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Global biogeography of traits and extinction risk in birds: an elevational perspective

By

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Thesis submitted for the degree of Doctor of Philosophy in Biodiversity Management

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Abstract

Mountains are hotspots of terrestrial species richness and endemism, but the reasons why are poorly understood. Extensive reviews of the literature, across taxa, reveal that research on trait and extinction risk variation with respect to elevational distribution are outnumbered by studies on latitudinal gradients and geographical range size, and are taxonomically and geographically restricted.

The aim of this thesis is to analyse interspecific variation in morphology, life history, ecology, and extinction risk with respect to elevational distribution – at the global scale and across a broad taxonomic range. To achieve this, I use birds as a model system, a global avian trait database and a comparative approach – employing both bivariate and multivariate statistical techniques.

Elevational distribution is shown to be positively associated with reproduction and niche breadth, whilst being negatively associated with morphology, growth and survival – even when controlling for body weight, geographical range, and latitude. Birds with larger elevational ranges and higher maximum and midpoint elevations possess traits consistent with a fast life history, and vice versa. Fast life histories at high elevations may result from exposure to more variable/seasonal environments compared to lowland birds. Global avian extinction risk is found to be greatest in lowland species and those with small elevational ranges. Overall, these relationships remained robust at the family level, for species within biogeographic realms, endemic subsets, and across phylogenetically independent contrasts.

This research will add to current understanding of large-scale ecology, trait biogeography, and conservation biology – assisting the incorporation of an elevational perspective into biogeography and macroecology theory, and conservation practice. Future work should focus on further identifying the underlying processes for the patterns shown here, and investigating their generality across other vertebrate groups, e.g. mammals.

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CHAPTER ONE
General introduction

1.1 Macroecology and the comparative approach: gaps in knowledge

Macroecology comprises the study of relationships between organisms and their environment at large spatial and temporal scales, in order to characterise and explain statistical patterns of abundance, distribution and diversity, via the integration of ecological, biogeographical and macroevolutionary theory (Brown 1995; Gaston & Blackburn 2000). The term was coined by Professor James Brown and Professor Brian Maurer (Brown & Maurer 1989), although the discipline has been practiced for around a century and a half (McGill & Nekola 2010). Macroecology has recently been revolutionised by a combination of the availability of high-resolution datasets (e.g. on geographical distributions), large molecular phylogenies, extensive computational power and new advanced analytical approaches (Keith *et al.* 2012). Consequently, the last two decades have seen an explosion of research in macroecology, which has now established itself as a major line of ecological research (Beck *et al.* 2012).

Methodologically, macroecology differs from 'classical' ecology in its substitution of experimental manipulations for comparative statistics (Blackburn 2004). Such an approach involves comparing the distributions of traits among species, or comparing patterns in variables measured for different communities or in different regions, with the aim of identifying causes of variation in those traits or variables (Bennett & Owens 2002). The comparative approach is typified by large-scale, multi-species comparisons, and the use of statistical correlations to investigate general patterns (Gaston & Blackburn 2000).

As stated by McGill & Nekola (2010), ecologists often believe the discovery of processes (i.e. mechanisms) to be the central goal of scientific research. However, most of the focus of macroecological research to date has been on reporting and describing patterns in species and ecological communities, whilst the identification and understanding of the underlying processes has ultimately lagged behind (Gaston & Blackburn 2000; McGill & Nekola 2010; Beck *et al.* 2012). This is due largely to the fact that macroecological diversity patterns are generated by a complex interplay of environmental and historical factors, interactions between the traits of species and the attributes of communities, and is scale-dependent (Bennett & Owens 2002). However, as macroecological studies increase in number, there is a noticeable shift from reporting to explaining large-scale diversity patterns (see Beck *et al.* 2012; Keith *et al.* 2012).

Many of the most severe anthropogenic pressures facing biodiversity today, such as destruction of habitat and climate change, occur at regional to global scales. These threats to biodiversity cannot effectively be addressed solely using information from traditional, small-scale ecological experiments. In part, because there is not sufficient time, money, or personnel to conduct studies of each species, habitat and process (Gaston & Blackburn 2000). In addition, results from such small-scale, experimental studies cannot validly be extrapolated to regional and global scales, because qualitatively different processes often assume importance at larger spatial scales (Brown 1995). Therefore, addressing regional and global problems of environmental change and decreasing biodiversity requires macroscopic studies, that trade-off the precision of small-scale experimental science to seek general robust solutions to ‘big problems’ (Brown 1995). However, it is important to emphasise that the two approaches are clearly complementary, with studies at a variety of spatial and temporal scales necessary for effective biodiversity conservation.

As will be shown and dicussed in subsequent sections of both this chapter and the next, recent global-scale analyses on spatial patterns of species richness and species’ traits utilise a grid-cell (averaging) approach, rather than classic interspecific comparative studies. In addition, large-scale ecological studies to date are biased towards investigating latitudinal gradients over elevational gradients – in relation to both measures of diversity and trait biogeography.

Finally, it is important to note that some scientists use the terms *biogeography* (defined in Section 2.1.2) and *macroecology* interchangeably, whilst others see them as distinct yet overlapping disciplines (see Kent 2005 and references within). As both terms can relate to describing and interpreting large-scale patterns and processes in the spatial distribution of diversity and underlying traits, for the purposes of this thesis, I also use them interchangeably.

1.2 The biodiversity hotspot concept

Available resources for conservation are limited (Balmford *et al.* 2003), and as such, priority sites for conservation must be identified by the scientific community. The most prominent spatial conservation prioritisation method is the biodiversity hotspot approach, conceptualised by Norman Myers (Myers 1988, 1990) and then further revised (Myers *et al.* 2000), as areas featuring ‘*exceptional concentrations of endemic* [plant] *species and experiencing exceptional loss of habitat*’. However, the definition of biodiversity hotspots has since been expanded and generalised to equate to areas of extraordinary concentrations of species richness, endemic species richness, and number of rare or threatened species (Orme *et al.* 2005; Possingham & Wilson 2005).

Originally, the biodiversity hotspot concept was promoted as a ‘silver-bullet’ strategy for conservation planners (Myers *et al.* 2000), despite considerable criticism (e.g. Kareiva & Marvier 2003). However, a number of global studies have since highlighted that this is not the case, and that the hotspot approach should only be used as part of the conservationists’ toolkit. For example, Orme *et al.* (2005) discovered, using a global avian database, that hotspots of species richness, threat and endemism are not geographically congruent. Only 2.5% of hotspot areas were shown to be common to all three aspects of diversity, with over 80% of the identified hotspots being idiosyncratic. They concluded that different mechanisms were therefore responsible for the origin and maintenance of different aspects of diversity. In a related study, Grenyer *et al.* (2006) used a database on the global distribution of bird, mammal and amphibian species to show that, although the distribution of overall species richness is very similar among these groups, congruence in the distribution of rare and threatened species was found to be significantly lower. They suggested that this low congruence may arise from differences among groups in their sensitivity to particular threatening processes, which in turn vary in their global distribution (e.g. invasive species and overexploitation are key threat sources in birds, whereas pollution and transmissible disease are more important in amphibians). These findings of both a general lack of overlap between spatial patterns of different measures of diversity and a lack of congruence of the same measure of diversity across taxa were further supported by a recent global vertebrate study conducted at the finest spatial grain yet – 10 x 10 km (Jenkins *et al.* 2013).

Overall, the studies that indicate a lack of congruence between different types of diversity and between taxa, suggest that identifying priority areas for biodiversity conservation requires both the use of multiple indices of diversity and high-resolution data from multiple taxa. In addition, as has been previously highlighted (e.g. Kareiva & Marvier 2003; Possingham & Wilson 2005), biodiversity hotspots (and many other large-scale conservation prioritisation schemes) need to explicitly account and incorporate factors including: (1) economic and social aspects, (2) measures of phylogenetic and higher taxonomic-level diversity, and (3) dynamic spatial changes in anthropogenic threat patterns and intensity.

1.3 Importance of mountains for biodiversity and correlates of altitudinal species richness

Despite the inherent limitations of the biodiversity hotspot concept as a tool for prioritising sites for conservation, recent global studies of geographical range sizes, utilising a grid cell approach, have undisputedly shown that major mountain chains, predominately within the tropics, are the richest areas for avian species richness (e.g. Orme *et al.* 2005; Davies *et al*. 2007; Thomas *et al.* 2008; Jenkins *et al.* 2013). For example, of the species richness hotspot regions identified by Orme *et al.* (2005), 89% (eight out of nine biogeographic regions) were located in mountainous areas of mainland continents (the top five ranges are highlighted in Fig. 1.1). These global studies concur with previous regional analyses that have identified highlands as important regions of avian diversity (e.g. Rahbek & Graves 2001; de Klerk *et al.* 2002; Jetz & Rahbek 2002; Jetz *et al*. 2004; see also Fjeldså *et al.* 2012 and references within). Even higher-taxon richness for birds has been shown to peak in certain mountainous regions, e.g. generic richness peaks along the Andes, with the highest levels of family richness located across parts of the Himalayas (Thomas *et al.* 2008). To a lesser extent, the tendency for mountains to harbour large numbers of species has also been documented for various non-avian taxa (e.g. plants: Myers *et al.* 2000; Lobo *et al.* 2001; mammals: Simpson 1964; Tang *et al.* 2006; Grenyer *et al.* 2006; amphibians: Poynton *et al.* 2007).

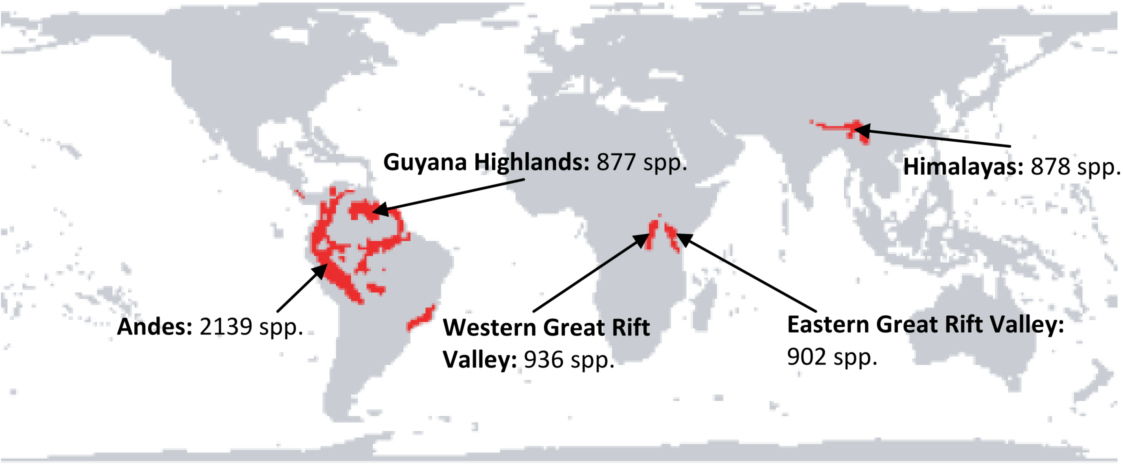


Figure 1.1 Top five mountainous hotspots of avian species richness (Orme *et al.* 2005).

Despite bird diversity consistently being shown to be highest in tropical montane regions, models of diversity mechanisms consistently under-predict montane diversity (e.g. Rahbek *et al*. 2007). One reason given for this disjunct is scale – the strong elevational shifts in climate, habitat and topography occur at scales of 1–10 km, whereas the scales of global analyses are orders of magnitude larger, e.g. grid cells of 110–10,000 km^2 (McCain 2009a). Such large scales therefore average much of the important variation in the potential drivers, which are vital for identifying and interpreting the high richness of montane systems (e.g. Ruggiero & Hawkins 2008).

Until relatively recently, it was believed that species richness patterns of birds, in fact all faunal and floral groups, decreased with increasing elevation, in a manner analogous to the latitudinal pattern (e.g. MacArthur 1972; Terborgh 1977; Brown & Gibson 1983; Stevens 1992). However, Rahbek (1995) noted that few studies controlled adequately for differences in area and/or sampling effort at different altitudes, both of which are often greater at low altitudes, and both of which have the potential to create artefactual results by inflating the richness of the lowest altitudes (Herzog *et al.* 2005). To overcome such pitfalls, Rahbek (1997) analysed a Neotropical land bird data set, firstly without area being taken into account and found richness declined montonically with elevation; when area was factored out, the richness-elevation relationship was hump-shaped. Similarly, when Terborgh (1977) controlled for variation in the effort expended in sampling his Peruvian bird community, the monotonic unstandardised relationship between altitude and richness developed a mid-altitudinal hump. Recently, McCain (2009a) has shown conclusively using well-sampled datasets worldwide, that neither decreasing nor mid-elevational peaks are the sole predominant pattern for bird species richness on mountains. Instead, bird diversity on mountains follow four general patterns in nearly equal frequency (Fig. 1.2): decreasing, low-elevation plateaus, low-elevation plateaus with a mid-elevational peak, and unimodal with a mid-elevational peak (McCain 2009a). These patterns are seen across all comprehensive bird assemblages studied, across both the eastern and western hemispheres, and within each biogeographical region. Christy McCain also investigated global patterns of elevational diversity in non-avian vertebrates, where she found reptiles to display the same four patterns as birds (McCain 2010), mid-elevational peaks for non-volant small mammals (McCain 2005), and equal support for declining species richness with elevation and mid-elevational peaks for bats (McCain 2007).

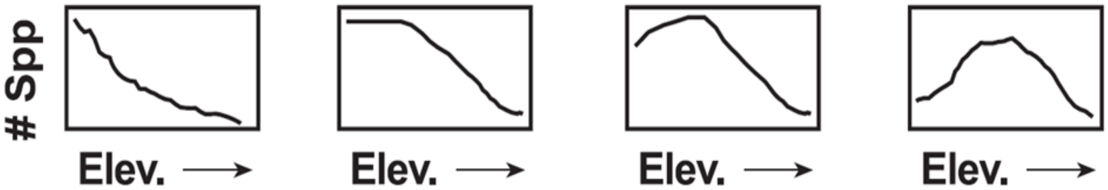


Figure 1.2 The four elevational richness patterns displayed by birds globally. From left to right: decreasing, low plateau, low plateau with a mid-elevational peak and mid-elevational peaks (McCain 2009a). # Spp = number of species, and Elev. = Elevation.

The elevational variability seen in avian species richness is poorly understood, due primarily to a lack of focused studies on mountain systems and elevational gradients at large spatial scales, yet is believed to be largely attributable to current climate, particularly combined trends in temperature and water availability (McCain 2009a). Temperature decreases with increasing elevation on all mountains, while rainfall and water availability follow more complex relationships with elevation depending on the local climate (Section 1.4). These relationships appear relatively robust as they have also been found for a variety of other taxa at large/global spatial scales (e.g. plants: O'Brien 1993; Bhattarai *et al*. 2004; Krömer *et al*. 2005; non-volant small mammals: McCain 2005; bats: McCain 2007; see

Hawkins *et al*. 2003a, and references within, for similar findings with respect to geographical patterns). Further analyses are required to determine the relative importance of direct (physiological limitations) and indirect (food resource) effects of water and temperature on avian diversity, although several mechanisms that attempt to explain the relationship are summarised in Evans *et al.* (2005) and McCain (2009a).

There are numerous alternative proposed drivers of elevational variation of species richness in the scientific literature, with one notable concept being the importance of geometric constraints or, as coined by Colwell & Lees (2000), the 'mid-domain effect' (MDE). The theory underlying the MDE can be applied to both altitudinal and latitudinal dimensions. Focusing on the former, for any altitudinal gradient, species altitudinal distributions are constrained to fall between the lowest and highest possible altitude on the gradient (Gaston & Blackburn 2000). If species altitudinal distributions are chosen at random from a feasible set of values and placed at random on the gradient, then the highest number of species is expected by chance alone to be found at mid-elevations (Colwell & Hurt 1994; Colwell *et al*. 2004, 2005). There is an extensive theoretical, empirical and review literature on the MDE, with respect to both altitude and latitude, and the debate regarding its role as a driver of species diversity gradients is ongoing (e.g. Zapata *et al.* 2003, 2005; Colwell *et al*. 2004, 2005; Hawkins *et al.* 2005; Storch *et al.* 2006; Dunn *et al.* 2007). Nevertheless, with respect to elevational gradients globally, empirical evidence across taxa for the MDE is often shown to be weak or non-existent (see Dunn *et al.* 2007; McCain 2010 – and references within both).

It is important to note that most studies of the MDE have used one-dimensional models to study patterns of species richness (in latitude, elevation or depth), with only a few having developed two-dimensional latitude-longitude models (see Zapata *et al.* 2003). Such a lack of multi-dimensionality may limit the predictive power and applicability of these MDE models (Bokma & Mönkkönen 2000). Consequently, VanDerWal *et al.* (2008) developed and tested the first three-dimensional mid-domain models to assess the effects of geometric constraints on species richness in North American bird, mammal, amphibian and tree species. Although complex to interpret, multi-dimensional mid-domain models reflect a more realistic geometry of geographical range shapes. Variation in species richness explained by MDE predictions has so far been found to decrease with increasing number of spatial dimensions being accounted for in the models (e.g. VanDerWal *et al.* 2008).

Niche conservatism posits that most large-scale richness patterns result from taxonomic groups diversifying when the majority of the earth was dominated by a tropical-like climate (Wiens & Donoghue 2004). Using birds as an example, if most species evolved niches in warm, wet conditions, then bird diversity should be concentrated at warm, wet elevations on mountains. This theory is supported with respect to both elevation (McCain

2009a) and latitude (e.g. Hawkins *et al*. 2003b, 2007). However, these studies do not test niche conservatism directly. In future avian studies, time-calibrated phylogenies are therefore needed to test whether the oldest species are concentrated in the areas of highest diversity, and whether niches of those species are more constrained to warm, wet conditions than younger species, across mountain systems (e.g. Stephens & Wiens 2003; Wiens *et al*. 2007).

1.4 Environmental change along elevational gradients

It is important to ask the question: '*What is elevation a gradient of?*' By itself, elevation above sea level, like degree of latitude, means nothing to organisms. Instead, it is an umbrella term (or proxy) for the underlying correlated environmental variables, past and present, abiotic and biotic, that in turn generate and maintain patterns of abundance, distribution and diversity (Brown 2001). Körner (2007) draws attention to the fact that there are two categories of environmental changes with respect to elevation, namely: (1) those physically tied to meters above sea level (i.e. global altitude-related phenomenon), and (2) those that are not generally elevation specific. In more detail, those falling under category one are:

a) declining atmospheric temperature – approximately 0.6°C per 100m elevational gain (Barry 1992),
b) declining (total) atmospheric pressure and partial pressure of all atmospheric gases (of which O_2 and CO_2 are of particular importance for life),
c) increasing radiation under a cloudless sky, both as incoming solar radiation and outgoing night-time thermal radiation (due to reduced atmospheric turbidity), and
d) higher fraction of UV-B radiation at any given total solar radiation.

In fact there are no other climatic/atmospheric factors relevant for organisms which exhibit consistently global unidirectional trends with elevation.

As most mountains erode to produce gradually sloped, roughly conical land forms, land surface area also decreases relatively continuously with increasing elevation (Fig. 1.3). Although it is important to remember that there are a number of expansive high-elevation plateaus, e.g. Tibetan plateau and the Andean altiplano. A further consequence of uplifting and erosional processes is that the tops of mountains tend to be more isolated than sites at lower elevations (Brown 2001).

The more numerous and complicated variables falling under category two (Körner 2007), include:

a) precipitation (and related ecologically relevant variables, such as soil moisture and evapotranspiration),
b) seasonality,
c) wind velocity,

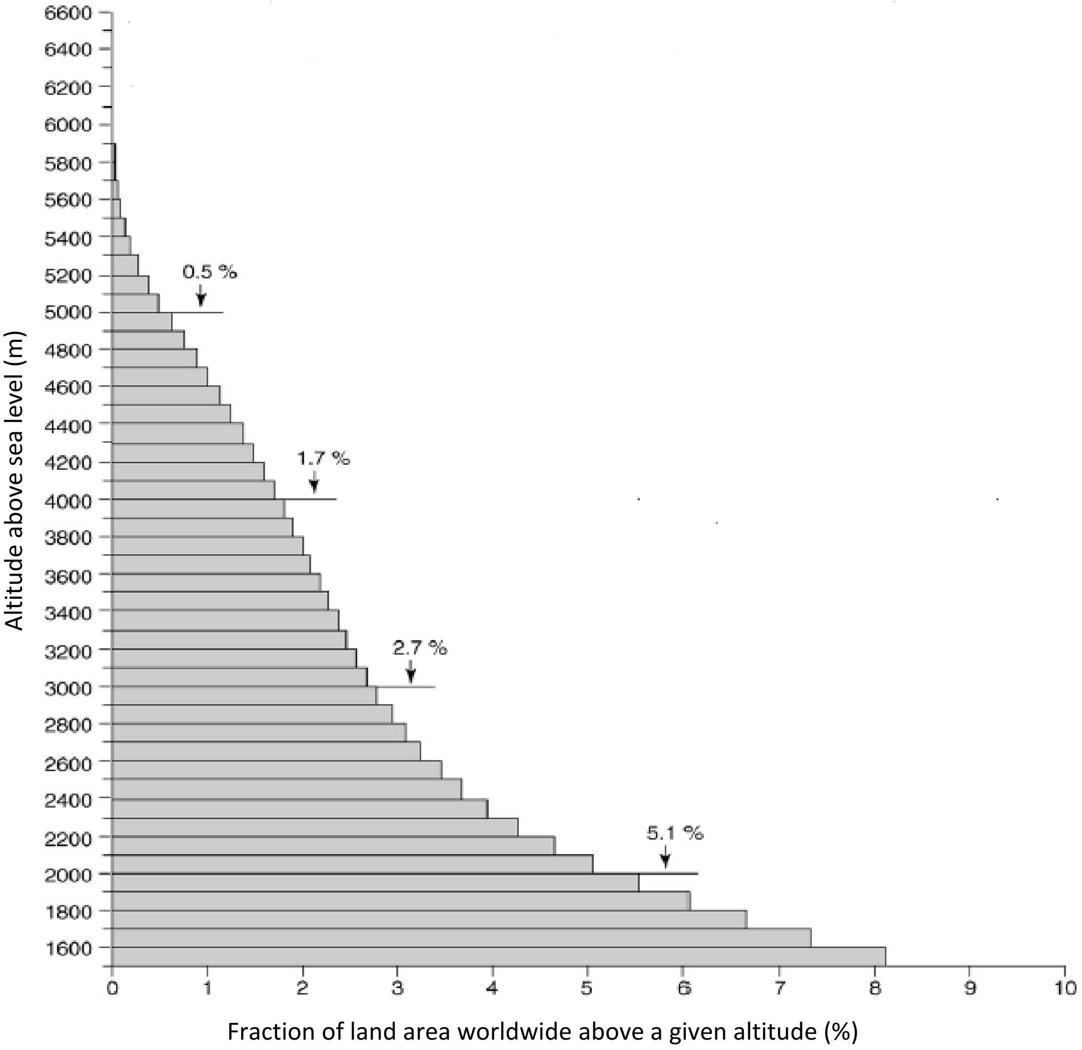


Figure 1.3 The global pattern of land area outside Antarctica per altitude in 100m steps above sea level (a.s.l.), starting from 1500m a.s.l. (land area above 1500m = 11 Mio km^2 – total world terrestrial area = 135 Mio km^2). From Körner (2007).

d) geology (differential erosion of substrates creates a heterogeneous topography of ridges, valleys, stream networks, and other features),

e) biotic interactions (e.g. competition, predation, mutualism), and

f) human land use.

These linear (category one), non-linear and highly variable (category two) covariates of elevation are discussed in detail in Körner (2007) and Brown (2001).

In essence, environmental variation with elevation is inherently complex and scale dependent. As stated by Körner (2007), any data collected along elevational gradients will reflect the combined effect of general altitude phenomena and regional environmental idiosyncrasies. This confounding of the first category by the latter has introduced confusion in the scientific literature on altitude-related phenomena, especially when attempting to compare the results and trends of studies along different altitudinal gradients. Ultimately, such variation justifies the difficulties of obtaining a general (i.e. global) altitude-related theory of biological phenomena, such as gradients of species richness and productivity, trends in physiology and morphology, or life-history and ecological traits. Nevertheless, the two most influential factors for life that are globally associated with increasing altitude are the reduction of land area and the decline in air temperature (Körner 2007). In order to obtain general altitude-related organismal responses, multivariate analyses of data from altitudinal gradients replicated across a variety of regions are of great value (Körner 2007). In other words, large-scale comparative research provides the most convincing tests for contributing to a furthering of the theory of altitude-related life phenomena, such as those conducted by Christy McCain (e.g. McCain 2007; McCain 2009a,b).

Finally, as highlighted and discussed by Brown (2001), it is important to stress that there are considerable differences between elevational and latitudinal gradients, i.e. the former '*are not simply equator-to-pole transects in small, replicated, easily studied units*'. For example, environmental variables such as precipitation, productivity and structural complexity of vegetation, often show non-linear (e.g. hump-shaped) patterns with respect to elevation, but decline more or less continuously from equator to pole. In addition, because of the tapering shape of mountains, the influence of historical dispersal, extinction and speciation processes are understandably quite different along elevational gradients on mountains than along latitudinal gradients on continents.

1.5 What is a mountain?

Although mountains may, on first consideration, appear clearly defined in space, there is no consensus method for marking the transition to lowlands, and consequently no consistent way of precisely defining the geographical limits of a mountainous region (Gerrard 1990). The core of the problem is that environmental gradients are continuous (from sea level to mountain top), and so any spatial dichotomy is unavoidably subjective (Platts *et al.* 2011). In addition, it is very difficult to offer a quantitative generalised scientific definition of what a mountain is, and as such, there is no universally accepted definition of a mountain *per se* (Körner *et al.* 2011).

Early attempts to define mountains go back to the 19th century, and used several criteria such as elevation, volume, relief and steepness, but have been inconsistent on a global scale (Gerrard 1990). The advent of freely available digital elevation data, together with improvements in desktop mapping software, have brought recent advances in the development of a systematic process by which to define and study mountains at a global scale (Platts *et al.* 2011). It is important to note that the only common topographical feature of mountains is their steepness, i.e. slope angle to the horizontal (Körner 2004). However, steepness is a slope-specific feature that cannot realistically be quantified at a global spatial scale (Körner *et al.* 2011). Consequently, global mountain classification schemes instead adopt ruggedness/roughness as a simple and pragmatic proxy for steepness, broadly defined as the maximal elevational difference among neighbouring grid points (e.g. Kapos *et al.* 2000; Meybeck *et al.* 2001; Körner *et al.* 2011).

Meybeck *et al.* (2001) used a hydrologically oriented approach to classify mountains globally, based on a simple fixed relief roughness (RR) indicator and on mean elevation in 30’ x 30’ cells (RR = maximum minus minimum elevation per cell divided by half the cell width). They imposed a minimum cut-off elevation of 500 m. Körner *et al.* (2011) used essentially the same approach and resolution as Meybeck *et al*. (2001) to provide the first quantitative attempt at a global areal definition of ‘alpine’ and ‘montane’ terrain, by combining geographical information systems for topography with bioclimatic criteria. Körner *et al.* (2011) defined the world’s mountains by a common ruggedness threshold (>200 m difference in elevation within a 2.5’ cell, 0.5’ resolution). Unlike Meybeck *et al.* (2001), the mountain definition Körner *et al.* (2011) adopted refrains from any truncation by low-elevation thresholds, and used a higher ruggedness threshold.

The most widely adopted global mountain definition used in recent ecological studies is arguably the 2002 UNEP-WCMC version of the ‘world mountain map’ first developed by Kapos *et al*. (2000). It was originally created to support the mountain agenda of the Commission on Sustainable Development (CSD), and to provide a platform for developing a map of the world’s mountain forests (Kapos *et al.* 2000). It was the first global mountains map at a 1 km resolution to use consistent objective definitions of mountain classes based on elevation, slope, and local relief in combination (Körner & Oshawa 2005).

Specifically, Kapos *et al.* (2000) used topographical data from the GTOP030 global digital elevation model (USGS EROS Data Centre 1996) to generate slope and local elevation range on a 30 arc-second (approximately 1 km) grid of the world. These parameters were combined with elevation to arrive at empirically derived definitions of six mountain (elevation) classes, with terrain constraints strictest at low elevations, and a lower cut-off elevation of 300 m imposed. A seventh class was introduced in the 2002 revision of the original 2000 system (UNEP-WCMC 2002). Table 1.1 provides a summary of all seven classes and the criteria used to define them. This definition identifies mountains as covering 26.5% (39.3 million km^2) of the world’s total terrestrial area, or 24.8% (33.3 million km^2) of the terrestrial area outside Antarctica (Rodríguez-Rodríguez *et al.* 2011). More information on the classification scheme along with numerous summary statistics can be found within Kapos *et al*. (2000), UNEP-WCMC (2002) and Körner & Oshawa (2005).

Table 1.1 Global mountain classes as defined by UNEP-WCMC (2002)

Mountain class	Criteria
1	Elevation ≥4500 meters
2	Elevation <4500 & ≥3500
3	Elevation <3500 & ≥2500
4	Elevation <2500 & ≥1500 & slope >2°
5	Elevation <1500 & ≥1000 & slope ≥5° OR local (7 km radius) elevation range >300 m
6	Elevation <1000 & ≥300 & local (7 km radius) elevation range >300 m
7	Isolated inner basins and plateaus (≤25 km^2 in size) that are surrounded by mountains but do not themselves meet criteria 1–6.

1.6 What constitutes a 'montane' species?

From reviewing the literature, it is apparent that there is no consensus definition of a montane (highland) species. Examples of definitions from avian studies in the tropics alone include species that exist above 200 m (Harris & Pimm 2004), 500 m (Patterson *et al.* 1998; Manne & Pimm 2001), 1000 m (Manne *et al*. 1999; La Sorte & Jetz 2010) or 1200–1500 m (Renjifo *et al*. 1997; Romdal & Rahbek 2009). Other definitions have instead been based upon a species having a certain percentage of their geographic distribution overlapping a mountain region (e.g. Ruggiero & Hawkins 2008). Justification of a particular definition is often not robustly justified or appears somewhat arbitrary (e.g. Harris & Pimm 2004). However, some studies justify their chosen cut-off point based upon the elevational band where a noticeable shift in species assemblages is identified, which is taken to demarcate a transition from lowland to montane bird communities (e.g. Herzog *et al*. 2005), although this is likely to be an oversimplification. Ultimately, the lack of a consensus definition for both lowland and highland species reduces the comparability of studies that use such terms. It should be noted that a consensus definition is unlikely to be made, as in reality no globally clear cut-off boundary between lowland and highland communities exists. Such a boundary varies due to a number of factors including latitude, slope and anthropogenic pressures (Brooks *et al.* 1999).

1.7 The 'enigma' of endemism

1.7.1 Defining Endemism: an issue of semantics and scale

The earliest known and most common usage of the word *endemic* is in medical literature – referring to a disease that is constantly present in a population living in a specific area (see Anderson 1994). The word has since been adopted by ecologists and biogeographers, although numerous definitions exist, leading Crisci *et al.* (2003) to state that defining endemism is analogous to the attempt of defining the species concept in systematic biology.

For a detailed discussion on the semantic problems of endemism, see Anderson (1994). In essence, the ambiguity created by the presence of various definitions and usages in the ecological/biogeographical literature means that caution is needed when using the term endemic, particularly when comparing and interpreting outputs from different studies.

In general, the term endemic has been defined relative to particular geographical regions, and traditionally implies that '*for a given area, a species (or other taxonomic entity) is naturally confined only to that area*' (Ladle & Whittaker 2011), with most accepting that the term can be applied on any scale to any size of region. Accordingly, a species could be classified as endemic to the entire Northern Hemisphere, to Venezuela, or to a single mountain slope. Therefore, when using the word endemic, it is vital, in terms of research transparency, for scientists to clearly indicate what the intended meaning is when the term is used – to state that a species is endemic without specifying an area is meaningless.

Although sometimes hindered by its reference to political units (for example countries, which are often ecologically/biogeographically meaningless) or habitat definitions, a geographical/regional approach to defining endemism provides an unambiguous list of taxa found nowhere outside of the focal region, and proves useful in applications addressing conservation priorities within countries (Peterson & Watson 1998). However, endemism defined in this way is useful only for that particular region, i.e. it precludes comparisons and generalisations to be made with other regions.

Consequently, a number of studies instead use area-based definitions, whereby those species with ranges smaller than a specified area are deemed endemic (referred to here as *restricted-range* species, but sometimes termed *threshold endemics* or *local endemics* in the scientific literature). Following Terborgh & Winter (1983), many studies have adopted an arbitrary fixed threshold value of 50,000km^2, including BirdLife International's Endemic Bird Area (EBA) concept (Bibby *et al.* 1992; Stattersfield *et al.* 1998). Nevertheless, several problems are associated with this approach, as discussed in Peterson & Watson (1998) and Kessler *et al.* (2001), including: (a) as the area threshold changes, scaling of endemism also changes, producing a different picture of endemism at each spatial scale; (b) the areal definition assumes equal levels of heterogeneity in different landscapes (which is clearly an oversimplification); (c) thresholds are subjective and abrupt, potentially leading to error by omission of taxa with slightly larger ranges than the threshold, but which may be of importance; (d) range sizes of different higher taxa are known to differ (e.g. Grenyer *et al.* 2006), precluding the use of a single arbitrarily determined cut-off value. In response to this last point, Gaston (1994b) suggested using the lower quartile of species with the smallest range sizes as the limit between restricted-range and widespread species (e.g. as used by

Orme *et al*. 2005; Grenyer *et al.* 2006). However, this definition is dependent upon the selection of species included in the analysis.

The importance of distinguishing the regional definition (endemism) from the areal definition (range restriction) of endemism has been emphasised by Peterson & Watson (1998), who attempt to clarify these two concepts. Briefly, *endemism* should be used to refer to restriction to a stated geographical region, based on either political boundaries or natural geographic features, whereas *range restriction* should be used to refer to geographical distributions less than a particular cut-off value in areal extent, without reference to a particular geographical feature. Both quantities are of interest and relevance to biodiversity conservation research.

A fault in some studies of endemism is that they apply a terminology that may confound separate aspects of the geographic distribution of a species (Estill & Cruzan 2001). For example, while endemism, rarity, and endangerment may sometimes be synonymous, it is important to recognise that they represent different aspects of the biogeography of a species. With respect to range size, a species is rare if it is limited to a small number of occurrences, endemic if it is restricted to a given area, and endangered if it is likely to undergo range contraction to the point where it is threatened with extinction (Gaston 1994b). Therefore, not all endemic species are rare, just as not all rare species are endemic. For example, Orme *et al.* (2005), in a study investigating global congruence in different types of hotspot for birds, defined species as endemic using the lower quartile method (Gaston 1994b) outlined above (strictly speaking, a measure of range restriction). However, in a related and complementary study by Grenyer *et al.* (2006), the same bird data and methodology was used as in Orme *et al.* (2005), but instead those species were labelled rare.

Finally, I think that it is necessary to emphasise the fact that studies to date are heavily biased towards defining both endemic and restricted-range species in terms of two-dimensonal geographical range size. In other words, there is a distinct lack of studies that attempt to define and study elevational endemics or restricted elevational range species. In fact, a search for peer-reviewed papers and conference proceedings whose title, abstract/summary or keywords contains phrases pertaining to ‘mountain endemics’ or ‘restricted elevational range’ species on the ISI Web of Knowledge database found very few references (Table 1.2).

1.7.2 Biogeography of endemism and restricted-range species

Compared to the numerous studies investigating large-scale spatial patterns and processes of overall species richness, there have been few focusing on the distribution of endemic (or restricted-range) species richness, and even fewer on the evolutionary and ecological factors

Table 1.2 Number of peer-reviewed studies investigating either 'mountain endemics' or 'restricted elevational range' species.

Key search term	Number of reference results in ISI Web of Knowledge database
'Elevation endemic'	7
'Altitude endemic'	24
'Mountain endemic'	28
'Montane endemic'	17
'Highland endemic'	13
'Alpine endemic'	41
'High-elevation endemic'	6
'High-altitude endemic'	18
'Restricted elevational range'	1
'Restricted altitudinal range'	1
'Narrow elevational range'	7
'Narrow altitudinal range'	4

Search date: 01/08/2013; http://webofknowledge.com

responsible for generating and maintaining endemism. A potential reason for this could be the difficulties in generalising a definition of *endemic* over a large area (Section 1.7.1).

Across taxa, the global species-range area distribution is strongly right-skewed, with the majority of species having small geographical ranges, as shown for birds by Orme *et al.* (2006) – see also Fig. A3.1. Despite this, a number of grid-cell based studies have shown that geographical patterns of overall avian species richness are determined by the distribution of wide-ranging (i.e. common, generalist) species, rather than narrow-ranging (i.e. rare, restricted-range) species – with both showing markedly different species richness patterns (e.g. Jetz & Rahbek 2002; Lennon *et al.* 2004; Orme *et al.* 2005; Jenkins *et al.* 2013). As succinctly stated by Jetz & Rahbek (2002): '*Geographic patterns in species richness are mainly based on wide-ranging species because their larger number of distribution records has a disproportionate contribution to the species richness counts*.' This lack of congruence implies that different mechanisms are responsible for the geographical patterns of wide-ranging and narrow-ranging species (Jetz & Rahbek 2002; Magurran & Henderson 2003).

Although a simplification of reality, regional studies of both birds and mammals (biased towards sub-Saharan Africa and the Neotropics) have found topographic heterogeneity (measured as altitudinal range) to be the most important (positive) predictor of narrow-ranging species distribution, whereas energy availability/productivity is believed to be the main driver of wide-ranging species distribution (e.g. Jetz & Rahbek 2002; Bonn *et al*. 2004; Ruggiero & Kitzberger 2004). Specifically, endemic species richness is thought to be a product of either refugia from past extinctions or of high rates of ecological and allopatric speciation, with topographic heterogeneity viewed as being a rough surrogate variable reflecting historical opportunities for speciation (Rahbek & Graves 2001; Jetz & Rahbek 2002; Jetz *et al.* 2004).

Regarding, the global spatial distribution of endemic (i.e. restricted-range) species, Orme *et al.* (2005) found avian endemic richness hotspots to be predominantly located on large islands and island archipelagos (60%), followed by continental mountains (45%) – although the Andes hotspot region was found to contain by far the largest number of endemic species (*n* = 483 species). At a finer resolution, Jenkins *et al.* (2013) found restricted-range birds and mammals to both have concentrations in the Andes, Madagascar, Southeast Asian islands, and other scattered localities. They also found amphibians to be a special case; so many species have small ranges that relatively few places have large concentrations. In essence, both islands and mountainous regions have consistently been highlighted as hotspots of endemism across terrestrial vertebrates. In fact, the first global study of variation in species range sizes across an entire taxonomic class (Aves), found the smallest range areas of birds to be located on islands and in tropical and sub-tropical mountainous areas (Orme *et al.* 2006).

As discussed in Voleker *et al.* (2010), the high levels of endemism found in montane tropics cannot be explained by models of current climate alone, as many tropical montane regions are areas that have experienced long-term climatic (and habitat) stability. This stability of montane habitat through time is believed to occur as a consequence of macroclimate interactions with topographic relief, creating sharp local habitat gradients (see Fjeldså & Lovett 1997; Fjeldså & Bowie 2008). In addition, low seasonality in the tropics means reduced seasonal overlap in thermal regimes between low- and high-elevation sites, which in turn selects for organisms with narrow ecological tolerance (Janzen 1967; Ghalambor *et al.* 2006). Collectively, these factors may allow species and communities to persist locally, promoting population isolation, persistance and speciation (Voelker *et al.* 2010).

Endemism, mountains and elevational gradients: In contrast to elevational gradients of species richness, little is known about elevational gradients of endemism as they have attracted less research attention. Available studies are geographically biased towards the tropics (specifically Central and Southern America), and taxonomically towards plants, which in turn are limited to small-scale/regional research conducted on spatially disparate elevational gradients – with a resulting lack of large-scale comparative studies. Plant-oriented studies reveal heterogenous patterns; although endemism predominantly either increases with elevation or displays a unimodal trend (see Kessler 2002; Trigas *et al.* 2013 – and references within both). Interpreting such variation is inherently complex, yet the explanations put forward typically involve abiotic factors including the biogeographical setting, orography and palaeoecological changes. An increase of endemism with elevation (and the observation that endemic species richness usually peaks at higher elevations than total species richness) is most commonly interpreted as a result of increasing isolation and decreasing surface area of high-mountain regions, leading to small, fragmented species populations that are prone to speciation (e.g. Kruckeberg & Rabinowitz 1985). As summarised by Trigas *et al.* (2013), observed decreases of endemism at the highest elevations has been explained by recent mountain uplifts providing too little time for speciation, or by glaciations that might have led to alpine endemic extinctions. Related to this, Kessler (2002) discussed that the high connectivity of many of the mountain plateaus in the Andes allows high-montane species to be widely distributed, whereas species inhabiting the steep, topographically complex slopes have narrow, fragmented ranges.

Focusing on the vascular plants of Ecuador, one of the most extensive studies on endemism and elevational gradients to date was by Kessler (2002). He found such patterns to differ significantly between the different genera and families, and suggested that these patterns were influenced both by taxon-specific traits (e.g. reproduction, dispersal, demography, spatial population structure, and competitive ability) in their specific interaction with historical processes and by environmental factors such as topographical fragmentation. Although he states that the degree to which these influences become visible along the elevational gradient is determined by the combination of species analysed. Concerning underlying traits and patterns of endemism, it is plausible that only the most adaptable and therefore widespread species can survive at the highest elevations, which could in turn contribute to hump-shaped endemism distributions. Evidently, further comparative studies that explicitly incorporate traits into their analyses are needed in order to separate the influence of taxon-specific traits and topography on the development of elevational patterns of endemism.

As with plants, studies on non-plant taxa have repeatedly reported contrasting patterns in total and endemic species richness along elevational gradients (e.g. Peterson *et al.* 1993; Stotz *et al.* 1996; Stotz *et al.* 1998; Patterson *et al.* 1998; Kessler *et al.* 2001; Fu *et al.* 2004; Fu *et al.* 2006). This mirrors the lack of congruency between latitudinal gradients of overall and endemic species richness. Focusing on birds, species richness and endemism have been found to be inversely related (e.g. Peterson *et al.* 1993; Patterson *et al.* 1998) and, more generally, the number or proportion of endemic bird species has been shown to increase with elevation (e.g. Graves 1985, 1988; Kessler *et al.* 2001; Young *et al.* 2009; Mallet-Rodrigues *et al.* 2010; Swenson *et al.* 2012). Interestingly, for Neotropical birds, Stotz (1998) found elevational patterns of strictly montane species to be largely similar to that of montane endemic species, i.e. unimodal. The only study that could be found investigating differences in both elevational and latitudinal distribution of endemics and non-endemics was conducted by Blackburn & Ruggiero (2001) for Andean passerines. Non-endemics were found to possess wider latitudinal ranges and tend to have latitudinal range maxima, minima and midpoints further from the equator, whereas endemics were instead shown to have higher elevational range minima, maxima and midpoints. However, their elevational distributions tend to span smaller ranges than those of non-endemic Andean passerines. The interpretations offered for the above-mentioned avian patterns are limited, with many associated studies offering no explanation in their discussions (e.g. Blackburn & Ruggiero 2001). Overall, current understanding of the drivers that create areas of high species endemism lags considerably behind existing knowledge of elevational patterns of endemism.

It should also be noted that very few studies have explicitly investigated elevational gradients of non-endemics or compared patterns with those of endemics occurring within the same study area, however, see Nogué *et al.* (2013) and references within. Although limited, such studies typically find non-endemic species richness to peak either at low elevations or towards the middle of the respective elevational range.

A number of studies on montane bird communities have found that endemic species (with narrow geographical ranges) were more likely to have high local abundance (e.g. Manne *et al.* 1999; Manne & Pimm 2001; Reif *et al*. 2006). Such a pattern contradicts the positive relationship generally found between range size and abundance (see Gaston & Blackburn 2000). This may suggest the combination of narrow geographical range and high local abundance is common in endemic species that have evolved in relatively stable high-elevation montane regions (Isaac *et al.* 2009). Reif *et al*. (2006) propose that the high abundances of endemic montane species could be a result of adaptation to local environmental conditions, enabled by climatic stability and isolation of montane habitat. They also suggest that species restricted to high-elevation montane areas may previously have had larger ranges but have become restricted after retreat of montane forest.

It is important to highlight that mountain tops can be considered terrestrial analogues of oceanic islands. In fact, the term *sky island* (or *continental island*) is used to refer to biogeographically isolated mountains that, like oceanic islands, may act as ‘cradles of evolution’ (Robin *et al.* 2010). However, they differ from oceanic islands in that they are connected by lowland valleys and terrain that act as both barriers and bridges to dispersion and colonisation (for a global overview of sky islands, see Warshall 1995). Such dynamic systems have been the focus of a number of studies investigating genetic divergence among populations and allopatric speciation events (Knowles 2000; DeChaine & Martin 2005; Robin *et al.* 2010). The interplay between isolation and connectedness results in these sky islands harbouring high levels of both species richness and endemism, making them important regions to target conservation efforts (e.g. Mayr & Diamond 1976; Peterson *et al.* 1993; Burgess *et al.* 2007).

1.7.3 Endemism and restricted-range as a tool for conservation prioritisation

Scientists are commonly interested in identifying centres of richness and endemism (i.e. 'CORE areas') for conservation prioritisation, with most emphasis being given to endemics (Ladle & Whittaker 2011). Orme *et al.* (2005) found that global avian endemism hotspots provide an effective way of capturing a high proportion of other aspects of diversity (i.e. overall species richness and threatened species richness), supporting the use of endemism as a criterion for identifying areas of avian conservation priority. Similarly, a global vertebrate study across ecoregions found that regions selected for high levels of endemism capture significantly more species than expected by chance, and are therefore a useful surrogate for the conservation of all terrestrial vertebrates (Lamoreux *et al.* 2006). For example, they show that 10% of the world's land area chosen on the basis of bird endemism captures 60% of all vertebrate endemics. At a much finer resolution (10km x 10km), Jenkins *et al.* (2013) concluded that the most efficient conservation prioritisation method from a '*space-for-species perspective*' would rely on small-ranged species, based on their finding that global centres of diversity for small-ranged vertebrates cover 93% of all vertebrate species in just over 8% of the world's land area. However, both Grenyer *et al.* (2006) and Jenkins *et al.* (2013) stress that the extent to which restricted-range species from one vertebrate class can act as a surrogate for corresponding species in other classes is limited – especially at the finer scales most relevant to conservation. Nevertheless, to date, a number of global biodiversity conservation prioritisation schemes have been centred on the concept of endemism and restricted range, most notably:

1) Conservation International's (CI) hotspots scheme (Myers *et al.* 2000). This is based on two criteria: (1) identifying areas of the world possessing more than 0.5% of the world's plant species as endemics, and (2) areas that have lost more than 70% of their natural vegetation.

2) BirdLife International's Endemic Bird Areas (EBAs) are delimited based on the possession of as few as two restricted-range (<50,000km^2) bird species (Stattersfield *et al.* 1998).
3) 'Criteria B' of the IUCN Red List classifies species as threatened based purely on their geographical range (IUCN 2001). Concerning extent of occurrence, a species is considered Vulnerable if it covers an area <20,000km^2, Endangered (<5,000km^2) and Critically Endangered (<100km^2).

It should be highlighted that all three of these prioritisation schemes are based on measures of two-dimensional geographical range, with no consideration of elevational distribution. In addition, EBAs and the IUCN Red List 'Criteria B' for birds are, arguably, non-independent measures of conservation prioritisation, as they are inherently linked by utilising the same range maps and comprising approximately 33% of the same species (BirdLife International 2013), i.e. a third of all bird species defined as restricted-range species by BirdLife International are also classified as Threatened under the IUCN Red List. Which of these methods are most efficient and effective at conserving the world's biodiversity is difficult to judge and somewhat subjective, and it is important to reiterate that a species considered endemic under one definition may be disregarded under another (Section 1.7.1), which can lead to considerable confusion and uncertainty in conservation decisions.

1.8 IUCN Red List status as a response variable of extinction risk correlates

The most comprehensive global assessment of perceived species extinction risk is the International Union for Conservation of Nature (IUCN) Red List (http://www.iucnredlist.org/), which places evaluated species on a coarse scale of extinction risk – the current categories and criteria (IUCN 2001) are summarised in Fig. 1.4. Species are evaluated against each criterion, where data permit, and the highest level of extinction risk attained under any criterion is assigned as the species' extinction risk category (Mace *et al.* 2008).

Studies investigating the correlates of extinction risk, particularly for birds and mammals, typically use the IUCN Red List categories as their response variable. However, there are three often cited issues of particular concern regarding this, as outlined below:

1) ***Translation to interval scale – the 'unequal units' problem****:* In a number of comparative studies of extinction risk (e.g. Bennett & Owens 1997; Purvis *et al.* 2000a; Gage *et al.* 2004; Cardillo *et al.* 2008), the IUCN Red List threat rating is treated as a coarsely measured continuous variable. This conversion from a ranked scale to a linear interval scale – necessary for analysing multiple correlates simultaneously at the level of species – assumes that the 'distance' between pairs of

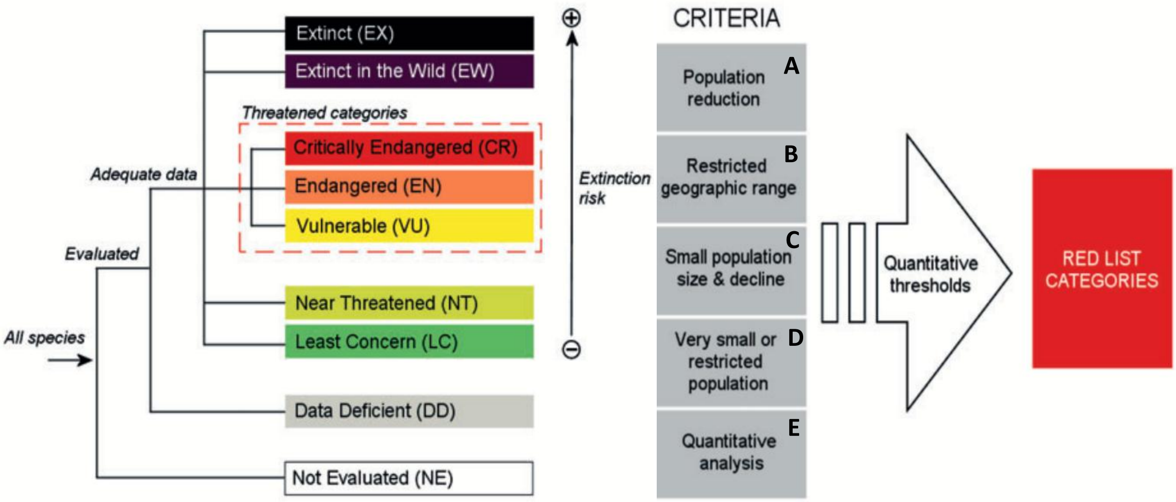


Figure 1.4 The IUCN Red List categories and five criteria (A-E). Adapted from Vié *et al.* (2008).

successive points on the scale is equal, i.e. the categories of extinction risk are assumed to be equal in width. This assumption, is not part of the design of the IUCN Red List categories, and is certainly not met in full (Purvis *et al.* 2005). The true function linking threat status to a continuous scale is likely to be quite complex. Although there are comparative techniques that handle both freely continuous variables and discrete characters (e.g. Purvis & Rambaut 1995), there are no current methods to handle ordered discrete characters with differing probabilities of transition between states (Purvis *et al.* 2005). Even if there were, there is still no empirical basis for determining those probabilities for IUCN Red List ratings. As stated in Purvis *et al.* (2005), there is little option at present but to accept the inaccuracies introduced by linear transformations, and interpret the resultant findings accordingly.

2) ***Circularity:*** An obvious, but often overlooked issue with using IUCN Red List threat ratings as the response variable, is that some likely predictor variables actually feature in the Red List criteria themselves (Harcourt 2005). Most notably, species can be listed on the basis of small geographic range size, either on its own (Criterion D), or in combination with fragmentation, decline and fluctuations (Criterion C). A significant correlation between geographic range size and threat rating is therefore essentially inevitable. Attempts have been made to avoid this issue of circularity (e.g. Keane *et al.* 2005; Lee & Jetz 2011). For example, ‘Criterion A’ considers population or range decline, but is concerned only with changes over time and not with the current range size. Therefore, correlating geographic range size against risk for species listed only under criterion A would not be circular (e.g. Purvis *et al.* 2000a; Cardillo *et al.* 2008).

3) ***Equivalence among criteria:*** Another assumption when using IUCN Red List categories as the response variable is that extinction risk of species in a given category is independent of the criteria under which it qualified for listing (Purvis *et al.* 2005). For example, it is assumed that species listed as Endangered on grounds of rapid population decline are, on average, at the same risk of extinction as those listed on the basis of restricted geographic range. The criteria were designed with this intention in mind (Mace & Stuart 1994), and revisions to the threshold conditions of some criteria are somewhat motivated by a need to improve equivalency among criteria (Mace *et al.* 2008). However, the degree to which the criteria are equivalent is difficult to assess.

1.9 Distribution and correlates of avian extinction risk

1.9.1 Distribution of avian extinctions

As neatly summarised by Szabo *et al.* (2012), '*extinctions have probably been better documented among birds than for any other comparable group of organisms, and indeed more bird species are known to have gone extinct in recent centuries than organisms of any other class*'. According to the 2012.2 update of the IUCN Red List, a total of 130 species have gone Extinct since 1500, with a further four species deemed to be Extinct in the Wild, surviving only in captive populations (BirdLife International 2013). Despite being comparably well studied, these totals are likely to be underestimates, due to the inherent difficulties in declaring an extinction event. A number of other species currently categorised as Critically Endangered have probably gone Extinct too, but cannot be designated as such until certain (Butchart *et al.* 2006). Fourteen such species are categorised as Critically Endangered (Possibly Extinct) and one as Critically Endangered (Possibly Extinct in the Wild) (BirdLife International 2013). Thus, a total of 149 species may have been lost in the past 500 years or so. However, it should be noted that, although only approximately 1.3% of bird species have gone extinct since 1500 (Sekercioglu *et al.* 2004), the global number of individual birds is estimated to have experienced a 20–25% reduction during the same period (Gaston & Blackburn 2003), indicating that avian populations are declining faster than species extinctions would indicate.

Since 1500, the vast majority of documented avian extinctions (between 89–95%) have been on islands (Butchart *et al.* 2006; Loehle & Eschenbach 2012; Szabo *et al.* 2012), even though most bird species (>80%) live on continents (Johnson & Stattersfield 1990). Many island extinctions resulted from the introduction of invasive alien species such as cats, rats and goats, which predated the native 'predator naïve' species, or degraded their habitats (Manne *et al.* 1999). However, the extinction rate on islands has declined over the past century, presumably because many susceptible species are already extinct, while conservation interventions are successfully improving the status of some of the remainder (Butchart *et al.* 2006). By contrast, the extinction rate on continents is increasing (see Szabo *et al.* 2012), with predictions of massive future extinctions stemming from the current clearing of lowland continental, tropical forests (Pimm *et al.* 1995; Manne *et al.* 1999; Pimm *et al.* 2006).

1.9.2 Geographical distribution of currently threatened bird species

Understanding the geographical distribution of extinction risk and its causes are key challenges in conservation biology, and are central to determining spatial priorities for the focus of conservation efforts. Unfortunately, there have been few quantitative studies of the spatial distribution of threatened species for any taxa. Concerning birds, as with historical avian extinctions, a disproportionately higher number of currently threatened species occur on islands: almost equal numbers are found on islands as on continents, with few shared between them (Manne *et al.* 1999; BirdLife International 2013). Although threatened bird species can be found worldwide, Orme *et al.* (2005) identified global hotspots of avian threatened species richness. They found 60% and 40% of threat hotspot regions were located on large islands (e.g. Philippines, New Zealand, Hawaii and Madagascar) and in continental mountains (e.g. Andes and Himalayas), respectively. Another global study by Davies *et al.* (2006) confirms that the global distribution of threatened avian species richness exhibits marked large-scale spatial heterogeneity, being highest across much of the Indo-Malay realm and parts of the Neotropics (including areas of the Andes).

Previous research has shown that the geographical distribution of threatened species richness is, to some extent, dependent on that of overall species richness (e.g. Kerr & Currie 1995; McKee *et al*. 2003). However, Davies *et al.* (2006) found that the proportion of species threatened was still far from constant and does not simply mirror the patterns for absolute numbers of either threatened or non-threatened species. These regional variations in numbers of threatened birds depend largely upon a combination of evolutionary history (which influences species diversity, range size, behaviour and ecology) and past and present threatening processes (BirdLife International 2013).

1.9.3 Correlates of extinction risk in birds

Extinction risk varies among species, and comparative analyses can help clarify the causes of this variation (Purvis 2008). Identifying the underlying causes of high extinction risk is an important step in understanding the processes contributing to current species declines, and predicting the probable future declines in the face of escalating human pressure on biodiversity (Purvis *et al.* 2005). Although the set of circumstances contributing to extinction risk may be unique for each species (and often for populations), comparative studies have begun to reveal general patterns and correlates of extinction risk for a variety of taxa (Cardillo *et al.* 2008). In general, the distribution of extinction risk among species is phylogenetically non-random, with some taxonomic groups more likely to contain threatened species than others (Purvis 2008). For example, Bennett & Owens (1997) showed that certain families, such as Psittacidae (parrots), Columbidae (pigeons) and Rallidae (rails) contain significantly more threatened species than would be predicted by chance alone. This implies that biological differences among taxa are at least partly responsible for extinction risk variation (Cardillo *et al.* 2008). Indeed, a wide variety of ecological and life-history traits are often associated strongly with extinction risk in comparative analyses. An overview of the proven and potential correlates of extinction risk in birds is beyond the scope of this review. However, a commonly cited predictor of high avian extinction risk is large body size (e.g. Gaston & Blackburn 1995; Bennett & Owens 1997; Gage *et al.* 2004; Lee & Jetz 2011). Yet, it is difficult to determine if this is a direct or indirect effect, as large body mass is often correlated with other extinction-promoting traits, such as low population densities, slower life histories and larger home ranges (see Gaston & Blackburn 1995). Consequently, body size is an extremely difficult variable to interpret and should be treated with caution (Bennett & Owens 1997).

It is not only intrinsic factors that determine a given species threat of extinction, but also extrinsic factors, including climatic variables, human population density (HPD) and habitat loss (Purvis *et al.* 2000a). Threat therefore varies across species and space due to the combined and often synergistic influence of a broad-array of life-history, ecological, geographical and anthropological factors (Lee & Jetz 2011). Focusing on HPD, the greater the number of people in a given area the greater their likely effect on other species. Consequently, extinction risk has been predicted to increase with human population density (e.g. Keane *et al.* 2005). In reality, both contemporary HPD and extent of agricultural activity in an area are known to be important predictors of the numbers of threatened species (e.g McKinney 2001; McKee *et al*. 2003; Scharlemann *et al*. 2005; Davies *et al*. 2006). In extension to this, Lee & Jetz (2011) found at a broad, global scale that simple quantifications of past human encroachment across species ranges emerge as a key factor in predicting avian extinction risk.

An important finding by Owens & Bennett (2000) is that different taxa are threatened by different mechanisms. For example, they showed for birds that extinction risk incurred through persecution and introduced predators is associated with large body size and long generation time, whereas extinction risk incurred through habitat loss is associated with habitat specialisation and small body size. This may go some way to explain why it has previously proven so difficult to identify simple ecological correlates of overall extinction risk.

To conclude, it is imperative that future comparative studies of extinction risk control for interrelatedness among independent variables, avoid circularity, ensure statistical (phylogenetic) independence across taxa, and examine differences across spatial scales and taxonomic levels.

1.9.4 Extinction risk and elevation

In comparison to numerous papers published exploring the relative role of geographical range and distribution on extinction risk across taxa (e.g. Manne *et al.* 1999; Orme *et al.* 2005; Grenyer *et al.* 2006; Harris & Pimm 2008), only a few studies to date have investigated elevation as a potential predictor of extinction – the findings and limitations of those that could be found for birds are summarised in Table 1.3. Out of these studies, six explicitly analyse avian elevational distribution as a predictor variable of extinction risk, however, they are spatially and/or taxonomically focused (Manne *et al.* 1999; Manne & Pimm 2001; Gage *et al.* 2004; Keane *et al.* 2005; Krűger & Radford 2008), lack transparency and/or a multivariate assessment (Sekercioglu *et al.* 2008, and also Sutherland 2003; Sekercioglu *et al.* 2004). The two other research efforts are global in extent and cover all landbirds, but utilise a grid-cell approach and model potential elevational distribution rather than actual recorded elevational limits of bird species (Davies *et al.* 2006; Lee & Jetz 2011).

Despite differences in aim, extent and methodology of the studies presented in Table 1.3, overall, they provide evidence for the following: (a) a negative relationship between avian extinction risk and elevational range, and (b) lowland birds being currently more threatened with extinction than montane species. Explanations for these patterns are not widely discussed in the associated literature. Both Gage *et al.* (2004) and Keane *et al.* (2005) proposed that having a large elevational range raises the chance that a given species will have a large, continuous distribution, which in turn is more likely to provide refuges from the impacts of humans, thus lowering risk of extinction. Keane *et al.* (2005) suggest that species living in lowlands may face more habitat destruction and overexploitation than upland species, increasing their risk of extinction. Manne *et al.* (1999) explained their own results via ‘competitive release’ (MacArthur *et al.* 1972), by stating that montane (and island) species tend to be relatively common within their restricted ranges, compared to continental lowland species, and their increased abundance reduces their likelihood of being threatened. Evidence for this explanation was empirically found in Manne & Pimm (2001). In addition, Blackburn & Gaston (2002) found threatened bird species living at higher altitudes tend to have larger global population sizes.

Table 1.3 Summary of studies, in chronological order, that have investigated the role of elevational distribution in avian extinction risk

Author (year) and study title	**Geographic, taxonomic extent and sample size (*n*)**	**Main extinction risk and elevation conclusions**	**Limitations of study**
Manne *et al.* (1999) *Relative risk of extinction of passerine birds on continents and islands*	All passerines of the Americas and their associated islands (*n*=2286 species)	For species with range sizes between 1000 and 100,000 km^2, a much higher proportion of 'lowland' continental than of either 'montane' continental or 'island' species were classified as threatened.	Uses simplistic dichotomous measure of elevation: continental species were classified as 'montane' if they do not occur below 1000m, with the remainder defined as 'lowland'.
Manne & Pimm (2001) *Beyond eight forms of rarity: which species are threatened and which will be next?*	All passerines of the Americas and their associated islands (*n*=2074 species)	Species with narrower elevational bands suffer higher levels of threat across lowland, montane and island species. For a given range size, lowland species suffer higher levels of threat than island or montane species. Overall, elevation is a consistent, yet relatively unimportant factor in determining threat status; abundance and range size are much more important.	Uses simplistic dichotomous measure of elevation: continental species were classified as 'montane' if they breed only above 1000m and are therefore restricted to high-altitude areas, with the remainder defined as 'lowland'.
Gage *et al.* (2004) *Ecological correlates of the threat of extinction in Neotropical bird species*	Neotropical species (*n*=1708)	Found minimum elevation and elevational range to be positively and negatively associated with threat respectively (raw species analysis), and not significant for independent contrasts. Confining the analysis to species restricted to a single zoogeographic region revealed elevational range to be negatively correlated with threat for both raw and independent contrasts.	Only approximately half of all described Neotropical bird species were included due to data availability. As such, the data are likely to be subject to sampling biases, and are potentially unrepresentative of the Neotropical bird community as a whole.
Keane *et al*. (2005) *Correlates of extinction risk and hunting pressure in gamebirds*	Global study of 232 (out of 284) species of Galliform	Found elevational range to be negatively associated with extinction risk globally, and when broken down into certain families and regions (raw data and independent contrasts). Elevational (and latitudinal) range found to explain a large proportion of the variance in extinction risk alone.	Small sample sizes, particularly for independent contrast analyses of individual families and regions.

Table 1.3 Continued

Author (year) and study title	**Geographic, taxonomic extent and sample size**	**Main extinction risk and elevation conclusions**	**Limitations of study**
Davies *et al*. (2006) *Human impacts and the global distribution of extinction risk*	Global study of landbirds (*n*=9626 species)	Calculated the number of threatened bird species and determined elevation range (a measure of topographic variability) for 1° latitude x 1° longitude grid cells. Found elevation range to be a positive predictor of threatened avian species richness globally, and for the Neotropical and Australasian biogeographic realms, which is counter-intuitive.	Uses a binary measure of extinction risk (Threatened vs. Non-threatened), and grid cells rather than species as study units. Large number of cells in global analysis have: i) low elevation range (e.g. Russian flatlands), and ii) minimal threatened species (due to isolation, or human extinction filter). These large numbers of zero-sum squares hugely bias results towards a positive correlation between threatened spp. richness and elevation range.
Sekercioglu *et al*. (2008) *Climate change, elevational range shifts, and bird extinctions*	Global study of landbirds (*n*=8459 species)	Elevational limitation of range size significantly explained 97% of the variation in the probability of being 'at risk of extinction' (CR, EN, VU, NT). Species with wider elevational ranges were less likely to be threatened.	Extinction risk variation explained by elevational range is incredibly high. Methodology and data sources are not explicit, and supporting information cannot be accessed. Likely used interpolation to obtain elevational data for 8459 species, which is not advisable for geographical traits where the majority of variation occurs at the species level (Section 3.5.1.). No multivariate analyses.
Krűger & Radford (2008) *Doomed to die? Predicting extinction risk in the true hawks Accipitridae*	Global study of the 237 species in the family Accipitridae.	No significant covariation was found between extinction risk and median breeding altitude.	Explores a large number of explanatory variables (26 in total). Fails to discuss the lack of a significant association between extinction risk and elevation for this taxonomically restricted set of birds.
Lee & Jetz (2011) *Unravelling the structure of species extinction risk for predictive conservation science*	Global study of landbirds (*n*=8664 species)	Both minimum elevation and potential elevational range across all species were found to have no association with threat status.	Uses a binary measure of extinction risk (Threatened vs. Non-threatened), and potential rather than known elevational limits for all bird species studied. Extracted minimum elevation and potential elevational range (minimum elevation – maximum elevation) across each species' geographical breeding range.

Briefly considering non-avian taxa, it has been widely noted that most declines and disappearances of amphibians have occurred, and are predicted in the future to occur, in high-altitude areas, particularly in the Neotropics (e.g. Young *et al.* 2001; Morrison & Hero 2003; Stuart *et al.* 2004; Sodhi *et al.* 2008; Caruso & Lips 2013). In addition, Lips *et al.* (2003) found small elevational range to be a correlate of population decline in the amphibians of Central America, and Pounds *et al.* (2006) found a mid-elevation peak in extinction risk for New World amphibians. The drivers of these patterns are complex and currently unclear; however, habitat loss, climate change and diseases such as chytridiomycosis are likely to be key drivers (Wake & Vrendenburg 2008), along with the intrinsic life-history characteristics of high-elevation species (Morssison & Hero 2003).

Concerning plants, Yessoufou *et al*. (2012) explored elevational variation in the distribution of threatened angiosperm species in the Eastern Arc Mountain hotspot, and found a positive relationship between elevational range and threatened species richness. However, this study doesn't explicitly use the elevational range of individual species, but instead the elevational distribution of differing forest blocks. They suggest that this finding could be due to the fact that species in more topographically diverse forest blocks occupy smaller geographical distributions, or that such a trend is simply because such forest blocks contain a greater total richness of plant species at higher elevations.

No studies could be found investigating the elevational distribution of extinction risk for other taxa (e.g. mammals, reptiles or invertebrates), and this knowledge gap needs to be addressed to assess the generality of relationships across taxa. In addition, it is evident that the existing scientific literature is missing a study that explicitly investigates and highlights the role of elevational distribution as a predictor of extinction risk. Such a study would form a valuable basis for recommendations on future conservation efforts, and would need to:

a) be global in scale;
b) be conducted primarily at the species level, but also control for phylogeny;
c) be conducted across an entire taxonomic class;
d) consider bivariate relationships, but also control for other intrinsic and distributional traits known to be predictors of extinction risk in a multivariate environment;
e) break analyses down into regional subsets to test for geographical generalities in any patterns found.

Such an analysis is provided below (see Chapter 7).

1.10 Anthropogenic threat and elevational distribution

Mountains are typically perceived as wilderness areas unspoilt by human presence, and consequently under low human threat, due to factors including their limited accessibility, economic potential and low human population density. Approximately 22% of the world's human population (90% of which live in developing countries) inhabit mountainous areas (UNEP-WCMC 2002), with numbers of people decreasing faster than exponentially with increasing elevation (Cohen & Small 1998). Less attention has therefore been focused on the current and potential threats facing mountainous regions than has been for lowlands. For a general overview of the current pressures facing mountain systems and their spatial distribution, see UNEP-WCMC (2002).

More specifically, Rodriguez-Rodriguez & Bomhard (2012) assessed the degree of human impact on global mountains via the 'Human Influence Index' (HII) (see Sanderson *et al.* 2002), using it as a proxy to estimate the degree of threat to mountain biodiversity. They found that there are still large proportions of mountainous areas (outside Antarctica) under low to moderate human influence (52.9% and 40.6% of total mountain area respectively). Most of the lowest human influence mountains were identified as occurring at high northern latitudes, and, unsurprisingly, the most heavily influenced mountain areas were found to largely overlap with the most densely populated regions in the world. However, their results are likely to be underestimates of the true extent of human influence in mountains, for a number of reasons, including the fact that the HII does not take into account indirect human impacts such as climate change. In a similar, but regional study, Burgess *et al*. (2007) showed that high-biodiversity mountain areas of sub-Saharan Africa have higher levels of human influence than the mean across the whole region. Implying that, for certain mountainous regions at least, the potential threat from humans is greater than adjacent lowlands.

A key global study by Nogués-Bravo *et al*. (2008) concluded that human activities have generally affected lower and upper elevational regions more than mid-altitudinal habitats. Specifically, they found deforestation to be most extensive in both lowland (via clearance for settlements and exploitation of forest resources) and high altitude (via grazing and fire practices) regions, and overall human impact to be greatest in the lowlands, decreasing nearly monotonically with increased elevation. However, the authors do stress the importance of acknowledging the fact that different elevational gradients and mountain ranges worldwide have a unique history of human intervention.

In recent decades, tropical montane forests have disappeared, due to human activities, at a greater rate than forests in any other biome (Price *et al.* 2011). In fact, montane forests (particularly cloud forests) are considered by some to be one of the world's most threatened ecosystems (Aldrich *et al.* 2001). However, while montane forest cover is typically declining in developing countries (especially in tropical regions), throughout most of the temperate zone (industrialised countries), the area and/or density of montane forests is generally stable or gradually increasing (Price *et al.* 2011). Using a regional case study, deforestation rates in South-east Asia are among the highest globally and remain the primary threat to its biodiversity (Miettinen *et al.* 2011). Related to this, a number of studies conducted in this region have investigated and shown the vulnerability and sensitivity of native montane birds to even low levels of deforestation and habitat disturbance, much more so than lowland species (e.g. Brooks *et al.* 1999; Lee *et al.* 2005; Soh *et al.* 2006). Soh *et al.* (2006) suggested that montane birds are unusually sensitive to slight deforestation because a higher proportion of these species have restricted ranges and/or specialised physiologies.

1.11 Impact of climate change on avian range distributions

Birds are the best-known class of organisms when it comes to climate research (Sekercioglu *et al.* 2012). However, few studies have explicitly examined how life-history traits, ecology and climate envelope influence the ability of bird species to respond to climate change (e.g. Jiguet *et al.* 2007). A pioneering new study by Foden *et al.* (2013) examined biological traits of all extant bird species (and amphibians and corals) and their modelled exposure to projected climate change, in order to identify species and underlying geographic areas most vulnerable to climate change. They found that between a quarter and a half of all extant bird species have traits that make them particularly vulnerable to climate change (e.g. specialised habitat requirements, narrow environmental tolerances, rarity, poor dispersal ability, low genetic diversity, and long generation times). The five most climate change vulnerable bird families are all tropical in distribution: Thamnophilidae (antbirds), Trogonidae (trogons), Bucerotidae (hornbills), Pipridae (manakins) and Trochilidae (hummingbirds). What is most concerning is that up to 83% of these bird species are not yet considered threatened on the IUCN Red List.

Climate is a critical factor in determining species geographical ranges at the global scale, and it is because of this paradigm that species are expected to shift their distributions, with respect to both latitude and elevation, under climate change (Pigot *et al.* 2010). Although it is difficult to causally link an observed shift in the range of a given species to changes in climate, a number of studies have identified bird species undergoing latitudinal (i.e. poleward) range shifts worldwide (e.g. Thomas & Lennon 1999; Brommer 2004; La Sorte & Thompson 2007; Hitch & Leberg 2007; Olsen 2007; Zuckerberg *et al*. 2009). However, as is generally the case in ecology and conservation, the temperate zone has been the focus of most studies of climate change and most modelling exercises on the changes in species distributions (Sekercioglu *et al.* 2012). As highlighted by Rosenzweig *et al.* (2008), less than 1% of the long-term climate change data sets come from the tropics. So, although most bird species are tropical and sedentary (BirdLife International 2013), the majority of current understanding on climate change impacts on birds is based on research of temperate species that are largely migratory (Sekercioglu *et al.* 2012). Despite this research and knowledge bias, tropical mountain birds, along with those species without access to higher elevations and restricted-range species, are some of the most vulnerable groups to the potential impacts of climate change (Sekercioglu *et al.* 2008; Sekercioglu *et al.* 2012 – and references within both).

The literature on climate change is extensive and often both contentious and ambiguous. The aim of the following subsections is not to provide an exhaustive review of the impact of climate change on avian range distributions, but instead to highlight current theory and evidence for climate change impacting on species inhabiting mountains and their elevational distributions.

1.11.1 Evidence for upward elevational shifts in avian distributions

Species are not only expected to track climatic warming by shifting polewards in latitude, but also upwards in elevation. Whilst evidence for latitudinal extensions or shifts has been observed in birds from a wide number and variety of studies, elevational shifts have received less attention to date (in comparison to other taxa, particularly plants and Lepidoptera – see Lenoir *et al.* 2011). Archaux (2004) provides two potential explanations for this:

a) Comparisons of bird atlases over time, which have contributed to current evidence of latitudinal shifts in birds, are not as useful in studies of altitudinal shifts, due to their broad scale. Instead, surveys using transects or point counts are used to investigate elevational shifts in birds.
b) Relatively few bird communities have been studied along altitudinal gradients in the past (for meaningful time periods).

Only a few studies (predominantly within the temperate Holarctic) could be found explicitly investigating upward shifts in bird species' ranges that have already occurred – the results of which are ambiguous (e.g. Pounds *et al*. 1999; Archaux 2004; Tryjanowski *et al*. 2005; Peh 2007; Popy *et al.* 2010; Maggini *et al.* 2011). In the tropical cloud forests of Monteverde in Costa Rica, between 1979 and 1998, lowland and foothill species, such as *Ramphastos sulfuratus* (Keel-billed toucan), extended their ranges up mountain slopes in response to elevated cloud-base levels (Pounds *et al.* 1999). However, species that extended their distribution upslope often shifted downwards too. Archaux (2004) investigated altitudinal shifts in forest breeding bird distributions in the French Alps between the 1970s and 2000s, and found that the bird communities did not shift their distribution upwards despite a 2.3°C increase in spring temperatures, although they did suggest that there might be a time lag effect. Studying *Ciconia ciconia* (White Stork) in the Tatra Mountains of southern Poland, Tyrjanowski *et al.* (2005) provided what is believed to be the first well-documented evidence of a bird species ascending to higher elevations as a result of both changes in habitat and climate. An analysis of the elevational distributions of Southeast Asian birds over a 28-year period by Peh (2007) provides evidence for a potential upward shift for 94 common resident species. However, over the same time period 93 species exhibited downward shifts in both their upper and lower boundaries. Popy *et al.* (2010) found only a weak upward elevational shift in the distribution of breeding birds in the Italian Alps over an 11-year period with an approximate 1°C increase in temperature in the area. They state that the observed elevational shift in the distributions of the avifauna cannot unambiguously be attributed to climate warming. Finally, Maggini *et al.* (2011), found relatively even proportions of Swiss birds (95 species) to significantly shift upwards, downwards or display no significant change, between 1999-2002 and 2004-2007 – with associated increases in mean temperature over this time period.

As can be seen from the above studies alone, only a subset of species shift upslope as expected under warming temperatures, whereas a number of species ranges have been found to remain unchanged with respect to elevation or to move/expand towards lower elevations. Such heterogeneous shifts in elevational ranges have been identified across taxa (see Lenoir *et al*. 2010; Tingley *et al.* 2012). Focusing on potential mechanisms for downward shifts or expansions, some have attributed it to a strong precipitation response (e.g. Tingley *et al.* 2012). In addition, Lenoir *et al.* (2010) propose that both climate warming and/or habitat modification may increase levels of disturbance leading to: (1) a temporary reduction of the importance of competition as a limiting factor on species distributions (i.e. competitive release), and (2) an associated potential range expansion towards lower elevations for species whose lower elevation margin was previously strongly limited by competition (however, see Jankowski *et al.* 2010).

It is important to note that a widely cited meta-analysis by Chen *et al.* (2011) estimated that the distributions of terrestrial organisms have recently shifted to higher elevations at a median rate of 11.0 meters per decade. However, focusing on birds, only four temperate studies were included. In turn, birds were found to respond least in terms of elevational shifts, with considerable interspecific variation in response – likely based on differences in physiology, ecology and environment.

Only a few avian studies could be found examining the effects of particular species' life-history and ecological traits on interspecific variability in elevational range shifts – regardless of direction (e.g. Relf & Flousek 2012; Tingley *et al.* 2012). For example, Tingly *et al.* (2012) found bird species in the North American Sierra Nevada Mountains were more likely to shift elevational ranges if they had small clutch sizes, defended all-purpose territories and were year-round residents. This went against their *a priori* hypothesis that traits concerning dispersal and colonisation should be positively related to range movements (Angert *et al*., 2011), i.e. migration during the nonbreeding season, large clutch size, large home range size, small body size, low territoriality, and a generalist diet. Without more studies spanning a broader taxonomic and geographic range, and investigating consistently defined traits, it is impossible to propose any general relationships between avian traits and climate change related range shifts.

As a final point, in some studies, evidence for altitudinal range shifts has been derived from a single or small number of permanent sampling plots established at a select position along the climatic gradient (e.g. Pounds *et al.* 1999). However, such studies assume that change at one point can be unambiguously interpreted as range shifts, rather than merely local density changes, range expansions or contractions (Shoo *et al.* 2006). A simulation study by Shoo *et al*. (2006) found that smaller range shifts are detectable by analysing change in the mean altitude of presence records rather than upper or lower range boundaries. Similarly, Archaux (2004) reasoned that change in species at the mean altitude was more indicative of a population response than change measured at range boundaries (see also Maggini *et al.* 2011).

1.11.2 Predicted elevational shifts in avian distributions

As with observed elevational range shifts, studies predicting future elevational range shifts in avian distribution are fewer in number than their latitudinal counterparts. This is despite the fact that existing studies predict extinctions and heightened extinction risk for a large proportion of montane bird species – especially those that are endemic and tropical (e.g. Williams *et al*. 2003; Shoo *et al.* 2005; Sekercioglu *et al.* 2008; Gasner *et al.* 2010; La Sorte & Jetz 2010, but see Peterson 2003). In fact, it has been suggested that, if global temperatures rise more than 2–3°C in coming decades, high-elevation specialists in the tropics could be among the most threatened species on Earth (see references within Laurence *et al.* 2011). In north-east Queensland, Australia, the distributional extents of 13 bird species endemic to montane tropical rainforests are expected to shrink dramatically (30% with a 1°C temperature increase, 96% with a 3.5°C rise), as suitable climate space retreats to higher altitudes (Williams *et al.* 2003). Within the same study region, Shoo *et al.* (2005) used extensive abundance data and expected range shifts across altitudinal gradients to predict changes in total population sizes in response to climate warming. According to their most conservative model scenario, 74% of rainforest birds of north-eastern Australia are predicted to become threatened within the next 100 years. A particularly interesting result of this study, was that extinction risk varied according to where along the altitudinal gradient a species is currently most abundant, with upland birds being identified as immediately threatened by even small increases in temperature. Climate-envelope modelling at high resolution (c. 1 km^2) in the Albertine Rift Valley of East Africa has shown that suitable climatic conditions for 14 endemic bird species are to move upslope by, on average 350m by 2085 – with at least one of these species, *Kupeornis rufocinctus* (Red-collared Mountain-babbler) projected to lose all suitable climate within the region (BirdLife International 2013, and http://www.africa-climate-exchange.org/albertine-rift/). Sekercioglu *et al.* (2008) modelled elevational range shifts at the global scale, and using an intermediate estimate of surface warming of 2.8°C, projected 400–550 land-bird extinctions. In addition they predicted that approximately 2,150 additional land-bird species would be at risk of extinction by 2100, of which only 21% are currently considered threatened with extinction.

Most recently, a key study by La Sorte & Jetz (2010) provided a global baseline assessment of expected global warming-induced geographical range contractions and extinction risk (between 1980-1990 and 2080-2099) for the world's 1009 montane bird species that breed ≥1000m (i.e. high-elevation specialists). In a novel analysis they considered three dispersal scenarios, namely:

1) No-dispersal (ND) scenario – allowing only the lower elevational range boundary to shift in response to warming temperatures;
2) Vertical-dispersal (VD) scenario – allowing both lower and upper elevational range boundaries to shift;
3) Vertical dispersal plus lateral-dispersal (VD+LD) scenario – additionally allows LD to a maximum distance of 1000 km from the edge of the range.

Under the ND scenario, projected median range sizes declined by 54% worldwide. Vertical range extent was the greatest predictor of projected species' extinction risk, with those possessing narrow distributions most at risk (lateral range extent was only of minor importance), and at least a third of montane bird diversity (327 species) found to be severely threatened (i.e. projected as losing ≥50% of their range, resulting in range sizes <20,000 km^2). In the VD scenario, median losses in range size declined to 27%, and the location and structure of mountain systems emerged as a strong driver of extinction risk (e.g. the availability of higher elevation area within a given species range). Even under the VD+LD scenario (i.e. the 'best-case' scenario), lateral movements offered little improvement to the 'fate' of montane species in the Afrotropics, Australasia and Nearctic (due to the geographical patterns of projected warming and the extent, orientation and isolation of mountains in these realms). Overall, the results of La Sorte & Jetz (2010) demonstrate the particular roles that the distribution of species richness, the spatial structure of lateral and especially vertical range extents, and the specific geography of mountain systems have in shaping the vulnerability of montane biodiversity to climate change. However, they do acknowledge that a broad array of additional environmental and ecological factors (e.g. species interactions) will shape individual species' responses to climate change, and that the projected outcomes could be more severe for less vagile vertebrates.

A number of potential explanations for montane species being a high risk group under impeding climate change have been suggested, although none have been explicitly tested. In general it is believed that their risk is associated with their geographical isolation, limited range size and unique environmental adaptations (La Sorte & Jetz 2010). Due to the nature of mountain area declining with increasing elevation, as a species shifts upwards, contraction in range size is inevitable, increasing the extinction risk of many species (Sekercioglu *et al.* 2008), especially those living at the highest elevations that have little or no remaining habitat to colonise (Williams *et al.* 2003). Vertical dispersal may be hampered by declines in the quantity and quality of habitable land area and the development of vertical gaps between current and future suitable elevation bands: 'range-shift gaps' (La Sorte & Jetz 2010). Lastly, the potential for lateral dispersal by mountain-top species is limited, severely so for tropical species, owing to the lack of latitudinal temperature gradients and weak seasonality in temperature (see Janzen 1967; Ghalambor *et al.* 2006).

Regarding projected elevational range shifts, research to date has focused overwhelmingly on predicting shifts with respect to global increases in temperature, despite the additional importance of changes in precipitation regimes – which in turn are more difficult to model, assess and measure (Tingley *et al.* 2012). However, a recent study by McCain & Colwell (2011), attempted to address this knowledge gap by modelling local population extirpation risk for a range of temperature and precipitation scenarios over the next 100 years for vertebrate populations (including birds) distributed along elevational gradients globally. They found average population extirpation risks to increase 10-fold when changes in precipitation were considered in addition to warming alone – highlighting the importance of conducting more realistic and complex predictions of future climate change risks.

It is important to appreciate the limitations of projecting the rate of extinction with respect to elevational shifts in the face of climate change. For example, different habitat-loss and surface-warming scenarios often predict substantially different extinction risk futures for species (e.g. Sekercioglu *et al.* 2008). In addition, extinction risk projection is also challenging due to lags in species population responses, incomplete knowledge of natural adaptive capacity and the complexities of inter-specific interactions within communities (La Sorte & Jetz 2010).

Anthropogenic land-use change and climate change are predicted to be the two primary drivers of biodiversity loss this century (Sala *et al.* 2000), a problem exacerbated by interactions between both drivers (Jetz *et al.* 2007, Malhi *et al.* 2008). For example, habitat loss and fragmentation can limit the dispersal and colonisation ability of species that might otherwise track a changing climate (Travis 2003). It is therefore of great importance that future studies incorporate both climate change parameters and other anthropogenic threat measures into their models.

1.11.3 Lowland tropical biodiversity under global warming

As with montane species, it should also be highlighted that the responses of tropical lowland species to global warming remains poorly understood, with an array of differing opinions (Corlett 2011). The latitudinal gradient in temperature levels-off to a plateau between the Tropic of Cancer and the Tropic of Capricorn and, consequently, latitudinal range shifts are unlikely for species confined to the tropics (Lovejoy 2010). This leaves upslope range shifts as the only dispersal route for tropical species already living near their thermal limit, and that live in close proximity to mountains (Sekercioglu *et al.* 2012). One widely-cited scenario is that tropical lowland biodiversity may decline with global warming, due to a lack of a 'species pool' to replace lowland species that migrate to higher elevations, i.e. 'lowland biotic attrition' (Colwell *et al*. 2008). Alternatively (or in addition), lowland species may not be able to track suitable climates upwards due to a lack of adaptations required to survive and thrive at higher altitudes (see Buermann *et al.* 2011). There is therefore the potential for both 'lowland biotic attrition' and 'montane (high-altitude) biotic attrition' (Colwell *et al.* 2008; Buermann *et al.* 2011). For bird species that inhabit extensive flat areas such as the Amazon basin, where mountains are few and far between, poor dispersers are unlikely to make the required long-distance shifts in range (see discussion in Sekercioglu *et al.* 2012).

1.12 Mountains and protected areas

Formal protected areas (hereafter PAs) are considered to be the most widespread and important core 'units' for *in situ* biodiversity conservation (e.g. Chape *et al*. 2005; Boyd *et al.* 2008; Jenkins & Joppa 2009), although complementary conservation approaches are also required. The IUCN definition of a PA is the most widely recognised – adopted on both national and international levels. The most recent revised definition is: '*a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values*' (Dudley 2008).

In response to the failed global target of significantly reducing the rate of biodiversity loss by 2010, parties to the Convention on Biological Diversity (CBD) recently adopted a revised strategic plan containing 20 new targets for addressing biodiversity loss by 2020. Among these, Target 11 states that *'…at least 17% of terrestrial and inland water areas* […]*,* *especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of PAs and other effective area-based conservation measures…*' (CBD 2010). By the end of 2009, terrestrial PAs covered 17.3 million km^2 globally, equating to 12.9% of the total land surface outside Antarctica (Jenkins & Joppa 2009), but see Coad *et al.* (2010). Substantial progress is therefore needed before Target 11 is achieved worldwide.

Regarding the representativeness of PAs, a number of studies have highlighted that the geographic patterns of protection have a distinct bias and are not effectively safeguarding the world's hotspots of species richness, endemism or threat. The phrase 'rock and ice' refers to the common perception that PA locations are biased towards marginal lands where natural land cover might remain even without a PA, rather than towards locations where they can best mitigate rapid and extensive land-use change (Joppa & Pfaff 2010). Both national (e.g. Hunter & Yonzon 1993; Pressey & Tully 1994; Scott *et al.* 2001; Pressey *et al.* 2002; Maiorano *et al.* 2006) and global (e.g. Rodrigues *et al.* 2004a,b; Hoekstra *et al.* 2005; Gorenflo & Brandon 2006; Joppa & Pfaff 2010) studies assessing this issue have found evidence for PA location bias. A key study by Jenkins & Joppa (2009) showed the unrepresentative distribution of PAs with respect to realms, biomes and ecoregions. They found highly protected regions were typically those under low levels of land degradation pressure, such as temperate conifer forests and montane grasslands and shrublands. Joppa & Pfaff (2009) conducted a global assessment of national-level PA network distributions, and found them to be heavily biased towards higher elevations, steeper slopes and greater distances to roads and cities, with higher protection status PAs more biased than those with lower protection status. All of these studies conclude that future investment in new PAs needs to be better targeted, using tools such as gap analysis (Scott *et al.* 1993), systematic conservation planning (Margules & Pressey 2000) and global conservation prioritisation schemes (see Brooks *et al.* 2006).

Rodríguez-Rodríguez *et al.* (2011) conducted a comprehensive multi-scale evaluation of progress towards Target 11 with respect to mountains (excluding Antarctica). They found that the CBD's 17% target had already almost been met, with 16.9% of the world's mountain areas falling within PAs at the end of 2009 - representing 32.4% of the extent of the world's terrestrial PA network. In comparison, only 11.6% of the global lowland area was found to be protected. In a separate but complementary study, considering only mountain areas with the lowest 'Human Influence Index', Rodríguez-Rodríguez & Bomhard (2012) found the proportion protected increased to more than a third.

From a historical perspective, when PAs were first established, mountains were a favourite choice (see Kollmair *et al.* 2005 for a discussion on the history of PAs in mountainous regions). In fact, the first modern PA, declared back in 1872, was the mountainous Yellowstone National Park. However, as summarised by Körner & Oshawa (2005), many mountain PAs were historically established to '*protect the scenic high peaks of local or national value as cultural icons or for mountaineering and tourism'* – biodiversity values were not considered.

Although the world's PAs are clearly biased toward mountain areas, especially those under the least human influence, PA coverage is highly uneven across the world's mountains and inadequate at a range of scales (Rodríguez-Rodríguez *et al.* 2011). Protection of mountain areas has been shown to be uneven and largely insufficient, with 63% of countries, 57% of realms, 67% of biomes and 61% of ecoregions falling short of the 17% target (Rodríguez-Rodríguez *et al.* 2011). It should be noted that many global scale analyses of PAs (including Rodríguez-Rodríguez *et al.* 2011, 2012) exclude 'rock and ice' ecoregions, which comprise about 16% of the global mountain area. Focusing on the elevational distribution of PAs, a number of regional studies have clearly shown the highly skewed distribution of PAs towards higher-elevation zones, characterised by comparatively low species richness and anthropogenic threat (Sections 1.3 and 1.10, respectively), e.g. Himalayas (Hunter & Yonzon 1993; Shrestha *et al.* 2010), Western Ghats of India (Ramesh *et al.* 1997), Costa Rica (Powell *et al.* 2000) and Mexico (Cantu *et al.* 2004).

There is considerable evidence to suggest that existing mountain reserves do not cover sufficient areas to guarantee biodiversity conservation. For example, Rodríguez-Rodríguez *et al.* (2011) found only 17% of Important Bird Areas (IBAs) located (completely or partly) in mountain regions to be entirely protected, with 39% wholly unprotected. Rodrigues *et al.* (2004a) identified unprotected areas of the world that have high conservation value (irreplaceability) and are under serious threat. They found such areas to be concentrated in tropical and subtropical moist forests, particularly on tropical mountains and islands. In a related study, Rodrigues *et al.* (2004b) found the global distribution of 'gap species' to mainly reflect the presence of narrowly distributed, often threatened, species. The regions highlighted to contain many 'gap species' include many recognised centres of endemism, most of which are tropical montane regions (e.g. tropical Andes, Cameroon Highlands and the mountains of Southern China). Beresford *et al.* (2010) showed there to be poor overlap between the distribution of PAs and globally threatened birds in Africa, recommending expansion of the PA network in predominantly mountainous areas, e.g. Albertine Rift, Cameroon Highlands and the Eastern Arc.

Based on the findings from the studies above, the challenge in the future will not only be to establish new PAs in currently neglected mountainous regions of high biodiversity value, but to also enlarge existing mountainous PAs. In particular, to extend them to lower elevations, thereby promoting species, genetic, and community conservation, and providing functional landscapes for wide-ranging species (Körner & Oshawa 2005). Such, expansion from summits to lowlands is also of importance for climate change response (Section 1.11). As the majority of mountain PAs constitute discrete units, covering single mountains only, lateral connectivity of PAs is also vital where applicable, as it would aid migratory species, and potentially act as a buffer against climate change (Körner & Oshawa 2005). A number of these corridor initiatives are now in place, such as the Yellowstone-to-Yukon corridor in North America and the Condor Bioreserve in Ecuador. The IUCN World Commission on Protected Areas produced a set of '*Guidelines for Planning and Managing Mountain Protected Areas*' (Hamilton & McMillan 2004) to help rectify the current situation.

To conclude this section, it is important to note that mountainous regions are receiving increasing attention because of the wide range and importance of the ecosystem services they provide – both tangible and intangible (UNEP-WCMC 2002). As summarised by Rodríguez-Rodríguez *et al.* (2011), these include: '*water provision, air purification, agricultural diversity, minimisation of natural hazards, supply of natural resources, cultural diversity, leisure, landscape and spiritual values, income sources for local populations, research and early warning systems'*, and as already highlighted in Section 1.3, biodiversity. Based on this and the discussions in Sections 1.3, 1.10 and 1.11 it is therefore of great importance for humans to effectively conserve mountainous areas via PAs.

CHAPTER TWO

Introduction to trait biogeography

2.1 Trait biogeography: an overview

This section will provide a critical review of the literature on trait biogeography, highlighting knowledge gaps. This review is across taxa, but with a focus on birds where applicable. In addition, emphasis is placed on those studies that have investigated trait biogeography from an elevational perspective.

2.1.1 What is a trait?

Trait-based approaches are widely used in ecological and evolutionary research. In its simplest definition, a trait is a surrogate of organismal performance, and this meaning of the term has been used by evolutionary biologists since the time of Darwin (1859). However, over recent years, developments within all subfields of ecology have developed the concept of a trait beyond these original boundaries, and trait-based approaches are now used in studies ranging from the level of organisms to that of ecosystems. Consequently, a variety of types of traits can now be found in the literature (summarised in Violle *et al.* 2007). Despite some attempts to standardise the terminology, especially in plant ecology (e.g. Lavorel *et al.* 1997; Diaz & Cabido 2001), there is currently some confusion in its use, not only of the term 'trait' itself, but also in the underlying concepts it refers to. This is largely due to a lack of coordination and interaction across disciplines with respect to developing protocols for the quantification of traits (Naeem & Bunker 2009).

Violle *et al.* (2007) proposed a definition of 'trait' which they deemed unambiguous: *'a trait is any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization'*. This definition implies that no information external to the individual (environmental factors) or at any other level of organization (population, community or ecosystem) is required to define a trait. This definition is in contrast to the more open definition put forward by McGill *et al*. (2006): '*a trait is a well-defined, measurable property of organisms, usually measured at the individual level and used comparatively across species'*.

A further complication has arisen with the introduction of the term 'functional trait(s)', an expression coined with the emergence of functional ecology as a discipline (Calow 1987). As is the case for 'traits', the definition and use of 'functional traits' remains unclear (see Violle *et al*. 2007). Violle *et al*. (2007) provide the following definition: *'a functional trait* *is any morphological, physiological, or phenological trait which impacts fitness indirectly via its effects on growth, reproduction and survival*' – the three components of individual performance. Examples include: basal metabolic rate, beak size, seed or egg size, adult body weight, frost tolerance and potential photosynthetic rate (McGill *et al*. 2006).

Using the general trait definition of McGill *et al*. (2006), Tyler *et al.* (2012) suggest that those traits most relevant to large-scale ecology include: life history (e.g. life span, growth rate, body size), reproduction (e.g. egg size, fecundity), feeding ecology (e.g. trophic level, diet breadth) and behaviour (e.g. dispersal ability). Schleuter *et al.* (2010) note that a consequence of this diversity of relevant traits is that whereas a 'taxonomic' macroecological study requires information on the geographical distributions of species, trait-based analyses additionally require trait measurements for each species – sometimes for a complementary suite of traits. Yet, as stated by Naeem & Bunker (2009), trait data are *'…at best, dispersed throughout the literature, and at worst lacking altogether'*. Missing data can have a serious influence on statistical conclusions (Nakagawa & Freckleton 2008), and so the uneven availability of trait data are a potential obstacle to the trait-based approach to ecology (particularly macroecology); but there has been very little effort to quantify the degree to which trait data are available for entire, species-rich assemblages. Attempts to date include Tyler *et al.* (2012) with respect to demersal marine fauna of the United Kingdom, and TraitNet (Naeem & Bunker 2009; http://traitnet.ecoinformatics.org/). TraitNet is a network designed to facilitate trait-based research, and is aiding the development of a prototypical universal trait database called TraitBank. Its inception was due to the fact that existing trait databases, where they exist at all, have essentially remained specialised to particular regions, taxa, or sets of traits, and are typically not open-access.

2.1.2 Biogeography of traits

Defining biogeography: In its broadest definition, biogeography is the science that attempts to document and understand past and present spatial patterns of biodiversity (Lomolino *et al.* 2010). Modern biogeography includes studies of the patterns of geographic variation in biodiversity at all possible scales of analysis – from genes to entire communities and ecosystems – across geographic gradients, including: area, latitude, longitude, elevation, depth and isolation (Gaston 2000). The discipline has deep scientific roots, with some of the major themes already established as areas of enquiry by the early 1800s (see Ladle & Whittaker 2011).

From taxonomy to traits: Biogeography has both traditionally and predominantly been studied from a taxonomic perspective, focusing on patterns and underlying processes of species richness and composition within and among assemblages (Green *et al.* 2008; Olden *et al.* 2010). However, it is important to highlight that trait-based approaches to biogeography have been used for more than a century (e.g. Schimper 1898). In fact, the geographical variation in species' phenotypes has long been a focus in biogeography, generating many ecogeographical 'rules' (Section 2.1.3). Over the past 30 years, there has been a resurgence of interest in trait-based methodologies, across taxa, including an increasing trend in studies aiming to understand patterns in the distribution not only of taxa but also of the traits those taxa possess (McGill *et al.* 2006; Westoby & Wright 2006; Green *et al.* 2008; Olden *et al.* 2010). Plants have been the focal group in this re-emerging research area (e.g. Westoby & Wright 2006; Moles *et al.* 2007). Concerning birds, trait-based studies have been conducted for decades at a variety of spatial scales, primarily to understand adaptation and the evolution of morphological, life-history, ecological and behavioural trait diversity, but also to investigate allometry, and patterns of trait covariation in order to examine trade-offs (Bennett & Owens 2002, and references within) – often using a comparative approach (Harvey & Pagel 1991).

With the increasing availability of trait data being assembled into large databases for whole taxonomic groups, combined with the advent of high-quality satellite data and spatially-explicit models, the first studies on the spatial distribution of traits at a global scale, that have an explicit environmental focus and robust analytical framework, are starting to be undertaken for well-studied taxa such as plants (e.g. Moles *et al.* 2007, 2009; Swenson & Enquist 2007) and birds (e.g. Jetz *et al*. 2008a; Olson *et al*. 2009). Tailor-made software is also starting to be developed to aid in implementing such studies, e.g. the R package 'rangeMapper' (Valcu *et al*. 2012).

Knowledge on the biogeography of traits can be used to understand complex phenomena and shed light on fundamental questions in ecology, including: why organisms live where they do, how many taxa can coexist in a given place, and how they are responding, and could respond in the future, to environmental change (Green *et al.* 2008). In fact, macroecologists are gaining an improved understanding of the mechanisms behind large-scale patterns in biodiversity, by linking species traits to their abundance and distribution (Tyler *et al.* 2012). In addition, combining current trait spatial distributions with phylogenetic information may aid in advancing current understanding of how ecology shapes evolution and *vice versa* (Dawson *et al.* 2013). Ultimately, as stated by Dawson *et al.* (2013) '*traits allow for stronger testing of hypotheses that could not be addressed solely with data on environment and species localities or species' counts, demonstrating the potential for trait-based approaches to open the black box of biogeographical process*'.

Conservation biogeography: Conservation biogeography is a relatively new research area within the field of biogeography, formally defined by Whittaker *et al*. (2005) as: '*the application of biogeographical principles, theories and analyses, being those concerned with the distributional dynamics of taxa individually and collectively, to problems concerning the conservation of biodiversity'*. It is now recognised as a key subfield of conservation biology, and considerable research has been conducted in recent years (see Ladle & Whittaker 2011). There is increasing realisation that conservation at small scales is not sufficient for the task at hand (Richardson & Whittaker 2010). As summarised in Ladle & Whittaker (2011), in order to successfully manage biodiversity, we need to know: (a) where it is, (b) how it is arranged at different spatial scales, (c) how the different aspects of diversity co-vary spatially and temporally, and (d) how they respond to a complex suite of drivers that act and interact to mediate diversity and distributions via numerous mechanisms and processes.

Trait-based approaches have great potential to advance conservation biogeography, but studies at the taxonomic scale still dominate (Olden *et al.* 2010). A search for peer-reviewed papers and conference proceedings whose title, abstract/summary or keywords contains both the phrases 'conservation biogeography' and 'trait' on the ISI Web of Knowledge database returned only 18 references (search date: 01/08/2013; http://webofknowledge.com).

2.1.3 Ecogeographical rules

As stated by Lomolino *et al.* (2006), we are currently experiencing a resurgence of interest in ecogeographical rules. These are broadly defined as: general trends in morphology, physiology, life-history and range-related traits, within and/or across species/assemblages, with respect to biogeography – specifically geographical gradients, and particularly latitude (for a recent review, see Gaston *et al.* 2008). Examples include:

- *Bergmann's rule* = latitudinal increase in body size (Bergmann 1847).
- *Allen's rule* = latitudinal decline in limb length/surface area (Allen 1877).
- *Lack's rule* = latitudinal increase in avian clutch size (Lack 1947).
- *Rapoport's rule* = latitudinal increase in geographical range size (Stevens 1989).
    - *Steven's extension* = elevational increase in elevational range size (Stevens 1992).

The term 'ecogeographic rule' is arguably a misleading for two main reasons. Firstly, nearly all these patterns suggest not just an ecological but also an evolutionary basis for the pattern, and secondly, few, if any, of these patterns warrant the status of an invariant 'rule' of nature, with there often being exceptions to them (Lomolino *et al.* 2006).

Currently, there is a wealth of debate between both the observed patterns themselves and their underlying causal explanations. This debate is largely a result of differences in the study systems and biota, spatial and temporal scales, and/or methodologies used, and because none of these 'rules' applies independently of other influences. Consequently, in order to develop a more comprehensive understanding of the generality and underlying causal mechanisms for these patterns, Lomolino *et al.* (2006) devised a list of ten recommendations, which collectively emphasise the need for a more integrated research approach. Similarly, Gaston *et al.* (2008) stressed the importance of advancing our current understanding of the spatial patterns of traits at the intraspecific, interspecific and assemblage level, by assessing their distinctions and interactions.

2.1.4 Biogeography of body size

Body size variation with latitude: One factor that has repeatedly been proposed as a predictor of variation in body size is latitude, and the relationship between these two variables was first studied by Bergmann (1847). The tendency for a positive relationship between latitude and body size has since been formalised as Bergmann's rule, and has been extensively studied across a variety of taxa, for example:

- **Mammals:** Ashton *et al.* (2000); Freckleton *et al.* (2003); Blackburn & Hawkins (2004); Meiri *et al.* (2004); Rodriguez *et al.* (2006); Diniz-Filho *et al.* (2007); Medina *et al.* (2007); Rodriguez *et al.* (2008); Clauss *et al.* (2013).
- **Birds:** James (1970); Cousins (1989); Blackburn & Gaston (1996a); Blackburn & Ruggiero (2001); Ashton (2002a); Ramirez *et al*., (2008); Olson *et al.* (2009); Boyer *et al.* (2010).
- **Reptiles:** Lindsey (1966); Ashton & Feldman (2003); Reed (2003); Cruz *et al.* (2005); Olalla-Tárraga *et al.* (2006); Pincheira-Donoso *et al.* (2007, 2008).
- **Amphibians:** Ray (1960); Lindsey (1966); Ashton (2002b); Morrison & Hero (2003); Olalla-Tárraga & Rodriguez (2007); Adams & Church (2008).
- **Terrestrial Invertebrates:** Cushman *et al.* (1993); Kaspari & Vargo (1995); Hausdorf (2003); Shelomi (2012).
- **Marine invertebrates:** Roy *et al.* (2001); Berke *et al.* (2012).
- **Fish:** Ray (1960); Lindsey (1966); McDowall (1994); Belk & Houston (2002); Blanchet *et al.* (2010).
- **Plants:** Moles *et al.* (2009).

Numerous studies have resulted in a long and lively debate with respect to this ecogeographical rule – by far the most studied. However, despite doubts about its existence (e.g. McNab 1971; Geist 1987; Geist 1990; Paterson 1990), both the intra- and interspecific versions of Bergmann's rule have received broad support in mammals (e.g. Ashton *et al*. 2000; Meiri & Dayan 2003; Blackburn & Hawkins 2004; Clauss *et al.* 2013) and birds (e.g. James 1970; Blackburn & Gaston 1996; Ashton 2002a; Meiri & Dayan 2003; Ramirez *et al.* 2008; Olson *et al.* 2009; Boyer *et al.* 2010). The rule is most often applied to endotherms – empirically, evidence for the prevalence of Bergmann's clines in ectotherms is conflicting (see Hausdorf 2003; Adams & Church 2008; Pincheira-Donoso *et al.* 2008; Shelomi 2012). Despite the rule being formulated for interspecific comparisons, intraspecific patterns across all taxa have received the most attention.

A variety of hypotheses have been suggested to explain why body mass should vary systematically with latitude across species, and as of yet, there is no consensus mechanism. The most comprehensive avian study favouring Bergmann's rule, was a global study by Olson *et al.* (2009), utilising a grid-cell approach. They found temperature to be the single strongest environmental correlate of body size, with resource availability a secondary correlate.

Body size variation with elevation: If Bergmann's rule is a response to the harshness of the climate, it follows that latitudinal variation in body size should be mirrored by similar elevational variation. On average, air temperature decreases monotonically by about 0.6°C per 100 m elevational gain (Barry 1992). Indeed, elevational variation in avian body size has been documented in the literature (e.g. Rand 1936; Traylor 1950; Moreau 1957; Diamond 1973; Köster 1976; Altshuler *et al.* 2004; Soobramoney *et al*. 2005; Guillaumet *et al.* 2008), although it has been much less studied than variation with latitude, and most examples refer to intraspecific variation.

A recent study by Kennedy *et al.* (2012), focusing on the ecological limits of diversification of the Himalayan core Corvoidea (crows and allies: 57 species), found a positive trend between that of body size and elevation. However, they found this to contrast with the presence of many small-bodied species spanning all elevations within the Passerida (warblers, thrushes, finches, and other songbirds) of the region (approximately 400 species), and many large-bodied species at low elevations in the other non-passerines of the Himalayas (approximately 130 species). They discuss these contradictory findings with respect to competition.

Only one avian study could in fact be found that explicitly studies the relationship between interspecific body size variation and elevation (Blackburn & Ruggiero 2001). Focusing on Andean passerines (839 species), they found that across species, body mass is positively correlated with species' elevational distributions (midpoint, maximum and minimum, but not range). This relationship is maintained when controlling for phylogenetic relatedness and when focusing only on Andean endemics. The results of this study reflect those of Bergmann's rule. Nevertheless, the effects shown are very weak, with elevation explaining only a few percent of the variation in body mass (40 of 137 genera showed negative relationships between body mass and elevational range midpoint – counter to expectation).

Concerning non-avian relationships, elevational trends in intraspecific body size have been observed in mammals, although such trends are ambiguous. Some conform to Bergmann's rule (Ravosa 2007; Lin *et al*. 2008), whereas others show the opposite trend (Davis 1938; Taylor *et al.* 1985; Zammuto & Millar 1985; Dobson 1992; Yom-Tov *et al.* 2012), or do not change along an elevational gradient (Wasserman & Nash 1979; Medina *et al.* 2007). No interspecific studies for mammals could be found.

Bergmann's rule was originally proposed with respect to endotherms. However, a number of studies on ectotherms have been conducted. For reptiles, as with other taxa, results are ambiguous. The most rigorous study conducted to date is that by Pincheira-Donoso *et al.* (2008) on some 120 species of lizard within the *Lioaemus* genus. Both non-phylogenetic and phylogenetic analyses showed no evidence of increasing body size with increasing elevation (or latitude). Regarding amphibians, empirical evidence supporting the prevalence of Bergmann's clines with respect to elevation (and latitude) is controversial (Morrison & Hero 2003; Adams & Church 2008; Hu *et al*. 2011). Hu *et al.* (2011) found species of spiny frog to possess a significant negative correlation between body size and elevation. Among factors that might explain the disparity observed across studies testing Bergmann's rule in ectotherms, are their scarcity and poor representativeness, along with the limited availability of phylogenetic studies. Pincheira-Donoso *et al.* (2008) actually suggest as an alternative hypothesis, that large body size is unfavourable for ectotherms in cold-climates, as it demands longer basking times to achieve optimal metabolic temperatures, and that Bergmann's rule should be employed to investigate patterns of body size evolution only in endotherms.

Only one study could be found with the aim of investigating elevational patterns in body size for fish (Fu *et al*. 2004). They found Bergmann's rule could not be confirmed by the interspecific elevational body-size pattern of freshwater fishes in the Yangtze River basin. It should be highlighted that, with respect to freshwater/marine environments, the equivalent to terrestrial elevational gradient studies is that of bathymetric gradients. The phenomenon of 'deep-water gigantism', a trend towards increased body size with increasing depth (correlated with increasingly lower temperatures), has been studied for many groups of marine animals, but is most clearly seen in crustaceans, both benthic and pelagic, and is attributed to decreased predation and temperature (Timofeev 2001). However, the 'miniaturisation of taxa' has also been found with respect to increasing depth, and is thought to be related to the drastic decrease in food availability (see discussion in McClain *et al.* 2006). For fish, the interspecific relationship between body size and mean depth of occurrence has also been found to vary among classes and orders (Smith & Brown 2002).

Shelomi (2012) conducted an extensive review of the known literature on intra- and interspecific variation in insect size along elevational and latitudinal clines. The review found that there are nearly even numbers of studies showing Bergmann clines and converse-Bergmann clines, with the majority of studies suggesting no clines at all. Shelomi (2012) concluded that the validity of Bergmann's rule for insects is highly idiosyncratic and partially dependent upon study design. Only one study concerning elevational gradients and body size could be found for non-insect invertebrates (Hausdorf 2003). He found no significant correlation when investigating phylogenetically controlled interspecific variation in body size with elevation for snail species in north-west Europe.

Moles *et al.* (2009) investigated cross-species geographical variation in plant height at a global level (5784 species). Elevational gradients in plant height are well known within species (e.g. Totland & Birks 1996; Fernandez-Calvo & Obeso 2004; Macek & Leps 2008), and increases in elevation are often associated with decreases in plant height within a region (e.g. Kappelle *et al*. 1995; Wilcke *et al*. 2008). However, Moles *et al.* (2009) found elevation to be only weakly related to plant height at a global scale.

It should be noted, that some studies combine latitude and elevation into a single variable, justifying that both are generally similar with respect to temperature (e.g. Ashton 2002a; Ashton & Feldman 2003; Cruz *et al.* 2005; Pincheira-Donoso *et al.* 2007, 2008). However, this makes the added assumption that latitudinal and elevational gradients are similar in all other aspects additional to temperature, which is clearly inaccurate (Section 1.4).

Only one study could be found that examined the simultaneous effects of latitude and elevation on body size (Blackburn & Ruggiero 2001). Via multiple regression analysis, they found for Andean passerines that, across all species, there is a significant effect of elevation on body mass when controlling for latitude, but no effect of latitude when controlling for elevation. Both elevation and latitude were shown to be significant in the model for endemic species, while in the non-endemic model only latitude was significant.

Body size variation with geographical range: There is an extensive published literature centred on understanding interspecific variation in geographical range sizes. For a general summary of the correlation between body size and geographic range size, see Brown (1995), Blackburn & Gaston (2003), Gaston (2003). For the purposes of this review, key studies concerning birds will be the focus.

Confusion has always existed over the form of interspecific geographic range size-body size relationships, with published positive (e.g. Carrascal *et al*. 2008), negative (e.g. Glazier 1980), triangular (e.g. Brown & Maurer 1987; Coetzee *et al.* 2013) and non-significant relationships (e.g. Virkkala 1993). Blackburn & Gaston (1996) found patterns of breeding range size and body mass to vary with respect to latitude for New World birds. When controlling for phylogenetic relatedness of species and for population size, Gaston & Blackburn (1996a) found no relationship between body and geographic range size in Anseriformes.

A recent study by Laube *et al.* (2013) evaluated the effect of a suite of avian traits, including body size, on the global range sizes of 165 European passerines using path analysis. They found that body size effects were particularly complex, with both positive and negative effects acting over different pathways – the trait had a strong positive direct effect, which was reduced by negative indirect effects via annual fecundity, migratory behaviour and dispersal ability. Suggested causal mechanisms behind the direct and indirect paths between body size and range size are discussed in the paper in some detail. Briefly, Laube *et al.* (2013) comment that large body size in birds may directly increase range size because of body-size dependent spatial interactions with resources and the environment (Brown 1984). Smaller organisms are able to attain higher densities in small ranges, while larger ones tend to have less dense, more widely distributed populations (Brown 1984, 1995). They also suggest that large-bodied species have lower fecundity, which might lead to reduced range size (Gaston *et al*. 1997; Bohning-Gaese *et al*. 2000). Finally, large-bodied birds are less likely to be migratory (Hedenstrom 2008) and thus might have lower dispersal ability and hence smaller ranges than small-bodied birds (Holt *et al*. 1997; Dawideit *et al*. 2009).

Studies such as those conducted by Laube *et al.* (2013), demonstrate that a potential reason for the complex patterns observed between body size and range size might be the heterogeneity in mechanisms by which body size affects range size. Depending on the spatial scale of the analysis, the set of species analysed and other traits included in the study, this might result in positive, negative or no total effect of body size on range size. Gaston & Blackburn (1996b), in their review, conclude that much (though not all) body size-range size variation can be explained in terms of geographic coverage.

Body size variation with elevational range: Research relating to the study of body size variation with respect to elevational range size are scarce in comparison to those investigating body size relationships with geographical range size, with only three peer-reviewed studies found, all finding no direct relationship. McCain (2006) found body size to not be related to elevational range size in Costa Rican rodents. Blackburn & Ruggiero (2001) find no relationship between elevational range and body mass, either across species or within taxa for Andean passerines. Using structural equation modelling, Kubota *et al.* (2007), studying Neotropical tephritid flies, found no significant direct effect of body size on elevational range; however, it had significant indirect negative effects through plant host range and elevational midpoint.

2.1.5 Allen's rule: biogeography of non-body size morphological traits

Allen's rule is an extension of Bergmann's rule and proposes that the appendages of endotherms are smaller, relative to body size, in colder climates, in order to reduce heat loss (Allen 1877). In contrast to Bergmann's rule, Allen's rule has been largely ignored in the literature. Empirical support and debate concerning Allen's rule is nearly exclusively derived from occasional reports of geographical clines within individual species (mostly mammals) over their geographic range (e.g. Stevenson 1986; Fooden & Albrecht 1999). Interspecific research is thus far restricted to birds. Cartar & Morrison (2005) and Nudds & Oswald (2007) conducted two relatively small studies of leg dimension variation with latitude and temperature in shorebirds and seabirds respectively. Kennedy *et al.* (2012) found elevation to be positively correlated with relative tarsus length in the core Corvoidea of the Himalayas – contradictory to Allen's rule. They propose that this may reflect adaptations to foraging in more open habitats at higher elevations, especially hopping and walking on the ground (as high-elevation Corvidae typically do), whereas the low elevation species reside mainly in trees and bushes. By far the most comprehensive study to date, providing the strongest comparative support yet published for Allen's rule, is that by Symonds & Tattersall (2010). They used phylogenetic comparative analyses of 214 bird species from diverse taxonomic groups to examine whether bird bills and leg length conform to Allen's rule. Across all species, controlling for body size, there were strongly significant negative relationships between bill length and latitude, altitude and environmental temperature. Support for Allen's rule in leg elements was weaker.

Focusing on wing length in birds, it should first be noted that a number of ornithologists claim wing length to be the best measure of body size in birds (e.g. Gosler *et al*. 1998). A conflict thus arises – whereas wing length should decrease in association with increasing temperatures (i.e. with decreasing latitude or elevation) according to Bergmann's rule, the same measurement is expected to increase under the same conditions according to Allen's rule (see discussions in Yom-Tov *et al.* 2006; Salewski *et al.* 2010). As such, a lack of consensus concerning the trend in wing length with respect to temperature (latitude and elevation) is not surprising. Although feathers do not dissipate heat, Johnston (1969) found that in the house sparrow (*Passer domesticus*) across Europe there is a persistent positive relationship between summer temperatures and wing bone lengths, as predicted by Allen's rule. However, both intra- and interspecific comparisons of bird taxa provide evidence of relatively larger wings at higher altitudes (e.g. Traylor 1950; Hamilton 1961), an effect systematically demonstrated among hummingbird species (e.g. Feinsinger *et al.* 1979; Altshuler & Dudley 2002; Altshuler *et al.* 2004). Additional difficulty in interpreting the spatial variation in wing length arises from the fact that it is influenced by further divergent selection pressures including: flight performance and migration, microhabitat selection, foraging ecology and predator avoidance (Salewski *et al.* 2010).

2.1.6 Biogeography of life-history and ecological traits

Variation with latitude: Clutch size, which is central to avian reproductive effort, is probably one of the best-recorded of all animal life-history traits. As such, its spatial variation has been extensively studied, with increasing clutch size toward the poles long noted, both within and between species of birds (e.g. Moreau 1944; Lack 1947, 1948; Cody 1966; Kulesza 1990; Cardillo 2002). This so-called Lack's rule (Lack 1947) was confirmed by Jetz *et al*. (2008a), who analysed the global variation in clutch size across 5,290 bird species. Several factors have been hypothesised to influence interspecific spatial patterns of clutch size, which fall into four main categories: (1) proximate environmental constraints, (2) constraints based on predation; (3) constraints based on nest size and nest type, and (4) trade-offs with other life-history traits, e.g. adult life expectancy, egg size and body size (for a detailed discussion, see Jetz *et al.* 2008a; Boyer *et al.* 2010). However, the recent work by Jetz *et al.* (2008a) suggests that seasonality of resources is the predominant driver of clutch size variation across geographic gradients at the global scale - clutch sizes are smallest in species inhabiting relatively aseasonal environments and increase linearly with temperature seasonality. They provide two alternative mechanisms:

1) Classical life-history theory predicts that high seasonality, causing high adult mortality, will lead to the evolution of high investment in current reproduction and large clutch sizes, as the likelihood to survive until the next breeding season is low (Martin 2004).
2) Ashmole (1963) argued that high adult mortality in the temperate regions reduces population density, increases per-individual resource availability in the breeding season, and allows temperate birds to nourish large clutches.

Boyer *et al*. (2010) conducted a global scale study on birds concerning the, apparently conflicting, interspecific pairwise relationships among body size, clutch size and latitude (1,458 species). They found Lack's rule to be supported across clades and through the taxonomic hierarchy. However, the study illustrates the difficulty of interpreting individual pairwise correlations without recognition of interdependence with other variables, and as such, advocates the use of multivariate techniques to tease apart potentially conflicting interactions within macroecological systems.

To reiterate, compared to birds in temperate latitudinal regions, lowland tropical bird species experience less seasonality and more stable temperature and humidity regimes (Janzen 1967; MacArthur 1972; Ghalambor 2006). Although a simplification, these conditions in the tropics favour birds with ‘slower’ lives, that is, those with ‘k-selected’ life histories, as opposed to ‘faster’ lives or ‘r-selected’ life histories favoured in the temperates (Pianka 1970). Research based evidence has indeed found that, compared to temperate species, birds that breed near the equator tend to have:

a) smaller clutch sizes (see discussion above),
b) larger eggs (Martin *et al.* 2006, Martin 2008),
c) lower annual fecundity (Wiersma *et al*. 2007),
d) longer life spans (Wiersma *et al*. 2007),
e) longer parental care times (Russell 2000; Schaefer *et al*. 2004; Styrsky *et al*. 2005; McNamara *et al.* 2008),
f) greater age at first breeding (McNamara *et al.* 2008),
g) slower growth as nestlings (Ricklefs 1976; Bryant & Hails 1983),
h) delayed maturity (Russell 2000; Russell *et al*. 2004),
i) delayed senescence (Møller 2007), and
j) higher juvenile survival rates (McNamara *et al.* 2008).

The view that tropical birds tend to have high survival as adults was challenged by Karr *et al*. (1990), who found no difference in the survival of tropical and temperate forest birds, but debate surrounds this conclusion (see Johnston *et al*. 1997; Sandercock *et al*. 2000; Stutchbury & Morton 2001).

In contrast to the above trends, Geffen & Yom-Tov (2000) show that, among passerines in both the Old and New World, there is little or no difference in incubation or fledging periods between temperate and tropical areas. They conclude that tropical birds differ from temperate ones in clutch size and extended post-fledging periods, which are necessary for juvenile survival, but probably not in other life-history parameters. They state that the observed regional differences in incubation and fledging periods noted in prior studies can be accounted for by phylogeny.

With respect to latitudinal gradients in life-history traits, it is also informative to investigate and compare variation within each hemisphere. For example, studies have found that Southern Hemisphere birds have smaller clutch sizes, lower nest attentiveness, longer incubation periods and higher adult survival than Northern Hemisphere birds (e.g. Martin *et* *al.* 2000; Ghalambor & Martin 2001; Martin 2002; Samaš *et al.* 2013), which has been attributed to lower extrinsic adult mortality in southern latitudes, which select for lower effort and lower risk-taking (Martin 2002). However, overall, latitudinal variation in life history has been studied less in the Southern Hemisphere (see Cardillo 2002).

Although of uncertain origin, the latitude-niche breadth hypothesis predicts that niche breadth is positively associated with latitude, i.e. specialisation increases toward the tropics (MacArthur 1972). This hypothesis was formulated under the assumption that tropical regions are more stable and less seasonal than temperate regions, allowing for narrower species tolerances and hence specialisation. Related to this, it has been argued that specialisation facilitates local coexistence and thus high species richness, driving the widely observed decline in diversity with latitude (see Hillebrand 2004). A number of geographically restricted studies have investigated the relationship between specialisation and either latitude or species richness, with no consensus reached (see references in Belmaker *et al.* 2012). Furthermore, a meta-analysis by Vázquez & Stevens (2004) found no support for a general effect of latitude on niche breadth. However, at the global scale, using a grid-cell approach, Belmaker *et al.* (2012) found bird species richness to increase with both diet and habitat specialisation, with specialisation highest at low latitudes, decreasing towards middle latitudes, and increasing again at extremely high latitudes.

Variation with elevation: In birds, studies aiming to examine elevational variation in life-history traits are reasonably numerous, yet highly dispersed and taxonomically focused – studying either a single-species (e.g. Bears *et al.* 2009; Lu *et al.* 2010; Lu 2011; Lee *et al.* 2011; Li & Lu 2012), or a small group of closely related species (e.g. Krementz & Handford 1984; Badyaev 1997a,b; Badyaev & Ghalambor 2001). These cited studies (among others) have found that, purportedly due to environmental harshness (i.e. colder temperatures, greater variation in climate/seasonality, predation-levels, and greater fluctuations in food availability), higher elevation birds begin breeding later, experience shorter breeding periods, make fewer nesting attempts per year (fewer broods per year), produce smaller clutches (lower annual fecundity) and larger eggs, and have higher survival rates and longer life-spans. In addition, these studies have found high-elevation birds to possess longer nest-building, incubation and nestling periods, and provide longer post-fledgling care compared to their low-elevation counterparts (especially males). These findings suggest a trade-off between fecundity and parental care (survival) along the elevational gradient: high-elevation birds produce fewer offspring, but provide greater parental care per offspring than low-elevation birds (Badyaev 1997b). In other words, the observed patterns are consistent with an adaptive life history strategy (Roff 2002), with birds whose reproductive output is constrained in stressful environments such as high altitudes tending to have reduced fecundity, but allocating more energy into each offspring (high survival strategy) as a buffer to the harsh conditions.

It is important to note that for some single species studies, opposite trends to those described above have been found, for example in clutch size and egg size (e.g. Weathers *et al*. 2002; Johnson *et al.* 2006; Camfield *et al.* 2010). One potential factor contributing to these conflicting results concerning the effects of elevation on clutch and egg sizes could be differences among studies in the elevational gradients over which data were collected (e.g. Lu 2005). However, Boyce (1979) suggested that the supposed existence of larger clutches at higher elevations was related to a combination of a short but highly productive growing season, and low population densities during the reproductive season which 'released' more available resources.

Changing environmental conditions along elevational gradients have also been found to influence a species’ mating system, intensity of sexual selection, and development of sexual ornamentation (e.g. Saino & De-Bernardi 1994; Badyaev 1997a; Badyaev & Ghalambor 1998; Badyaev & Ghalambor 2001; Snell-Rood & Badyaev 2008; Li & Lu 2012). Badyaev & Ghalambor (2001) suggested that successful reproduction at higher elevations requires greater bi-parental investment due to colder, less predictable climatic conditions and the disjunct distribution of feeding and nesting habitats. High investment in parental care reduces mating opportunities and also requires greater assurance of social paternity, which in turn could constrain extra-pair fertilizations (Badyaev & Ghalambor 2001). Both of these consequences of greater bi-parental care have been suggested to reduce the differences in selection pressures between males and females, lowering the intensity of sexual selection on males, such that studies have shown a strong negative relationship between sexual dimorphism and elevation in birds (e.g. Badyaev 1997a; Badyaev & Ghalambor 2001), and mammals (Dobson & Wigginton 1996).

As already discussed, environments which possess high seasonality are expected to select for fast paces of life with high reproductive output, because mortality is high in such environments (Tieleman 2009). However, as stated by Sekercioglu *et al.* (2012), and as found in the studies discussed above, recent research suggests that high-elevation birds, rather than having life-history strategies similar to those of high-latitude birds, instead mirror those of low-latitude birds. Tieleman (2009) therefore suggested that variation in life-history strategies for bird species along elevational gradients cannot be explained by the same processes applied to life-history variation along latitudinal gradients. These findings, to date, raise further concerns about tropical high-elevation species with particularly slow life histories, as not only are high-elevation birds believed to be particularly susceptible to climate change, but most high-elevation endemic bird species are found in the tropics (Sekercioglu *et al.* 2012).

Focusing on non-avian taxa, greater investment per offspring with increasing elevation, as a strategy to increase offspring survival, has been reported across a wide diversity of terrestrial and aquatic ectotherms – predominantly at the intraspecific level, comparing high- and low-elevation populations. High-elevation populations of ectotherms have typically been shown to possess smaller clutches of larger eggs than low-elevation populations (e.g. reptiles: Rohr 1997, amphibians: Berven 1982a,b*;* Howard and Wallace 1985, invertebrates: Blackenhorn 1997; Hancock *et al*. 1998). In fact, some evidence suggests that mammals may compensate for reduced fecundity at high elevation by increasing the amount of parental care, especially male parental care, provided to offspring (Wynne-Edwards 1998). Although contentious, Badyaev & Ghalambor (2001) suggested that increased parental care may therefore be analogous to increasing egg size. As has been shown for birds, a strong negative relationship between sexual dimorphism and elevation in mammals has also been found (Dobson & Wigginton 1996). In the Colombian ground squirrel (*Urocitellus columbianus*), Dobson (1992) found that litter size decreases, age at maturity increases, the proportion of females that breed decreases, and adult and juvenile survival increases with increasing elevation. There is also evidence within reptiles for delayed reproduction, and higher survivorship and age at maturity at high elevations (Rohr 1997). However, in other studies of reptiles, high-elevation females were found to be smaller than their low-elevation counterparts (Mathies & Andrews 1995) or to produce larger clutches with smaller young (Sinervo 1990).

Morrison & Hero (2003) reviewed the intraspecific patterns and differences in life-history traits of amphibian populations living at different elevations (and latitudes). They found that the research published to date suggests that amphibian populations at higher elevations (and latitudes) tend to: a) have shorter activity periods and hence shorter breeding seasons, (b) have longer larval periods, (c) are larger at all larval stages including metamorphosis, (d) are larger as adults, (e) reach reproductive maturity at older ages, (f) produce fewer clutches per year, (g) produce larger clutches absolutely and smaller clutches relative to body size, and (h) produce larger eggs. However, they stress that these generalisations must be viewed with caution, due first to the small number of papers supporting them, and secondly to the inconsistent results published to date. Zhang & Lu (2012) performed a comparative study investigating both intra- and interspecific patterns of geographical variation in longevity of urodele and anuran amphibians. Controlling for body size and employing multivariate statistical procedures to determine the independent effect of elevation and latitude, they found maturation, mean and maximum age all increased with elevation but not with latitude in each sex of both amphibian groups.

Hodkinson (2005) conducted a thorough review on the response of terrestrial insect species to the changing environments experienced along elevational gradients. The review clearly highlights the variability in results obtained thus far.

Regarding plants, Jonas & Geber (1999) described patterns of trait variation among populations of Elegant clarkia (*Clarkia unguiculata*) along elevational and latitudinal gradients, and interspecifically within the genus – with inconsistent results produced. Although there was some evidence that traits varied clinally along environmental gradients, interaction effects between elevation and latitude dominated patterns of variation. They also found, that while some traits were correlated with one gradient in the expected way (e.g., development time with elevation, gas-exchange physiology with latitude), all traits were not consistently associated with each other along both gradients, and intraspecific patterns of variation differed from interspecific patterns. Fabbro & Körner (2004) looked at elevational differences in flower traits and reproductive allocation in lowland and alpine plant species in Switzerland, and found high-altitude plants to allocate more biomass to structures of sexual reproduction and prolonged flowering compared to lowland plants. At the global scale, elevation has been proved to be a poor predictor in global studies of seed mass (Moles *et al*. 2007) and wood density (Swenson & Enquist 2007). These results may partly be due to the sudden drop in plant height found at the tree line occurring at different elevations in different parts of the world (Moles *et al*. 2009).

Compared to latitudinal gradients, few studies have investigated variation in niche breadth with respect to elevation. Such studies focus on diet breadth and are both geographically restricted and taxonomically biased towards insects, with elevation found to have positive (Pellissier *et al.* 2012), negative (Rodríguez-Castañeda *et al.* 2010) and no effect (Novotny *et al.* 2005) on insect diet breadth. No studies could be found, across taxa, explicitly examining variation in habitat breadth with respect to elevation, with a number of studies instead using elevational range as a proxy of ability to tolerate environmental variability, i.e. habitat breadth (e.g. for birds, Badyaev & Ghalambor 1998; Bonier *et al.* 2007; Tobias & Seddon 2009).

Variation with geographical and elevational range: Among the most important factors that influence geographical range size are species life-history, ecological and morphological traits (Laube *et al.* 2013). A number of studies have found large geographical ranges to be exhibited by bird species with life-history traits associated with higher rates of population growth, i.e. fast development and high fecundity and mortality (e.g. Blackburn *et al.* 1996; Gaston &

Blackburn 1996a; Gaston *et al.* 1997; Duncan *et al.* 1999). Such a trend may be as a result of higher local abundances (Blackburn *et al*. 2006), which in turn, are often correlated with large range sizes (e.g. Brown 1984; Blackburn *et al*. 1996; Gaston *et al*. 1997; Borregaard & Rahbek 2010). A positive relationship between dispersal ability and geographical range size has also been identified (e.g. Dennis *et al*. 2000; Böhning-Gaese *et al*. 2006), and reviewed in Lester *et al.* (2007). Broader habitat niches have been found to be associated with larger range sizes (e.g. Symonds & Johnson 2006; Cofre *et al*. 2007; Hurlbert & White 2007; Carrascal *et al*. 2008), reflecting that the habitat niche directly constrains the area which can be colonised by a species (Brown 1984; Gaston *et al*. 1997). Equivocal results have been found for the effect of migratory behaviour on range size. Migratory birds have been shown to have smaller geographic ranges than non-migrants (e.g. Böhning-Gaese *et al*. 1998; Bensch 1999). However, long-distance migrants have been shown to have larger geographical ranges than sedentary birds among Anseriformes (Gaston & Blackburn 1996a).

Already discussed with respect to body size-range size relationships, the study conducted by Laube *et al.* (2013) investigated the combined influence of a multitude of species traits on global range sizes of European passerines. Confirming earlier studies, they found a direct positive correlation between geographical range size and: annual fecundity, dispersal ability and habitat niche breadth (which also had an indirect positive effect via higher annual fecundity). In addition, they found a direct negative correlation with diet niche position, i.e. bird species of a higher trophic level had smaller geographical ranges. However, it is important to note that no vertebrate-eating species were included in this study – many birds of prey have large geographical ranges (Schoener 1968). No significant direct relationship was found between geographical range size and migratory behaviour. Instead an indirect positive effect of migratory behaviour on range size, via dispersal ability was detected – migrants tend to be better dispersers (Dawideit *et al.* 2009). Contrary to habitat niche breadth, diet niche breadth did not have an effect on range size, which perhaps is not surprising considering different food sources can occur side by side in the same site, while habitat types cannot.

Only two studies could be found that investigate trait variation with respect to elevational range, and both are concerned with indices of avian sexual selection (Badyaev & Ghalambor 1998; Tobias & Seddon 2009). Sexual selection is thought to counteract natural selection on the grounds that secondary sexual traits are inherently costly and evolve at the expense of naturally selected traits (see Anderson 1994, and references within Tobias & Seddon 2009). Consequently, it is commonly predicted that increased sexual selection is associated with decreased physiological tolerance or ecological plasticity (e.g. McLain 1993). Both Badyaev & Ghalambor (1998) and Tobias & Seddon (2009) tested this prediction by assessing the relationship between interspecific sexual plumage dichromatism and elevational range in Cardueline finches and antbirds, respectively. It should be noted that elevational range is assumed in these studies to represent a measure of tolerance of environmental variability, and is used as a surrogate for both ecological plasticity and ecological generalism. Contrary to expectations, both studies found a positive, rather than a negative, relationship between elevational range and sexual dichromatism. Potential reasons for these findings are discussed within the respective papers, but the processes underlying this pattern remain to be investigated. Currently, we know next to nothing about whether or not trait patterns with respect to elevational range mirror those documented for geographical ranges.

2.1.7 Conclusions on the current status of trait biogeography

Having conducted a review of the literature concerning the variation in morphological, life-history and ecological traits with respect to latitude, elevation, geographical range size and elevational range size for both avian and non-avian taxa, the following can be surmised. Despite there being a number of studies that report research investigating variation in traits with respect to elevational distribution, such studies are:

a) Outnumbered by studies on latitudinal gradients and geographical range size;
b) Dispersed throughout the literature – no general review for birds;
c) Taxonomically restricted;
d) Geographically restricted;
e) Predominantly intraspecific, or, if interspecific, only compare a small number of (closely related) species;
f) Limited in terms of study design. Many involve comparing a high-elevation site, population or (sub)species with a low-elevation ‘equivalent’, rather than a continuous gradient;
g) Limited in terms of analysis. Predominantly look at bivariate/pair-wise relationships, without taking into account potentially important and confounding factors (e.g. body size, geographical range and latitude);
h) Certain traits have been studied far more than others, e.g. body size and clutch size;
i) Often contradictory with their findings – appears to be no real consensus;

There is a real need for such studies to shift from describing observed patterns and developing theory, to instead understanding and explaining results. To date, the interactions among morphological, life-history, and ecological traits along an elevational gradient have not been explicitly studied across species for any taxa. Very few studies control for other geographical traits (e.g. geographical range size and latitude) in a multivariate analysis.

Results from the studies conducted to date suggest that more studies on trait variation with elevational distribution are needed before any generalisations about patterns and processes can be made. There is also clearly a gap and a need for research that investigates interspecific trait variation with respect to elevational distribution at the global-scale, and this is addressed below (see Chapters 4–6). In fact, in a paper highlighting the utility of datasets on mountain biodiversity, Körner *et al.* (2007) formulated and discussed a number of questions that such data can and should be used to address, including: '*are there typical elevational trends in organismic traits across the globe?*'

2.2 Relationships between elevation, geographical range and latitude

2.2.1 Geographical range size relationships with latitude: Rapoport's rule

Changes in biodiversity patterns along environmental gradients have been an emphasis of research for decades, but less effort has been applied to understanding the patterns and processes of spatial variation in species range sizes, which underlie these diversity patterns. The majority of existing literature on range size distribution has tested the positive relationship of species geographical range sizes with increasing latitude, i.e. Rapoport's rule (Rapoport 1982; Stevens 1989). Conclusions on the generality of Rapoport's rule are precluded by the uneven taxonomic and latitudinal representation of organisms examined thus far. However, the various reviews of Rapoport's rule to date suggest that the overall support is weak (e.g. Rohde 1996; Gaston *et al*. 1998; Rohde 1999; Gaston & Chown 1999; Ribas & Schoereder 2006), principally due to the high degree of variability in the fit to predictions (e.g. support: Blackburn & Gaston 1996b; Lyons & Willig 1997; Price *et al*. 1997; Cardillo 2002; Arita *et al*. 2005; no support: Rohde *et al*. 1993; Roy *et al*. 1994; Ruggiero & Lawton 1998; Reed 2003). The 'rule' is believed by some to be merely a local effect, limited to the Northern Hemisphere (e.g. Rohde 1996; Gaston *et al.* 1998).

Until Orme *et al.* (2006), the global nature of Rapoport's rule was unknown, with studies largely being conducted within individual biogeographic realms or smaller biogeographic units – as such, these studies suffer from concerns about the generality of the patterns they identified. Orme *et al.* (2006) undertook the first global-scale analysis of spatial variation in the geographic range sizes of species for an entire taxonomic class – all extant bird species. They showed that there is no global tendency for avian geographic breeding range sizes to decline in area, or in latitudinal extent, toward the tropics, as proposed in the contentious Rapoport's rule. Instead, the smallest range areas were found on islands, in tropical and sub-tropical mountainous areas, and largely in the Southern Hemisphere. This leads to entirely different relationships between geographic range area and latitude in different biogeographic realms, with those in the Northern Hemisphere typically conforming to Rapoport's rule, and those in the Southern Hemisphere failing to do so. Therefore, this global study confirms that Rapoport's rule does not generalise – for birds at least. Orme *et al.* (2006) suggest that range size may be constrained by land availability within the climatic zones to which species are best adapted.

2.2.2 Elevational range size relationships with latitude and elevation

In comparison to latitudinal gradients of geographic range size, patterns of elevational range size with respect to both latitude and elevation have received much less attention. However, Janzen (1967) developed hypotheses for both (see Fig. 2.1). Janzen assumed that species evolve physiological adaptations reflecting the range of environmental variation encountered in their local vicinity. He predicted that temperate species experiencing high variability in temperature would evolve broad temperature tolerances and acclimation abilities, whereas tropical species experiencing low variability in temperature would evolve narrow temperature tolerances and acclimation potentials. Although his theory has been widely discussed within the scientific community, most of his assumptions and predictions have yet to be widely tested (Ghalambor *et al.* 2006). The first study to explicitly test Janzen's hypothesis was conducted by Huey (1978), who investigated extent of faunal overlap between high- and low-elevation sites for nine montane gradients using herpetofauna. Supporting Janzen, he found that faunal similarity was greatest between high and low elevations on temperate than tropical mountains. This test made the assumption that range sizes were larger on temperate than tropical mountains. Several other studies have documented small elevational range sizes on tropical mountains, but have not directly or quantitatively compared ranges from temperate and tropical latitudes (e.g. herpetofauna: Heyer 1967; Wake & Lynch 1976; Navas 2002; birds: Terborgh 1977; Rahbek & Graves 2001; Herzog *et al.* 2005; plants: Lieberman *et al.* 1996). McCain (2009b) conducted the first and only study to explicitly test whether tropical and temperate species do in fact have detectably divergent elevational range sizes, across taxa (herpetofauna, rodents, bats and birds). Overall, the study found strong evidence for vertebrates having smaller elevational range sizes in the tropics. For birds, they found elevational range size did not increase with latitude for all birds, but did for breeding birds (excludes potential bias from seasonal, long-distance migrants). However, despite attempts to remove the influence of mountain height for the bird analysis, it remained the strongest predictor of elevational range size.

Stevens (1992) showed for Venezuelan bird species (along with trees, insects, and other various vertebrate groups) that a pattern exactly analogous to Rapoport's rule holds for elevational distributions: within the same latitude, the elevational ranges of species increase with the elevation of the midpoint of their ranges. Large daily variation in temperatures

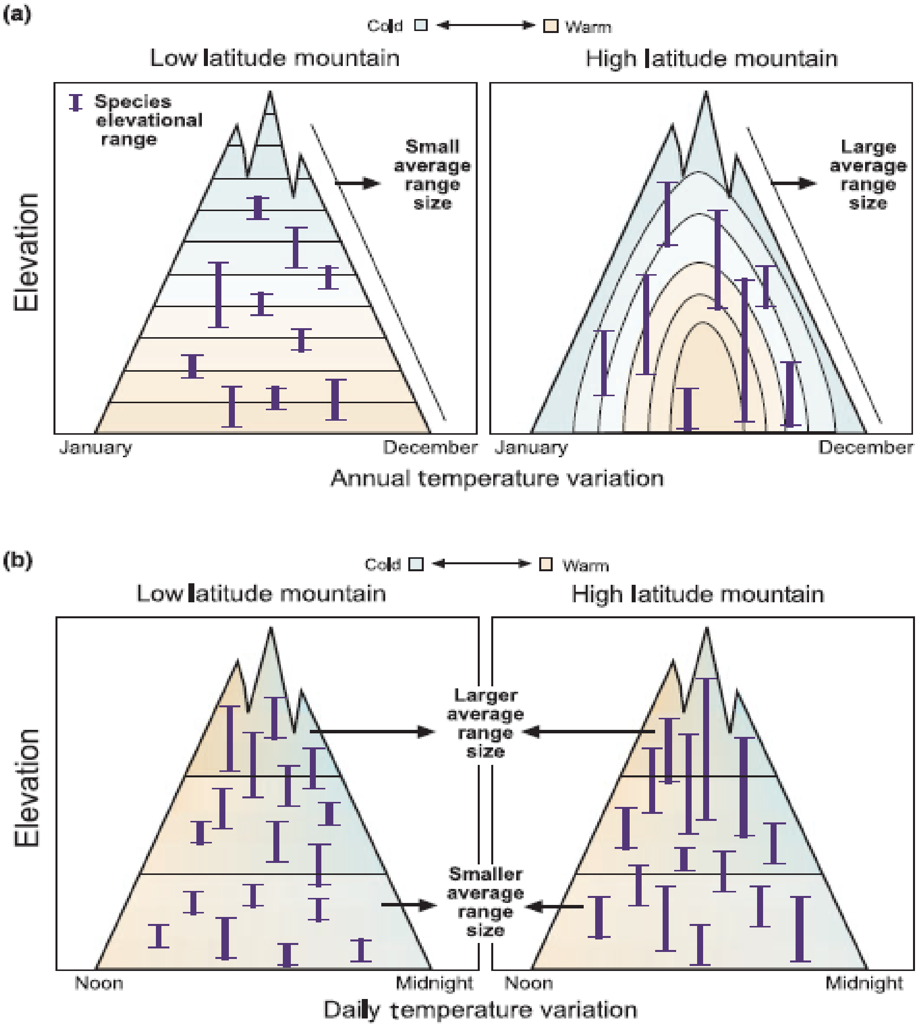


Figure 2.1 Diagram of Janzen's (1967) hypothesis: (a) annual temperature variation at single elevations on tropical mountains is remarkably stable and overlaps little with higher elevations, whereas temperature fluctuates greatly at single elevations on temperate mountains and overlaps substantially with higher elevations. Thus, in response to this variation, Janzen predicted that on average elevational range sizes should be smaller on tropical than temperate mountains. (b) Janzen's predictions can be extended to daily variation in temperature on single mountains where high elevations experience extreme variability in temperature within 24 hours, whereas low elevations experience relatively little daily variation in temperature, thus predicting that high elevation assemblages should have larger range sizes than lower elevation assemblages. From McCain (2009b).

experienced by high-elevation species, particularly tropical, can be just as pronounced as annual temperature variation experienced by temperate species (Figure 2.1b; Ghalambor *et al.* 2006). Thus, high-elevation tropical species should show larger physiological tolerances and acclimation abilities, and thus larger elevational ranges, than low-elevation tropical species (McCain 2009b). For various taxonomic groups, both empirical and theoretical support for the elevational Rapoport's rule has been highly variable (e.g. supportive: Price *et al*. 1997; Fleishman *et al*. 1998; Patterson *et al*. 1998; Blackburn & Ruggiero 2001; Sanders

2002; Chatzaki *et al*. 2005; Almeida-Neto *et al*. 2006; Hausdorf 2006; Ribas & Schoereder 2006; little or no support: e.g. Price *et al*. 1997; Rahbek 1997; Patterson *et al*. 1998; Ruggiero & Lawton 1998; Fu *et al*. 2004; Bhattarai & Vetaas 2006; Hausdorf 2006; Ribas & Schoereder 2006; Acharya *et al*. 2011; Hu *et al.* 2011). This conflict in findings is believed to be partly attributable to differences in study design, e.g. dividing data into endemic and non-endemics, controlling or not controlling for the influence of area, and differences in the elevational grain size, measure of central tendency and elevational range averaging method used (see Ruggiero & Lawton 1998; McCain & Knight 2012).

Some studies have instead revealed a triangular pattern for the relationship between elevational range size and elevation, with species at intermediate elevations having the broadest range amplitudes. For example, Fu *et al*. (2004) found, endemic and non-endemic, species of freshwater fish in the Yangtze River basin of China at mid-elevations displayed the complete range of range sizes, while species at lower elevations or higher elevations possessed only small range sizes. Similar patterns have been documented for birds and mice in the Andes of south-eastern Peru (Patterson *et al*. 1998).

The most geographically and taxonomically extensive study to date testing the elevational Rapoport's rule was conducted by McCain & Knight (2012), using 160 elevational datasets of montane vertebrates (bats, birds, frogs, non-volant small mammals, and herpetofauna) from mountains distributed globally. Overall, they found that, regardless of which methodology they used, support for the elevational Rapoport's rule was weak across all groups of montane vertebrates, being detected on average in 26% of cases. In addition, they undertook a literature review for elevational Rapoport's rule tests of the more species-rich invertebrates and plants, finding, in agreement with the vertebrate studies, highly heterogeneous results. McCain & Knight (2012) therefore concluded that the elevational Rapoport's rule is not a consistently predictive pattern for understanding montane patterns in range size.

2.2.3 Elevational range size relationships with geographical range size

Blackburn & Ruggiero (2001) briefly assessed the relationships between the various measures of latitudinal and elevational position (midpoint, minimum, maximum and range) of Andean passerine birds, calculated both across species and controlling for relatedness of taxa. Although they found most of these variables to be correlated to a certain degree, unsurprisingly, the strongest relationships were among the different measures of latitudinal position and elevational position, respectively (i.e. among variables in the same spatial dimension). The strongest relationships between variables assessing position in different spatial dimensions were those between elevational range and latitudinal maximum, and elevational range and latitudinal range. Taxa inhabiting a broad range of elevations tend also to inhabit a broad range of latitudes, and to have latitudinal range maxima further from the equator.

The only other studies, that I could find, to have investigated and found a positive relationship between elevational range and geographical range (or latitudinal extent) were conducted by Pielou (1979) for a subset of North American pines, by Stevens (1992) for Venezuelan birds, and by La Sorte & Jetz (2010) for montane bird species. However, McCain (2006) found geographical and elevational range sizes of Costa Rican rodents to be unrelated, in turn suggesting that perhaps the mechanisms underlying range size distributions differ for geographical and elevational ranges. Nevertheless, more analyses are needed to identify any generalities.

2.2.4 Two- versus three-dimensional ranges

When considering species-area relationships and latitudinal diversity gradients, whether quantified as extents of occurrence or areas of occupancy, species ranges are typically treated as two-dimensional and planimetric. This is of course a simplification taken in order to condense the spatial occurrence of a species into a single variable. However, the Earth is not flat, but topographically complex. Therefore, in reality, the positions of all individuals of all species at any one time should be defined not only by their longitudinal (x) and latitudinal (y) extent, but also by their altitudinal/bathymetric (y) extent. It can be argued that, relative to the magnitude of the differences in the latitudinal and longitudinal positions of individuals, differences in altitudinal position will be minimal, and can therefore be ignored (Gaston 1994a). However, Gaston (1994a) goes on to state that whilst this is likely to be true of species distributed over wide latitudinal or longitudinal extents, it is probably a weak argument when studying restricted-range species. As discussed in Section 2.2.3, the relationship between geographical and elevational range size has been largely ignored. Consequently, it is unknown whether or not geographical range size carries any information about elevational range size.

Non-planimetric range size is a measure of surface area that considers spatial variation in slope (La Sorte & Jetz 2010). A species that occurs only on a plateau and another species that occurs only on mountainous slopes will therefore possess considerably different surface area range size, even if their geographical range size is the same. As stated by Jenness (2004), '*Surface area provides a better estimate of the land area available to an animal than planimetric area*'. Despite recent advances in 3D GIS and statistical techniques, I could find only two studies that explicitly quantified non-planimetric range sizes and compared them to their two-dimensional equivalents. These two studies, by Smith *et al.* (2007) and Recio *et al.*

(2010), both investigated the spatial ecology of two introduced predators in New Zealand – the stoat (*Mustela erminea*) and feral cat (*Felis catus*), respectively – and estimated three-dimensional home ranges of radio-collared individuals to be 17% and 1% larger in extent than their planimetric home ranges. The only multi-species study that I could find explicitly quantifying non-planimetric range sizes, was a study by La Sorte & Jetz (2010), who investigated, using a grid-cell approach, projected range contractions under global warming for montane bird species at a global scale. In fact, although a number of studies have presented methods to estimate and incorporate aspects of the third dimension into ecology (particular landscape ecology), and tried to highlight the necessity to do so (e.g. Jenness 2004; Hoechstetter *et al.* 2008), 3D-analysis and the examination of 3D-patterns in large-scale ecology are still predominantly neglected.

Research aims and questions

The overarching research aims of this thesis are to test hypotheses and address knowledge gaps identified in the preceding two chapters, by analysing interspecific variation in morphology, life history, ecology, and extinction risk with respect to elevational distribution – at the global scale and across a broad taxonomic range. In order to achieve this aim, I use extant birds as a model system, a global avian trait database and a comparative approach to investigate the following broad research questions:

1) At the global scale, how and why do avian morphological, life-history and ecological traits vary with species-typical elevational distribution?
2) At the global scale, how and why does avian extinction risk vary with species-typical elevational distribution?
3) Are global relationships identified at the species level consistent at the following spatial and phylogenetic scales:
    a. within biogeographic realms,
    b. across higher taxonomic levels,
    c. for endemic and restricted-range species, and
    d. when controlling for phylogenetic non-independence?
4) How does avian elevational distribution vary with respect to latitude, geographical range and elevation?
5) How do elevational patterns in avian traits and extinction risk differ to those found with respect to both latitude and geographical range?

No studies to date have addressed such complementary and fundamental research questions at such a broad geographic and taxonomic scale. Consequently, this research will greatly benefit our current understanding of large-scale ecology, trait biogeography, and conservation biology. Ultimately, this research will assist in incorporating elevation into biogeography and macroecology theory and conservation practice.

Outline of thesis

This thesis is comprised of eight chapters, four of which are data chapters. All data chapters are set out in the style of a scientific paper, with an abstract, introduction, materials and methodology, results and discussion section. In addition, an appendix can be found at the end of Chapters 3–7, which provides relevant additional material to supplement the main body of work. Each data chapter can be read either as a self-contained unit, or as part of the narrative whole. However, the introduction to each data chapter is supplemented by the literature reviews contained within both Chapters 1 and 2. Specifically, the thesis is structured as follows:

Chapter Three: *'General materials and methodology'.* Describes and justifies common materials and methods used throughout the research presented in this thesis, with the aim of reducing repetition between chapters.

Chapter Four: *'Global biogeography of avian traits: an elevational perspective'.* Investigates the interspecific bivariate relationships between avian elevational distribution and key morphological, life-history and ecological traits, at the global scale. Relationships are additionally identified for species within biogeographic realms, and across both families and phylogenetically independent contrasts.

Chapter Five: *'Global biogeography of elevational distribution, and multivariate spatial patterns of avian traits'.* Firstly investigates the global species-level relationships between avian elevational distribution and geographical range, latitude and elevation. This chapter then examines the avian traits of Chapter 4 in a global multivariate spatial analysis. Relationships are additionally assessed for species within biogeographic realms, and across both families and phylogenetically independent contrasts.

Chapter Six: *'Elevational distribution and trait variation of endemic birds'.* Investigates the relationships first identified in Chapters 3 and 4, but for endemic and restricted-range bird species. Specifically, those species identified as: (a) biogeographic realm endemics (and also realm non-endemics), (b) species with the smallest geographical ranges, and (c) mountain range endemics. This approach removes any potential influence of wide-ranging species on patterns observed. The elevational range profiles of such species are also determined.

Chapter Seven: *'Global elevational distribution and extinction risk in birds'.* This final data chapter investigates global variation in species-level avian extinction risk with respect to elevational distribution. Relationships are analysed using both bivariate and multivariate techniques, and also for species within biogeographic realms and orders, and across both families and phylogenetically independent contrasts.

Chapter Eight *'Conclusions'.* Provides a critical synthesis and evaluation of the key findings and discussions arising from this thesis, along with their implications for both large-scale ecology and biodiversity conservation. This chapter concludes by identifying potential study biases and limitations, and suggestions are made concerning useful avenues along which future research should proceed.

References: Provides full references of the citations quoted throughout the entire thesis.

CHAPTER THREE

General materials and methodology

This chapter describes and justifies common materials and methods used throughout the research presented in this thesis, with the aim of reducing repetition between chapters.

3.1 Why use birds as a model system?

Birds are an ideal study group for large-scale comparative studies for a variety of reasons, including the following:

1) Birds are exceptionally well-studied in the wild, relative to other vertebrate groups (Bennett & Owens 2002). This is largely due to the comparative ease of surveying them. Most bird species are diurnal, often easily sighted, and distinguishable via external characters of plumage and song. For at least two centuries, both professional and amateur ornithologists have been collecting vast amounts of information on the natural history of birds (Bennett & Owens 2002).
2) Although constituting a minute fraction of the world’s total biodiversity, the 9,934 known extant bird species (BirdLife International 2013) are incredibly diverse, in terms of morphology, life history, ecology and extinction risk.
3) Bird distributions are relatively well known with respect to area, latitude and elevation. They are globally distributed, occupying most of the available terrestrial habitats on Earth, across a wide range of latitudes and elevations (Bennett & Owens 2002).
4) Birds are phylogenetically diverse and taxonomically well-studied compared to other classes (Bennett & Owens 2002). Relatively stable and comprehensive taxonomies and phylogenies exist across the entire avian class, using both morphometric (e.g. Cracraft 1981) and molecular (e.g. Sibley & Ahlquist 1990; Jetz *et al*. 2012) data.
5) Birds are mobile and relatively sensitive and responsive to environmental change, with enough species to show meaningful patterns.
6) Birds are ideal as flagship species to highlight conservation issues (Bennett & Owens 2002) – they are popular, charismatic and engage the public. In addition, all known extant species have been fully assessed under the IUCN Red List categories and criteria (IUCN 2001), with only 60 species currently listed as Data Deficient (DD) (IUCN Red List 2012.2 update; http://www.iucnredlist.org/). This in turn has allowed for the implementation of direct conservation action to protect both threatened birds and their habitats.

Collectively, these factors suggest that birds, perhaps more than any other taxonomic class, are an ideal group in which to explore the variability in life histories, ecology and extinction risk with respect to elevational distribution. For other major taxonomic groups the key data (i.e. information on elevational limits and/or life-history traits) are simply not yet available at a representative and/or accessible level.

3.2 Global avian database (GADB)

The main resource for this research was a comprehensive global (species-level) avian database (hereafter GADB). It contains available and up-to-date taxonomic, morphological, life-history, ecological and geographic information for over 10,200 extant and extinct bird species. The GADB is an unparalleled and highly valuable resource, from which numerous ecological, evolutionary and conservation driven questions can be answered at a global scale. In the following sub-sections, an overview will be provided of the GADB, including its history, the taxonomy followed, standard data entry protocol, and details of personal data entry.

3.2.1 Background: creation, development and usage to date

The GADB was created by Dr Peter Bennett during his doctoral research entitled '*Comparative studies of morphology, life history and ecology among birds'* (Bennett 1986), for approximately 3,000 bird species. It was expanded upon by the NERC funded '*Avian Diversity Hotspots Consortium*' (ADHoC) - a seven year collaborative research effort (including researchers from Imperial College London, University of Sheffield, Institute of Zoology and the University of Birmingham) that aimed to investigate the ecological and evolutionary processes that underlie biodiversity hotspots, using birds as a model system. Through their efforts, the GADB became the first global database of bird biodiversity, and was used in global-level studies testing hypotheses about hotspot congruence (Orme *et al.* 2005), latitudinal diversity gradients in taxonomic richness (Storch *et al*. 2006; Davies *et al.* 2007; Thomas *et al.* 2008), range size (Orme *et al*. 2006), beta diversity (Gaston *et al.* 2007), body size (Olson *et al.* 2009) and threat (Davies *et al.* 2006), as well as assessing levels of sympatric speciation via range overlap (Phillimore *et al.* 2008) and congruence between indices of richness for birds, mammals, and amphibians (Grenyer *et al.* 2006).

3.2.2 Taxonomy

Treatment of species listed in the GADB follows a standard avian taxonomy, namely that of Sibley and Monroe (1990, 1993). This classification recognises over 9,700 living species, which are distributed across 145 families and 23 orders. This taxonomy is adhered to because of its robustness and wide usage, and for reasons of consistency with previous studies undertaken by the ADHoC using the GADB. The GADB was updated for newly described species and recent splits and lumps using the '*BirdLife checklist of the birds of the world*, *with conservation status and taxonomic sources*' Version 5 (BirdLife International 2012), following the Sibley and Monroe nomenclature where applicable.

3.2.3 Standard data entry protocol

As emphasised by Bennett & Owens (2002), '*quantitative studies are only as rigorous as the data that underlie them, which in comparative studies varies widely in accuracy, quantity, and in the methods of collection'*. In this section, the broad guidelines used for data collection and input are discussed, along with potential sources of bias. Details referring to specific study variables are presented in Section 3.3.

Data sources: All data presented in the GADB were collected from the published literature. The primary literature is vast and widely distributed, with many thousands of studies by both professional and amateur ornithologists throughout the world. For this reason, great reliance was placed on studies which had already summarised much of the data. These took the form of handbooks, guidebooks, and books or journal articles on particular taxonomic groups, geographical areas, or life-history variables. Currently, the GADB is compiled from some 974 publications – the corresponding reference list is currently managed in an Excel database.

Intraspecific variation and species-typical values: As discussed at length in both Bennett (1986) and Bennett & Owens (2002), one of the frequent criticisms made about comparative studies is that intraspecific trait variation is too great to enable meaningful comparisons between species. It is undoubtedly true that individuals within a population and populations within a species can vary considerably for certain traits. However, when the range of taxa studied and geographical extent is wide, as in this research, interspecific variation is typically much greater than intraspecific variation.

This observation justifies the use of 'species-typical' values throughout this research. In doing so, it is important to select an unbiased measure of central tendency that provides a representative estimate for a species. Therefore, the descriptive statistic chosen was the median, defined here as the midpoint of the frequency distribution of values for a particular trait among individuals within a species. The median was chosen because it is relatively insensitive to outliers. When the number of observations (i.e. number of individuals within a species) is small, frequency distributions are often skewed. The median depends only on the frequency representation of outliers and not on their values. In contrast, the mean results in outliers having considerable weight, so that the mean moves in the direction of any asymmetry in the frequency distribution.

In practice, for many variables, the range of intraspecific variation is all that is reported. In such cases, the mean of the extreme values is the only appropriate description of central tendency. In exceptional circumstances where sample sizes are large or where the mean is the only summary statistic given, then the mean rather than the median has been used. For variables which are based on minimum (e.g. age at first breeding) or maximum (e.g. maximum elevation) values the median has, of course, not been given. It is important to note that species-typical values were only obtained after the data had been checked and cleared of extreme outliers and anomalies.

Throughout the development of the GADB, the aim has been to obtain large samples of species for each variable in order to minimise sources of bias, which may be introduced by differences in the number of individuals studied for each species or errors arising from differences in techniques of measurement. When the number and range of taxa studied is wide, these sources of bias should have little effect on overall results and will tend to cancel out (i.e. an overestimate by an observer will be matched by an underestimate by another, so that systematic biases are negligible).

The problems of missing data and data interpolation: Missing data are inevitable when dealing with large species-level databases. It is also an unavoidable fact that we know far more about some groups of birds and regions on the Earth than others, so that missing data are non-randomly distributed with respect to phylogeny and geography, respectively (Beck *et al.* 2012). For an overview of the representativeness of the global dataset used in this study, see Section 3.8.

Nakagawa & Freckleton (2008) reviewed the issues of missing data in evolutionary biology. In summary, they state that if data are not missing completely at random, then results will likely be biased. For example, if missing life-history data are more likely for species that are small or rare, the sample of included species will be biased with respect to these variables. A study by Gonzalez-Suarez *et al.* (2012) clearly highlights both the presence of non-random data biases within large trait databases (using the global mammal trait database PanTHERIA, Jones *et al.* 2009) and the associated difficulties in resolving them.

Tyler *et al.* (2012) recently summarised and discussed a number of approaches used to deal with data gaps, none of which are ideal, including: (1) replacing missing values with zeros (may break up co-evolved trait complexes), (2) deleting species or traits which include missing values (reduces degrees of freedom and consequently statistical power), (3) predicting missing values from congeners or confamilials (requires an accurate phylogeny and sufficient data to establish general patterns of phylogenetic conservatism in different traits).

Adopting standardised methods for dealing with missing data, such as multiple imputation (MI), is widely advocated by some statisticians (e.g. Little & Rubin 2002; Nakagawa & Freckleton 2008). However, it remains unclear as to how robust such techniques are for dealing with missing data in situations where available data are substantially outnumbered by gaps. Also, as stated by Cardillo *et al.* (2008), there are currently no MI algorithms capable of sufficiently dealing with the strongly hierarchical phylogenetic structure inherent in a comparative biological dataset. The result being that biological variables imputed using currently available MI algorithms suffer a loss of phylogenetic signal.

The decision has been made with this research and the GADB in general to only consider trait data that has been resolved to the species or subspecies level, i.e. when information on a trait was missing for a species, we did not consider information from a related species as a surrogate. Interpolation risks artificially inflating the sample size of the study variable in question, and might therefore result in spurious relationships being revealed, particularly for traits where the majority of variation occurs at low taxonomic levels (Section 3.5.1). Unlike some other trait databases, the GADB is an integrated archive of actual species data, based solely on observations in the field.

3.2.4 Personal data entry

Upon commencing this research, the GADB remained unedited since early 2006. Consequently, a period of personal data entry was undertaken to fill in gaps where possible and to significantly update the database, particularly with respect to elevational range limits. Specifically, the main phase of personal data entry commenced on 8th February 2011 and finished 15th April 2011. During this period, I predominantly went through each of the 15 published Handbook of the Birds of the World (HBW; del Hoyo *et al.* 1992-2010) in turn, cross-checking and adding missing data from pre-2006 volumes (1-10) and adding new data from post-2006 volumes (11-15) for all study variables where possible (see Section 3.3. for a list and descriptions of the study variables). Relevant data from the final HBW – *Volume 16: Tanagers to New World Blackbirds* (del Hoyo *et al*. 2011) was entered into the GADB in February 2012. Where necessary, the taxonomy used by the data sources was converted back to the standard avian taxonomy used throughout this research (Sibley & Monroe 1990, 1993).

Data recorded for subspecies were included within the parent species. Care was taken throughout data entry to avoid entering obvious cases of data taken from captive, vagrant, accidental and extreme cases.

3.3 Study variables

From the GADB, a complementary suite of 21 morphological, life-history (reproductive, developmental and survival), ecological niche breadth and geographical variables were chosen to investigate the overall thesis aim and questions, specifically:

- Four morphological traits: body weight, wing length, tarsus length and culmen length.
    - Two derived morphological traits: sexual weight dimorphism and wing-aspect ratio.
- Two reproductive traits: clutch size and egg weight.
    - One derived reproductive trait: annual fecundity.
- Three developmental traits: incubation period, fledging time and age at first breeding.
- One survival trait: adult survival.
- Two indices of ecological niche breadth: diet breadth and habitat breadth.
- Four geographical variables: geographical breeding range, raw mean latitude, absolute mean latitude and maximum elevation.
    - Two derived geographical variables: elevational range and elevational midpoint.

These variables were selected based on one or more of the following factors: (a) data availability and good taxonomic/geographic coverage, (b) their relevance to the research questions, and (c) their use in previous studies, related to this research, for comparative purposes. The life-history traits were split into the above three categories based on classic life-history theory (see Bennett & Owens 2002).

The following sub-sections (3.3.1-3.3.4) offer a concise overview of each study variable, providing definitions and highlighting any potential bias in the estimates. The study variables are an updated version of those used by Bennett (1986) and Bennett & Owens (2002), with the inclusion of the following novel variables: wing length, wing-aspect ratio, tarsus length, culmen length, maximum elevation, elevational range and elevational midpoint.

3.3.1 Morphological traits

Body weight: Species-typical adult body weight, with preference given to female weight where available. Where unavailable, species (unclassified) then male weight was taken.

Units: grams (g)

Transformation: $\log_{10}$

Value range: Minimum = 1.8 g (*Acestrura bombus*, Trochilidae)

Maximum = 100 kg (*Struthio camelus*, Struthionidae)

Wing length: Species-typical adult wing length, with preference given to female wing length where available. Where unavailable, species (unclassified) then male wing length was taken.
Units: millimetres (mm)
Transformation: $\log_{10}$
Value range: Minimum = 29.5 mm (*Acestrura bombus*, Trochilidae)
Maximum = 900 mm (*Struthio camelus*, Struthionidae)

Tarsus length: Species-typical adult tarsus length, with preference given to female tarsus length where available. Where unavailable, species (unclassified) then male tarsus length was taken.
Units: millimetres (mm)
Transformation: $\log_{10}$
Value range: Minimum = 6.6 mm (*Hemiprocne comata*, Hemiprocnidae)
Maximum = 445 mm (*Struthio camelus*, Struthionidae)

Culmen length: Mean adult culmen length, with preference given to female culmen length where available. Where unavailable, species (unclassified) then male culmen length was taken.
Units: millimetres (mm)
Transformation: $\log_{10}$
Value range: Minimum = 4.3 mm (*Psalidoprocne albiceps*, Hirundinidae)
Maximum = 410 mm (*Pelecanus crispus*, Pelecanidae)

As is typically the case in ecological studies, female preference was given to these four morphological traits, as they are typically under less pressure from sexual selection than males, and as such less prone to intraspecific variation. Two derivative variables of body weight and wing length were additionally calculated:

Sexual weight dimorphism: Sexual weight dimorphism (hereafter sexual dimorphism) was quantified as the residuals from a reduced major axis (RMA) regression of $\log_{10}$ male body weight on $\log_{10}$ female body weight.

Sexual dimorphism can be measured in a variety of ways (Lovich & Gibbons 1992; Ranta *et al*. 1994), and there has been much debate regarding the most appropriate method for expressing and analysing this variable in comparative studies (reviewed in Smith 1999).

The procedure selected for this research is widely accepted (Ranta *et al*. 1994). Residuals avoid the statistical pitfalls of ratios (discussed in Ranta *et al*. 1994; Sokal & Rohlf 2012), which were used in both Bennett (1986) and Bennett & Owens (2002). For example, residuals have the property of creating a measure of sexual dimorphism that is uncorrelated with body mass, whereas ratio measures of sexual dimorphism can lead to spurious correlations, since both variables contain body size and are therefore not mathematically independent.

Although to varying degrees, for the vast majority of bird species that display sexual dimorphism, the male is larger than the female (Székely *et al.* 2007). However, reversed sexual dimorphism (females being larger than males) occurs in a number of bird families, e.g. Accipitridae, Falconidae and Jacanidae (Krüger 2005). In this dataset, reversed sexually dimorphic species are those with strong negative values.

Units: none

Transformation: none

Value range: Minimum = – 0.4 (*Accipiter rhodogaster*, Accipitridae)
Maximum = 0.4 (*Otis tarda*, Otididae)

Wing-aspect ratio: Residual value from a RMA regression of $\log_{10}$ (cubed wing length) on $\log_{10}$ body weight. It is a quantitative measure of flight (and dispersal) ability – those species with low wing-aspect ratios having smaller wings relative to their body size (i.e. poorer flight ability) than those with higher wing-aspect ratio values.

Units: none

Transformation: none

Value range: Minimum = – 0.5 (*Dromaius novaehollandiae*, Casuariidae)
Maximum = 0.2 (*Collocalia leucophaeus*, Apodidae)

3.3.2 Life history traits

Reproduction

Clutch size: Species-typical number of eggs laid in a single nesting. This definition includes the ‘clutch’ laid as a series of eggs in mounds by megapodes (Megapodidae), but excludes data for obligate brood parasites.

Units: count

Transformation: $\log_{10}$

Value range: Minimum = 1 (455 species across 59 families)
Maximum = 20 (*Aepypodius arfakianus*, Megapodiidae)

Broods per year: Species-typical number of separate broods produced per year. This definition excludes second clutches (i.e. repeat layings after the failure of first clutches), but includes breeding attempts that occur after the successful completion of a previous brood, even though such attempts may fail. Data for obligate brood parasites were removed. Values less than one, arise from some species taking longer than a year to raise a brood, e.g. certain seabirds and raptors. Although broods per year was used to directly quantify annual fecundity (see below), it was excluded as a stand-alone study variable. This decision was made due to the low variation between minimum and maximum values, the fact that half (48%) of the species with data typically have one brood, and annual fecundity is a more informative measure of reproductive output (Bennett & Harvey 1988).
Units: count
Transformation: $\log_{10}$
Value range: Minimum = 0.4 (*Bucorvus leadbeateri*, Bucorvidae)
Maximum = 5.5 (*Streptopelia senegalensis*, Columbidae)

Egg weight: Species-typical egg weight.
Units: grams (g)
Transformation: $\log_{10}$
Value range: Minimum = 0.3 g (*Lophornis ornatus*, Trochilidae)
Maximum = 1444.3 g (*Struthio camelus*, Struthionidae)

In addition to these three basic reproductive characters, two derived variables were calculated:

Annual fecundity: Species-typical number of eggs produced per year. This was quantified as the product of clutch size multiplied by the number of separate broods produced per year (Bennett & Harvey 1988). Data for obligate brood parasites were removed.
Units: count
Transformation: $\log_{10}$
Value range: Minimum = 0.5 (*Puffinus newelli*, Procellariidae)
Maximum = 27.0 (*Alectura lathami*, Megapodiidae)

Development

Incubation period: Species-typical time taken to incubate a single egg, i.e. time between laying and hatching. As explained further in Bennett (1986), where possible the values used for incubation period are derived from calculations on the basis of marked eggs, yet in practice the mean of the extreme values of the usual intraspecific variation in incubation period found in the wild is instead typically used. Incubation period is the best measure of growth rate in this dataset. Data for megapodes (Megapodiidae) were excluded because they are mound builders that use geothermal heat to incubate their eggs, and so provide no parental care. Data for obligate brood parasites were also removed.

Units: days.

Transformation: $\log_{10}$

Value range: Minimum = 10 days (eight species across five families)

Maximum = 84 days (*Apteryx australis*, Apterygidae)

Fledging time: Species-typical time taken for first hatched individual to fledge. In the vast majority of cases this refers specifically to the elapsed time between hatching and first flying, because it can be more clearly defined for the majority of avian taxa compared to other measures (i.e. nestling time). See Bennett (1986) for a discussion regarding the exceptions to the stated method given here for measuring fledging time. Ultimately, due to the inherent difficulties in defining fledging time globally, especially for some precocial species, I set a minimum time period of seven days. Data for obligate brood parasites were removed.

Units: days

Transformation: $\log_{10}$

Value range: Minimum = 7 days (*Ptilinopus superbus*, Columbidae)

Maximum = 338 days (*Aptenodytes patagonicus*, Spheniscidae)

Age at first breeding: Modal age at which first breeding occurs. The minimum period was set at six months (following Bennett & Owens 2002). This allows for the inclusion of species that are known to breed in the wild within their first year, but for which an actual value is not available. As age at first breeding is a minimum measure, efforts were made to distinguish between estimates of age at earliest breeding as opposed to usual age at first breeding. As discussed in Bennett (1986), in some cases, especially in polygynous species, females are known to breed at earlier ages than males. In these cases the mean value for both sexes is given to provide a comparable measure to the majority of other species where possible sex differences in age at first breeding have not been investigated.

Units: months

Transformation: $\log_{10}$

Value range: Minimum = 6 months (seven species across five families)

Maximum = 152 months (*Phoebetria fusca*, Procellariidae)

Survival

Adult survival: Adult survival was taken as the annual survival rate among individuals above the modal age at first breeding. Values were not included for species threatened with extinction (i.e. Critically Endangered, Endangered, Vulnerable) under the IUCN Red List (2012.2 update) that are either receiving or have recently received considerable conservation action. Specifically, adult survival data were removed from those species recently undergoing one or more of the following: recent and extensive predator control, provision of artificial nests, provision of food, translocations, captive breeding and reintroductions, habitat restoration.

Units: percentage (%)
Transformation: arcsine
Value range: Minimum = 6.2% (*Chloebia gouldiae*, Passeridae)
Maximum = 97.3% (*Phoebetria palpebrata*, Procellariidae)

3.3.3 Ecological niche breadth traits

Diet breadth: Species-typical number of food sub-types consumed. Specifically, the final value assigned to each species with data was the sum of (1) vertebrate diet breadth – how many out of fish, amphibians, reptiles, birds and mammals are included in diet (integer from 0-5), (2) invertebrate diet breadth – how many out of annelids, molluscs, crustaceans, insects, echinoderms, other terrestrial invertebrates and other aquatic invertebrates are included in diet (integer from 0-7), (3) plant diet breadth – how many out of foliage, fruit/berries, seeds/nuts, nectar/sap and other plant parts are included in diet (integer from 0-5), (4) other diet breadth – how many other food types are included in diet, e.g. algae, carrion, eggs and beeswax/honey (integer from 0-5).

Units: count
Transformation: none
Value range: Minimum = 1 (839 species across 68 families)
Maximum = 19 (*Gallirallus australis*, Rallidae)

Habitat breadth: Species-typical number of distinct habitats used. Specifically, the 'Level 2' habitat types applied in BirdLife International's World Bird Database (http://www.birdlife.org/datazone/info/spchabalt) were used (see Table A3.1 for the full habitat classification breakdown). These habitats are the standard terms used in the IUCN Red List Habitats Authority File (Version 3.0). This classification uses familiar habitat terms that take into account biogeography and latitudinal zonation, and the resultant data are globally standardised.

Units: count

Transformation: none

Value range: Minimum = 1 (781 species across 78 families)
Maximum = 29 (*Gallirallus philippensis*, Rallidae)

Both measures of ecological niche breadth used in this research provide a simple count of the number of diets and habitats exploited by birds, and thus are indices of the degree of generalisation or specialisation.

3.3.4 Geographical traits

Geographical breeding range: Geographical breeding range (hereafter geographical range) was quantified as the number of equal-area grid cells, at a resolution of approximately 10,000km^2 (100 km [1°] x 100km [1°]), in which a species is known to breed. For details of sources and methodology used to produce the polygon breeding range maps and convert them into a grid-cell format from which geographical range size was derived, see Orme *et al.* (2005, 2006). Although this method, based on conservative extent of occurrence distribution maps, will tend disproportionately to overestimate the range areas of narrowly distributed species (see Jetz *et al.* 2008b and references within), it is unlikely to influence the global-scale results produced in this research.

Units: count

Transformation: $\log_{10}$

Value range: Minimum = 1, approximately 10,000km^2 (93 species across 31 families)
Maximum = 9138, approximately 91 million km^2 (*Falco peregrinus*, Falconidae)

Raw mean latitude: Raw mean latitudinal location of a species' geographical breeding range was quantified as the mean of the most northerly and southerly range points. Species whose midpoint is located in the Southern Hemisphere are denoted by negative values. This variable is a measure of geometric constraints given that, with the present configuration of continents, more than two-thirds of the world's land surface is located in the Northern Hemisphere (UNEP-WCMC 2002).

Units: degrees (°)

Transformation: none

Value range: Minimum = – 68.4° (*Thalassoica antarctica*, Procellariidae)
Maximum = 78.3° (*Pagophila eburnea*, Laridae)

Absolute mean latitude: Absolute mean latitudinal location of a species' geographical breeding range was quantified as the mean of the most northerly and southerly range points, irrespective of the hemisphere in which it falls, i.e. all values are positive. This variable reflects a species' average dispersion from the equator and was used as a proxy for temperature and seasonality, consistent with other studies (see Boyer *et al.* 2010).

Units: degrees (°)

Transformation: $\log_{10}$

Value range: Minimum = <1.0° (70 species across 32 families)

Maximum= 78.3° (*Pagophila eburnea*, Laridae)

Elevational distribution traits

Through reviewing the literature, it is evident that 'elevation' and 'altitude' are two terms often used synonymously within the field of ecology. There are studies that use elevation throughout, altitude throughout, and others that interchange between both terms. For consistency, this study uses elevation throughout, specifically elevation above sea level (a.s.l.).

For the purposes of this research, minimum and maximum known elevational limits have been taken, rather than minimum and maximum breeding elevational limits. The reason for this is that the former data type is more frequently reported and more reliable than the latter.

Species with an elevational range of zero metres, both those at sea level (130 species) and at higher elevations (seven species), were removed from the dataset. This was done because this research is primarily interested in avian trait and extinction risk variation with respect to elevational range distribution, and a value of zero provides no such variation to analyse.

The factors that limit species' elevational ranges are poorly understood (Gifford & Kozak 2012). In general, the most stressful conditions are found towards the end of a given environmental gradient (Brown *et al.* 1996). With this in mind, it is commonly proposed that the upper limit of a species' elevational/latitudinal range is typically constrained by its physiological tolerance towards the abiotically more stressful conditions, and the lower limit instead controlled by biotic interactions, such as competition (MacArthur 1972, Connell 1978, Brown *et al.* 1996; Brown & Lomolino 1998; Normand *et al*. 2009; Jankowski *et al.* 2010) – referred to as the '*asymmetric abiotic stress limitation hypothesis*' by Normand *et al.* (2009). Of course, maximum elevational limits are additionally constrained by topography.

Minimum elevation: Minimum elevation (a.s.l.) at which a species typically occurs – excluding unconfirmed, predicted, anomalous and extreme outlier records. Although minimum elevation was used to directly quantify both elevational range and elevational midpoint (see below), it was excluded as a stand-alone study variable. This decision was principally made due to the large proportion of species with a minimum elevation of approximately zero metres.

Units: meters (m)

Transformation: not applicable

Value range: Minimum = approximately 0 m (3857 species across 135 families)
Maximum = 4500 m (*Carpodacus roborowskii*, Fringillidae)

Maximum elevation: Maximum elevation (a.s.l.) at which a species typically occurs - excluding unconfirmed, predicted, anomalous and extreme outlier records.

Units: meters (m)

Transformation: $\log_{10}$

Value range: Min. = 30 m (one species each in the Rallidae, Sylviidae and Psittacidae families)
Maximum = 6540 (*Fulica gigantea*, Rallidae)

Elevational range: Elevational range over which a species is known to occur. Unless specifically stated in the literature, elevational range was determined via interpolation as the difference between species-typical maximum elevational limit and minimum elevational limit. Range interpolation makes the inherent assumption that a species observed at two different elevational levels is present everywhere between these levels, i.e. it assumes continuous species distributions, as is commonly done in ecological studies at all spatial scales (e.g. Patterson *et al*. 1998; Bachman *et al.* 2004; McCain 2004; Grytnes & Romdal 2008). If minimum and maximum elevational limits were available for different subspecies or regions of a given species' range, the lowest and highest values across them all were used to calculate elevational range.

Elevational range has regularly been used in previous studies of birds as a proxy measure of competitive ability, propensity to adapt to novel environments, and ability to tolerate environmental variability (e.g. Badyaev & Ghalambor 1998; Bonier *et al.* 2007; Tobias & Seddon 2009). As summarised by Tobias & Seddon (2009), elevational range has been used as a surrogate for both ecological plasticity (adaptability: i.e. the ability of individuals to adapt from one environment to another or to switch from one diet to another), and ecological generalism (broad niche: i.e. the ability of individuals to exploit a range of environments simultaneously).

Units: meters (m)

Transformation: $\log_{10}$

Value range: Minimum = 20 m (*Eriocnemis mirabilis*, Trochilidae)
Maximum = 6000 m (*Pyrrhocorax pyrrhocorax*, Corvidae)

Elevational midpoint: The mean between species-typical minimum and maximum elevational limits was used to represent the elevational midpoint of a species' elevational range. It is a measure of central tendency, providing an indication of the mean 'height' of a species' elevational range.

Units: meters (m)

Transformation: $\log_{10}$

Value range: Min. = 15 m (one species each in the Rallidae, Sylviidae and Psittacidae families)
Maximum = 5070 m (*Fulica gigantea*, Rallidae)

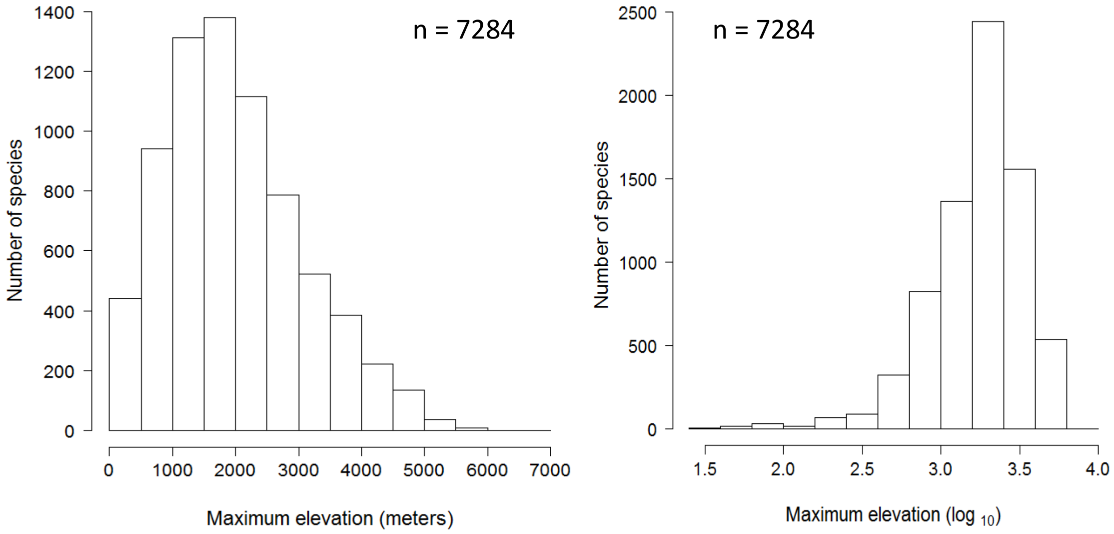
In total, the global dataset used contains maximum elevation data for 7284 bird species across 1567 genera, 139 families and 23 orders. Elevational range and elevational midpoint data were present for 5767 species across 1567 genera, 139 families and 23 orders.

3.4 Frequency distribution histograms

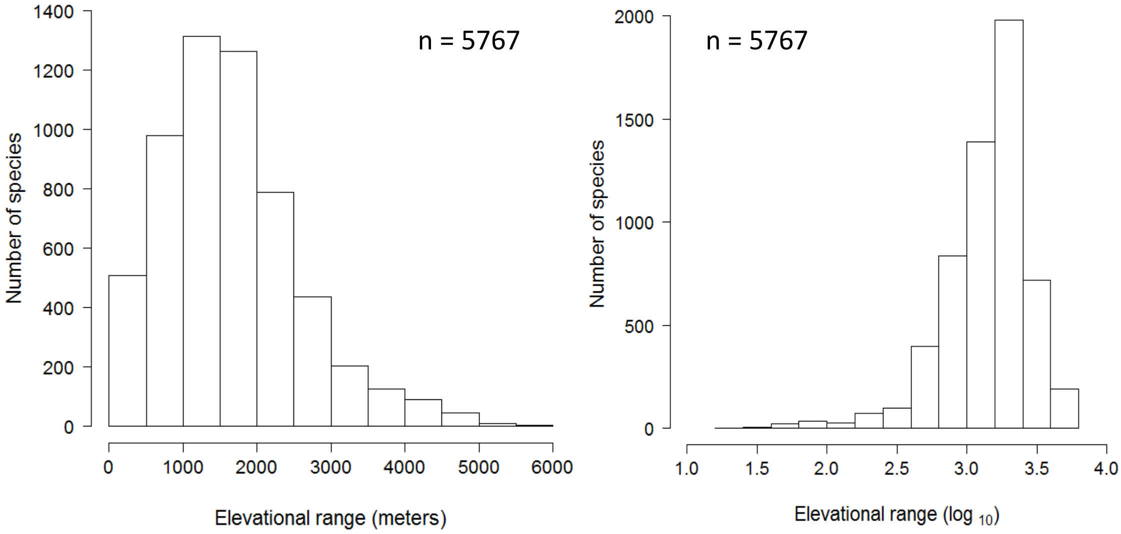
It is important, where necessary, to transform data to better comply with the assumptions of normality that parametric statistical techniques require (Sokal & Rohlf 2012). However, the results of formal statistical (goodness-of-fit) tests for normality (e.g. Shapiro-Wilk, Kolmogorov-Smirnov, Anderson-Darling) are essentially meaningless for large datasets, such as that used in this study (Läärä 2009). This is because, with large datasets, there is power to detect very minor deviations from normality, and since no ecological dataset is ever truly normal, this will almost always result in a rejection of the null hypothesis, i.e. data are not from a normally distributed population (Läärä 2009). The statistical literature instead advocates the use of graphical tools and visual inspection (see Zuur *et al.* 2010). Läärä (2009) provides seven general reasons for not applying preliminary tests for normality in ecological studies, including: most statistical techniques based on normality are robust against violation; for larger data sets the central limit theory implies approximate normality; and for larger data sets the tests are sensitive to small deviations (contradicting the central limit theory).

Consequently, frequency distribution histograms were produced for all study variables in order to visualise the need for data transformation and to guide the type of data transformation undertaken. Where a study variable was found to be not normally distributed, a variety of data transformations were applied, and the one that led to the data most closely

(a) Maximum elevation



(b) Elevational range



(c) Elevational midpoint

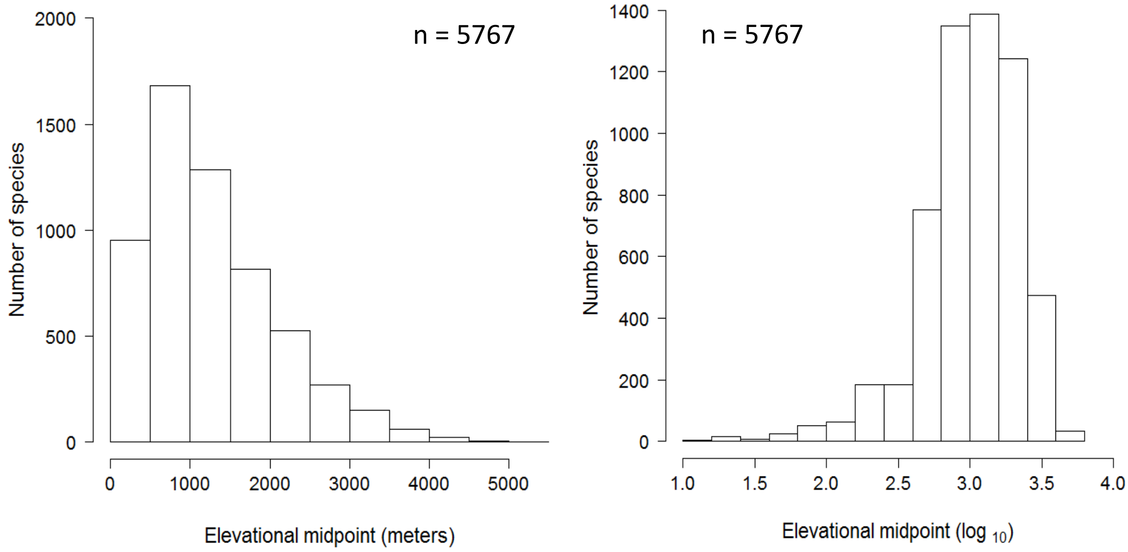


Figure 3.1 Global species-level frequency distribution histograms for the three avian elevational distribution study variables before (left-hand side) and after (right-hand side) $\log_{10}$ transformation. (a) maximum elevation, (b) elevational range, (c) elevational midpoint.

approximating a normal distribution selected. Accordingly, prior to analysis, continuous study variables were $\log_{10}$ transformed, apart from raw mean latitude. Adult survival, a proportional variable, was arcsine transformed. Sexual dimorphism, wing-aspect ratio, diet breadth and habitat breadth were untransformed. See Fig. 3.1 and Fig. A3.1 for the frequency distribution histograms, before and after data transformation (where applicable), for elevational distribution and non-elevational distribution study variables, respectively.

Focusing on the frequency distributions of the three elevational distribution study variables (maximum, range and midpoint), it is apparent that all three were right-skewed before $\log_{10}$ transformation (Fig. 3.1). If species recorded as having an elevational range of zero meters were included, then these distributions would be even more right-skewed. After $\log_{10}$ transformation, the distributions instead become left-skewed. However, the decision was made to use the $\log_{10}$ transformed elevational data because it better approximates a normal distribution, and conforms to previous global avian studies (e.g. Sekercioglu *et al.* 2008). The global frequency distribution of avian geographical range, before and after $\log_{10}$ transformation, and first described by Orme *et al.* (2006), is interestingly mirrored by that of elevational range. More than a quarter (25.8%) of bird species in the dataset have elevational ranges ≤ 1000 m, and 70.5% have elevational ranges ≤ 2000 m. Maximum elevation $\bar{x}$ = 2072 m; elevational range $\bar{x}$ = 1705 m; elevational midpoint $\bar{x}$ = 1299 m.

3.5 Taxonomic levels of analysis

3.5.1 Variance components analysis across successive taxonomic levels

One of the most important decisions that must be made in large-scale comparative studies, such as this, concerns the choice of taxonomic level for analysis. The technique used to do so in this study is a statistical analysis of the distribution of trait variation at successive taxonomic levels, via a hierarchical nested analysis of variance (nested ANOVA; see Sokal & Rohlf 2012). This method can be used on both discrete and continuously distributed characters, and locates the highest taxonomic level where there is the maximum amount of variation for a trait (dependent upon the taxonomic range of species in the sample and the trait under investigation). Such a method also enables a formal assessment of the problem of taxonomic independence, and provides a proxy measure of the origins of diversification in a given trait (Bennett & Owens 2002).

All study variables, in their transformed state where necessary (Section 3.4), were the dependent variables and the taxonomic classifications were the nested independent variables (species within genus within family within order within class). The nested ANOVA methodology first quantifies the amount of variance that can be attributed to variation among species within genera and then examines how much of the remaining variance is explained at successively higher levels in the taxonomic hierarchy (Harvey & Pagel 1991). The taxonomic level selected for analysis is that for which there is no appreciable increase in variation for the majority of the study variables at higher taxonomic levels. The analysis presented here is an extension of that conducted for avian life-history traits by Bennett (1986), Owens & Bennett (1995) and Bennett & Owens (2002), but with larger sample sizes, greater taxonomic and geographical representation and more study variables.

The nested ANOVA results for each study variable are presented in Table 3.1. Using a nested model, the majority of variation was found to occur at the family level and above for nine of the variables, and below the family level for the remaining 12 variables.

Morphological trait variation: Using a nested approach, out of the six morphological variables, four are most variable at the family level or above (body weight, sexual dimorphism, wing length and wing-aspect ratio). The discovery that the greatest variation in tarsus length and culmen length instead occurs at the level of genera within family and species within genera, respectively, is intriguing. This suggests that these two traits are more evolutionary labile and shaped by more recent environmental factors than either body weight or wing length, which both underwent the greatest amount of diversification (along with life-history traits) during the major avian adaptive radiation in the early Tertiary, over 40 million years ago (Bennett & Owens 2002).

Life history trait variation: Using a nested approach, all three reproductive variables display the greatest level of variation at the family level or above, suggesting that these traits are substantially phylogenetically conserved, i.e. possess a strong phylogenetic signal. This in turn means that closely related species exhibit similar trait values, with trait similarity decreasing as phylogenetic distance increases (Harvey & Pagel 1991).

Incubation period and fledging time both vary most at the family level using a nested model, whereas age at first breeding appears to be less phylogenetically conserved, with greatest variation instead occurring at the genera level. This finding differs from that found in both Bennett (1986) and Bennett & Owens (2002), where age at first breeding was found to vary most at the family level. This difference in results is likely due to the additional species added to this dataset that inhabit tropical regions, which typically display later onset of breeding than temperate species (Section 2.1.6).

Variation in adult survival is greatest at the family level, using a nested model, although percentage variation is relatively evenly partitioned below and above the family level.

Ecological niche breadth trait variation: Using a nested approach, the highest level of variation occurs at different taxonomic levels for diet breadth and habitat breadth: species level and family level, respectively. However, for both measures of niche breadth, percentage variation is relatively evenly partitioned below and above the family level.

Table 3.1 Variance components analysis via hierarchical nested ANOVA for each study variable. *n* is the number of species with available data. The remaining columns give the percentage of variance at successive taxonomic levels, along with total percentage variance below and above the family level. The taxonomic level where most variation is observed is highlighted in bold.

Variable	*n*	% species w/genera	% genera w/families	% families w/orders	% orders w/class	% below family	% family & above
MORPHOLOGICAL							
Body weight	8264	19.6	8.9	22.8	**48.7**	28.5	**71.5**
Sexual dimorphism	4112	9.9	0.3	**79.8**	10.0	10.2	**89.8**
Wing length	5657	12.8	12.6	**55.9**	18.7	25.4	**74.6**
Wing-aspect ratio	5135	5.9	8.1	**49.2**	36.8	14.0	**86.0**
Tarsus length	5221	24.6	**53.5**	13.5	8.4	**78.1**	21.9
Culmen length	5171	**32.1**	28.7	30.6	8.6	**60.8**	39.2
REPRODUCTION							
Clutch size	6983	0.0	0.0	**57.3**	42.7	0.0	**100.0**
Annual fecundity	2288	13.4	12.2	**59.9**	14.5	25.6	**74.4**
Egg weight	3493	17.2	21.0	**37.1**	24.7	38.2	**61.8**
DEVELOPMENT							
Incubation period	3118	17.7	18.2	**53.5**	10.6	35.9	**64.1**
Fledging time	2694	13.9	12.2	**45.5**	28.4	26.1	**73.9**
Age first breeding	1070	25.6	**37.8**	35.6	1.1	**63.4**	36.7
SURVIVAL							
Adult survival	469	23.3	27.7	**47.9**	1.1	**51.0**	49.0
NICHE BREADTH							
Diet breadth	3490	**32.7**	17.8	23.2	26.3	**50.5**	49.5
Habitat breadth	4127	43.9	11.8	**44.3**	0.0	**55.7**	44.3
GEOGRAPHICAL							
Geographical range	9369	**61.7**	2.9	10.1	25.3	**64.6**	35.4
Raw mean latitude	7588	2.8	38.5	**57.7**	1.0	**41.3**	58.7
Abs. mean latitude	7588	**79.9**	13.8	1.5	4.8	**93.7**	6.3
Maximum elevation	7419	**49.3**	15.6	35.1	0.0	**64.9**	35.1
Elevational range	5902	**55.8**	13.0	31.1	0.1	**68.8**	31.2
Elevational midpoint	5902	**55.8**	9.6	34.0	0.6	**65.4**	34.6

Study variables $\log_{10}$ transformed except adult survival (arcsine transformed), and sexual dimorphism, wing-aspect ratio, diet/habitat breadth and raw mean latitude (untransformed).

Geographical trait variation: It is believed that this is the first time, for any taxa, that partitioning in the variation of elevational distribution has been explored at the global level at successive taxonomic levels. Elevational distribution, geographical range and absolute mean latitude exhibit little evidence of phylogenetic conservatism, with the majority of variation in these traits being located at the species level using a nested model. In contrast to the other geographical variables, raw mean latitude displays the most variation at a higher taxonomic level (family within orders).

Although beyond the scope of this thesis, it is important to note that a considerable number of studies have investigated and heavily debated the heritability of, or more strictly phylogenetic signal in, geographical range size (see reviews by Gaston 2003; Waldron 2007; Vamosi & Vamosi 2012). Regarding the degree to which heritability is observed, there appears to be an influence of analytical method used (Hunt *et al*. 2005, Machac *et al*. 2011) and the taxonomic group being studied (Waldron 2007). For example, as reviewed by Waldron (2007), birds may generally have relative low heritability in geographical range size compared to other taxa, although the underlying mechanism for this outcome appears unknown. However, overall there is little evidence to date of a phylogenetic constraint on geographical range size (e.g. Hodgson 1993; Peat & Fitter 1994; Gaston & Blackburn 1997; Hurlbert & White 2007, and references in McCain & Knight 2012). Even if range size itself is not strongly heritable, Machac *et al*. (2011) suggest geographical range size could still exhibit a phylogenetic signal because related species tend to inhabit the same continents or ecozones and therefore tend to have similar abiotic limits exerted upon them.

To summarise, the nested ANOVA showed that the family taxonomic level typically displays the most variation in terms of life-history traits (morphological, reproductive, developmental, and survival), which is qualitatively the same as the results from previous studies that used a reduced avian dataset for some variables (e.g. Bennett 1986; Owens & Bennett 1995; Bennett & Owens 2002). However, the geographical variables display the greatest level of variation at lower taxonomic levels, i.e. species within genera. Consequently, for the purposes of this study, analyses will be conducted at both the species and family level.

A degree of caution must be taken in interpreting these results as a measure of global trait variation at successive taxonomic levels, due to both taxonomic and geographic biases (Section 3.8). However, regardless of such biases and to the best of my knowledge, this analysis is the most complete of its kind for birds.

3.5.2 Overview of study units

The decision was made to conduct analyses using three complementary units, namely:

1) **Species (the main study unit):** Although the concept of ‘what is a species’ is heavily debated, species are undoubtedly the fundamental unit of biodiversity and conservation, and preventing species from becoming extinct is arguably the primary goal of the current conservation movement (Ladle & Whittaker 2011). The importance of species as a unit for conservation was also the main reason that a grid-cell-based study approach was avoided, whereby species-level trait values are averaged within grid cells of a specified resolution (as utilised by the ADHoC research team, e.g. Davies *et al.* 2006; Orme *et al.* 2006; Olson *et al.* 2009). Species also represent the taxonomic level where the greatest level of variation occurs for geographical variables, using a nested model, including all three measures of elevational distribution (Section 3.5.1 and Table 3.1).
2) **Family:** Analysis at the family level accounts for the fact that the majority of variation for life-history traits is displayed at the family taxonomic level or above using a nested model (Section 3.5.1 and Table 3.1). In addition, conducting analyses at the family level minimises imbalances between samples sizes among variables, while the much reduced samples sizes ensure that the relationships need to be robust to be significant, i.e. hypothesis testing is more conservative and thus the possibility of spurious relationships arising less likely. Family-typical trait values were derived as the mean of constituent generic values, which in turn were calculated as the mean of constituent species values.
3) **Phylogenetically independent contrasts (PICs):** See Section 3.5.3 for a full justification of use and methodology. PICs were not exclusively used as the units of analysis for this research because they do not exist in the wild, i.e. PICs are not tangible units for biodiversity conservation.

Ultimately, the use of all three of these units of study allows for significant conclusions to be accepted with greater statistical validity.

3.5.3 Phylogenetic comparative methods overview

Over the past three decades, comparative biological analyses have undergone profound changes, with the incorporation of rigorous evolutionary perspectives and phylogenetic information. This change followed in large part from the realisation that traditional methods of statistical analysis implicitly assume independence of all observations. However, the phylogenetic relatedness of species means that they do not comprise independent data points for interspecific comparative analyses (reviewed by Harvey & Pagel 1991). Associations between traits evident in analyses across species may therefore arise because related species tend to share traits through their common ancestry, rather than because these associations have developed repeatedly over the course of evolutionary history (Fisher & Owens 2004). The consequences of ignoring non-independence (i.e. phylogenetic autocorrelation) are numerous. The main problem being that interspecific analysis will tend to artificially inflate sample sizes and overestimate the degrees of freedom for statistical tests, in turn elevating Type I error rates, i.e. false rejection of the null hypothesis (Harvey & Pagel 1991; Martins & Garland 1991; Harvey & Rambaut 1998).

Felsenstein (1985) proposed the first general statistical method for incorporating phylogenetic information into comparative studies, which he termed (phylogenetically) independent contrasts (PICs). Although this method is arguably the simplest of a suite of more complex statistical phylogenetic comparative methods, it is still the best understood and most widely used (Freckleton 2009). The most commonly employed software for conducting comparative analysis by PICs is the Comparative Analysis by Independent Contrasts (CAIC) software package (Purvis & Rambaut 1995). CAIC (employing Pagel's version of Felsestein's method; Pagel 1992) calculates PICs to determine whether there are associations between changes in sets of traits that have occurred since taxa last shared a common ancestor. Correlations between traits analysed in this way are therefore evidence for repeated independently evolved trait associations.

Although the PIC method helps circumvent the problem of phylogenetic relatedness, the extent to which it does depends on the degree to which its assumptions are met by the data analysed (Freckleton 2009). In particular, the method assumes a Brownian model of evolution, (i.e. that variation between tips accumulates along all branches of the tree at a rate proportional to the length of the branches), and that the hypothesis about the evolutionary relatedness of the species concerned, as represented by their phylogeny, is correct (Felsenstein 1985; Harvey & Pagel 1991). However, simulation studies indicate that PICs are reasonably robust even when character evolution deviates from Brownian motion (e.g. Martins & Garland 1991; Purvis *et al*. 1994; Diaz-Uriarte & Garland 1996; Harvey & Rambaut 1998), which is often the case, as most comparative analyses involve traits thought to be undergoing natural or sexual selection. Similarly, there is considerable evidence that using even a moderately accurate, if imperfect, phylogeny produces more accurate results in comparative studies than using no phylogeny at all (Symonds 2002). Increasingly, it is possible to quantify the uncertainty in phylogenetic reconstructions and to directly incorporate this into comparative tests using Bayesian methods (e.g. Huelsenbeck 2000).

Phylogenetic comparative studies of extinction risk: Extinction risk itself is not an evolved trait (Cardillo *et al.* 2005; Putland 2005). However, numerous studies have shown that extinction risk is phylogenetically non-random and often has a phylogenetic signal (e.g.

Bennett & Owens 1997; Russell *et al.* 1998; Purvis *et al.* 2000a; Bielby *et al.* 2006), as do many of the factors that predispose species to extinction. Consequently, the use of PICs has become widespread when testing proposed correlates of extinction risk (Fisher & Owens 2004; Purvis 2008). Despite this, the suitability of phylogenetic comparative methods in studies of extinction risk has been questioned (e.g. Putland 2005; Grandcolas *et al.* 2011, and see discussion within Purvis 2008; Bielby *et al.* 2010). For example, phylogenetic comparative analyses of extinction risk will tend to overcorrect for phylogenetic non-independence (Ricklefs & Starck 1996). However, remedial action is relatively straightforward (see Purvis 2008). As a result of this controversy, Bielby *et al.* (2010) performed a systematic comparison of techniques used to model extinction risk, namely: PICs, non-phylogenetic interspecific regressions and decision trees. They found that predictions were broadly consistent among techniques, but that predictive precision was best for PICs and decision trees. From their findings, and the fact that decision trees are unable to account for phylogenetic non-independence, they advocated the use of PICs as the mainstay of future efforts to model extinction risk.

Spatial and phylogenetic autocorrelation: Spatial autocorrelation is a well-known phenomenon, whereby the values of variables sampled at nearby locations are not independent of each other (Legendre 1993). The need for joint consideration of space and phylogeny in comparative analyses has only recently been recognised (within the past 10 years), and was summarised by Freckleton & Jetz (2009): both spatially structured environmental factors and phylogenetic processes may cause variation in traits. This means that species traits can be conserved across space and phylogeny as a consequence of ecological adaptation and evolutionary history (Kühn *et al.* 2009). In response to this, and due to the need for independence in comparative analyses, methods that simultaneously control for phylogenetic relatedness and spatial proximity in the analyses of traits are starting to be developed. For example, Diniz-Filho *et al.* (2007) used 'phylogenetic eigenvector filtering' (developed by Diniz-Filho *et al.* 1998) to partition phylogenetic and ecological components of interspecific body size variation in European carnivores, and then explained these signals by environmental variables using simultaneous autoregressive models (see also Ramirez *et al.* 2008; Kühn *et al.* 2009; Olalla-Tárraga *et al.* 2010). Safi & Pettorelli (2010) used both phylogenetic and spatial eigenvector filtering to aid in describing the independent influences of history, space and environment on the extinction risk of Carnivora. However, although the use of eigenvector filtering methods for controlling spatial and phylogenetic autocorrelation are being increasingly used in ecological analyses, they still face criticism (see Freckleton *et al.* 2011). Freckleton & Jetz (2009) provide an alternative method to simultaneously estimate spatial and phylogenetic influences on interspecific trait variation, by extending the use of PICs to incorporate spatial distances. At present, it is clear that such methods to control for both spatial and phylogenetic non-independence are still very much in their infancy.

Methodology used to control for phylogeny: PICs (Felsenstein 1985) were calculated and analysed within the R package 'caper' (comparative analysis of phylogenetics and evolution in R; Orme *et al.* 2012). The 'caper' package implements methods originally provided in the programs CAIC (Purvis & Rambaut 1995) and MacroCAIC (Agapow & Isaac 2002), along with additional tools.

The first complete dated phylogeny of all extant bird species has recently been published (Jetz *et al*. 2012). The decision was therefore made to use phylogenetic trees that they constructed for derivation of PICs in this thesis. Specifically, Jetz *et al.* (2012) used two separate backbones for constructing their distributions of trees: one based on the results and data from Hackett *et al.* (2008), and an alternative set based on the work by Ericson *et al.* (2006) – both sources provide recent reconstructions of relationships at the deep nodes, i.e. across families and above. Out of the 10,000 trees Jetz *et al.* (2012) developed for each backbone (all freely downloadable as nexus files from http://birdtree.org/), I decided to select the first tree using the 'Hackett backbone' and the first tree using the 'Ericson backbone'. For the full methodology used to construct the phylogenetic trees, see the supplementary methods of Jetz *et al*. (2012). As both trees are based on a calibrated phylogeny, the often applied, yet unrealistic assumption, of equal branch lengths was not necessary. Like all phylogenies, the trees contain biases and inaccuracies, and the methodology used has been critiqued (Ricklefs & Pagel 2012). However, it is arguably the best, and certainly the most comprehensive, avian phylogeny currently available.

For PIC analyses only, the scientific names adhered to in the GADB, following the taxonomy of Sibley & Monroe (1990, 1993), were edited where necessary to match the names used in the Jetz *et al.* (2012) taxonomy. Within caper, bivariate and multiple linear regressions were conducted using the 'crunch' algorithm which calculates PICs for continuous variables, using the method developed by Pagel (1992). Specifically, the 'caic.robust' function was used in order to remove any outlying studentised residuals greater than the commonly applied threshold of three (Garland *et al.* 1992; Jones & Purvis 1997). This is necessary as such outliers may exert undue influence over the obtained results. It is important to note that all PIC model functions enforce regressions through the origin. As the principal units of this research are species, PICs were only used for the main analyses conducted, as a means of checking for potential influenence of phylogenetic non-independence on the results.

3.6 Global scale of the study and data subsets

The primary spatial scale of this study is global. As discussed in Chapters 1 and 2, previous studies investigating trait variation and extinction risk variation with respect to elevational distribution have been geographically and taxonomically restricted. A global study of such patterns is now attainable for birds, due to the data contained within the GADB.

As summarised by Brown (1995), studies conducted at the global scale enable researchers to '*stand back and take a sufficiently distant view so that the idiosyncratic details disappear and only the big, important features remain*'. In other words, global scale studies enable an assessment of the generality of patterns and underlying processes found using more spatially restricted datasets. Studies at the global scale are also of great value from a conservation viewpoint. For example, results from such studies can inform global biodiversity conservation priority schemes (see Brooks *et al.* 2006).

In addition, data subsets can be highly informative, as they provide an evaluation of the strength of the relationships demonstrated across the global dataset. This is because there is less variation in each study variable and sample sizes are smaller. Although one would typically expect to find fewer significant relationships using data subsets, due to reduced statistical power, the robust relationships should remain.

3.6.1 Biogeographic realms

To test for any regional similarities and differences in the global patterns found, all analyses were also conducted for breeding bird species found within biogeographic realms, as delimited using the World Wildlife Fund ecoregions map (Olson *et al.* 2001, see Fig. 3.2), and

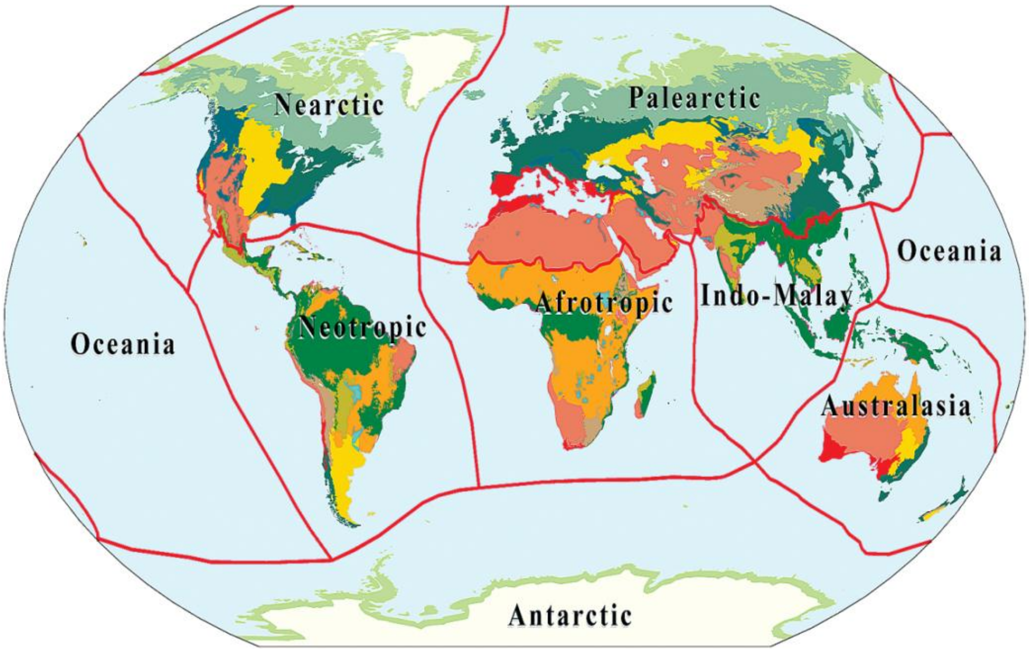


Figure 3.2 Map demarcating the boundaries of the seven biogeographic realms used for regional analyses (all realms excluding Antarctica). Taken from Olson *et al.* (2001).

devised by Udvardy (1975) and Pielou (1979). There are eight biogeographic realms in total: Afrotropical, Antarctica, Australasia, Indo-Malay, Nearctic, Neotropical, Oceania and Palearctic. However, the Antarctica realm was omitted from all realm analyses due to small sample sizes. Species were scored as present in a given biogeographic realm if any of their breeding range (Section 3.3.4) fell within the realm boundaries. Consequently, a species could occur in multiple biogeographic realms. Conducting analyses within individual biogeographic realms also provides a simple measure with which to address the issues of spatial autocorrelation by allowing repeated testing of patterns and relationships in multiple regions.

Figs. 3.3-3.5 show the minimum, maximum and mean values of all three elevational distribution study variables, for the global dataset and individual biogeographic realms. As can be seen, maximum elevation, elevational range and elevational midpoint are largely equivalent across realms, consequently avoiding a potential source of bias resulting from widely differing geometric constraints associated with mountain range size across realms.

3.6.2 Additional subsets

Analyses were also conducted for those species defined as realm endemics, realm non-endemics, restricted range, and mountain range endemics. See Chapter 6 for full definitions of these data subsets, along with the methodology used to derive them and the justification for their inclusion in this thesis. In addition, species were also analysed according to their extinction risk category under the IUCN Red List (2012.2 update; IUCN 2001). For the full methodology, see Chapter 7.

3.7 Common statistical proceedures

In this section, the reasons for the choice of common statistical techniques used throughout this thesis are discussed. In essence, a comparative approach was employed, with the decision made to use both bivariate and multivariate methods that are simple yet robust, and that produce biologically meaningful and intelligible results. All analyses were conducted within R.2.15.1 (R Development Core Team 2012).

3.7.1 Bivariate associations

Bivariate approaches enable sample sizes to be maximised, and promotes clarity in the identified trends. For the purposes of this research, both bivariate linear regressions and Pearson product moment correlations were used.

'Model II' regressions were used instead of standard 'Model I' ordinary least squares (OLS) regressions, because the later technique assumes that the independent variable is measured without error, i.e. it is under control of the investigator. This is an inappropriate

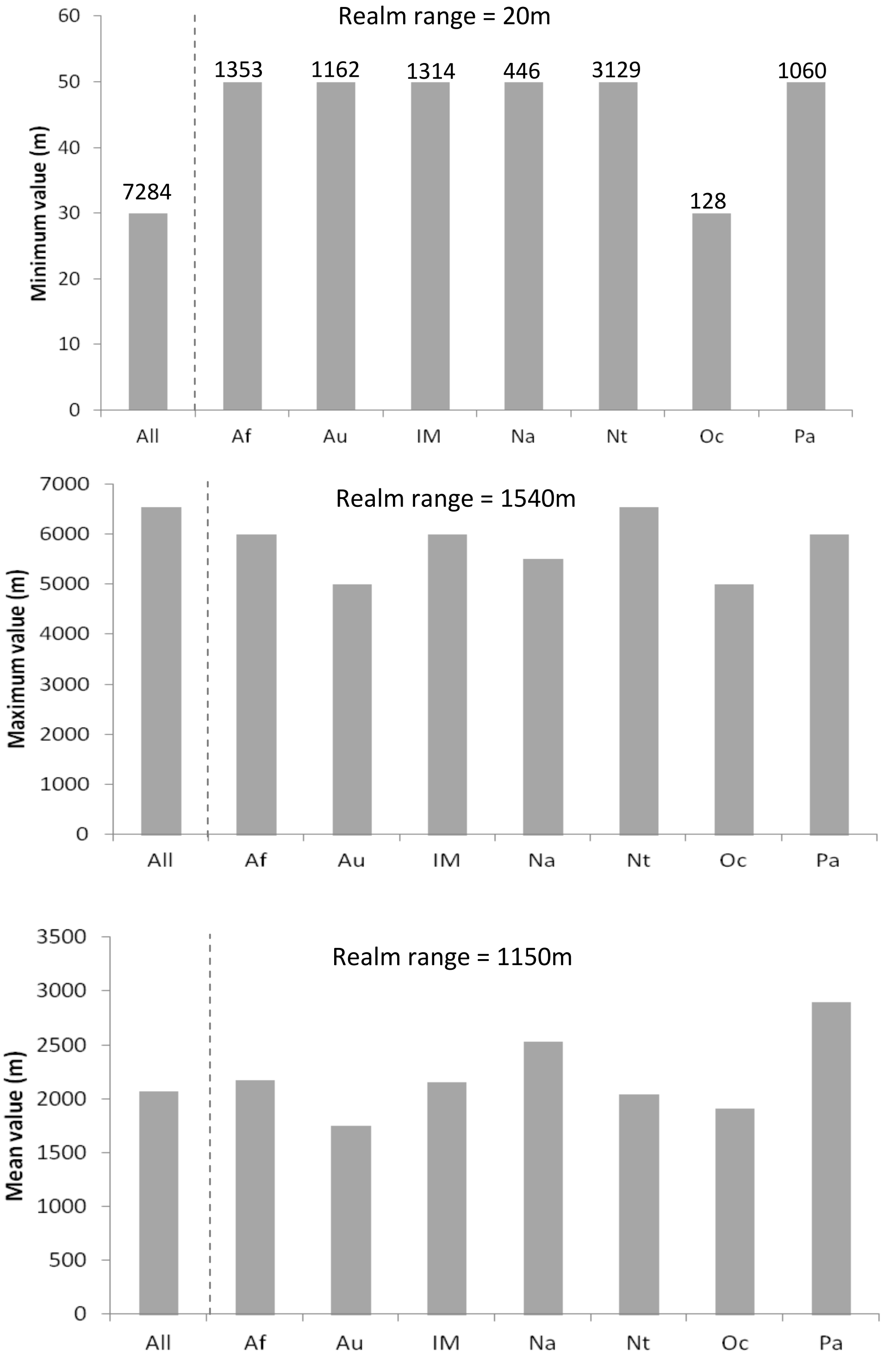


Figure 3.3 Minimum, maximum and mean values of avian species-level maximum elevation for the global dataset (All) and individual biogeographic realms. Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001). Sample sizes are located at the top of each column in the minimum value plot.

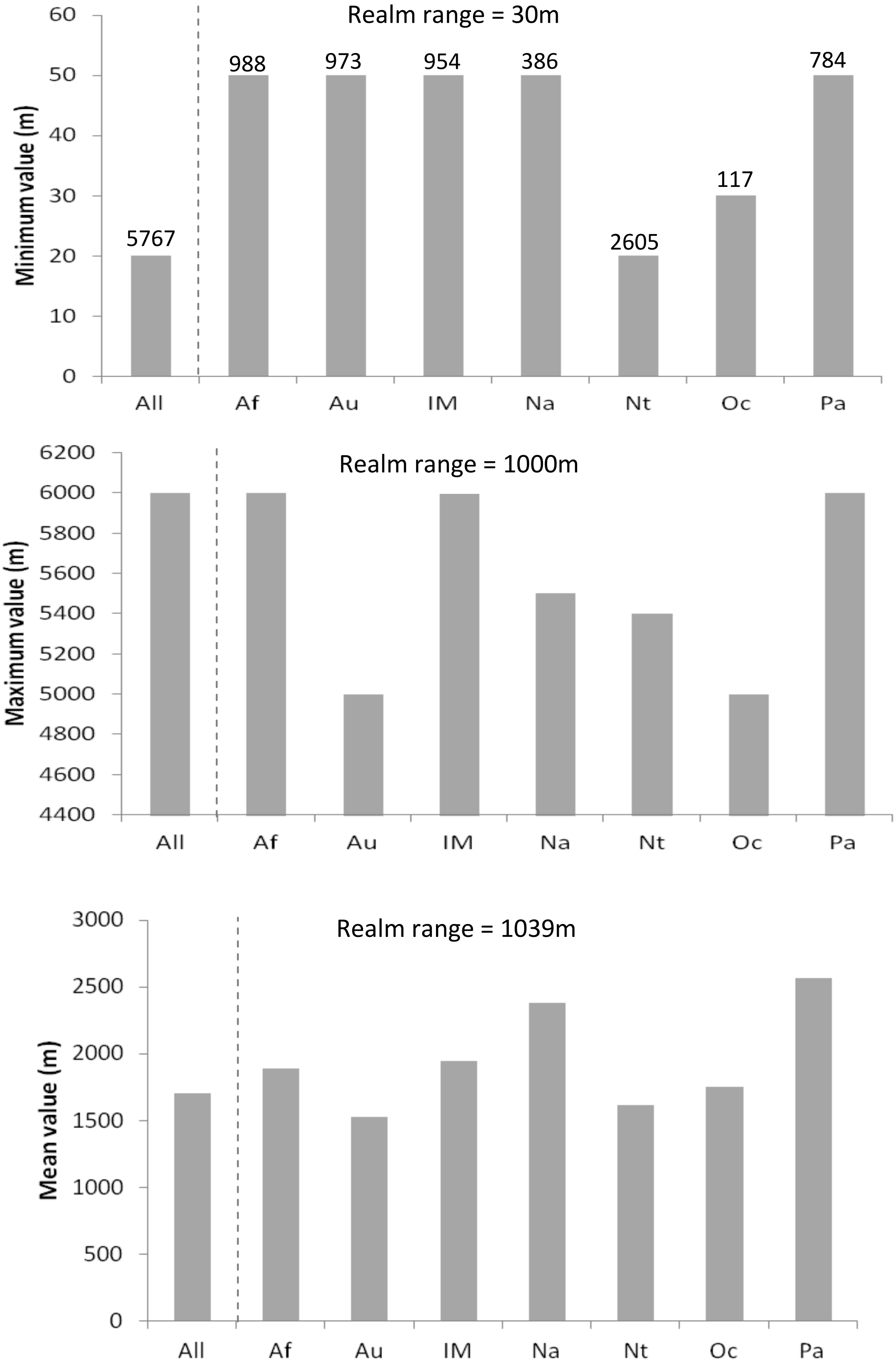


Figure 3.4 Minimum, maximum and mean values of avian species-level elevational range for the global dataset (All) and individual biogeographic realms. Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001). Sample sizes are located at the top of each column in the minimum value plot.

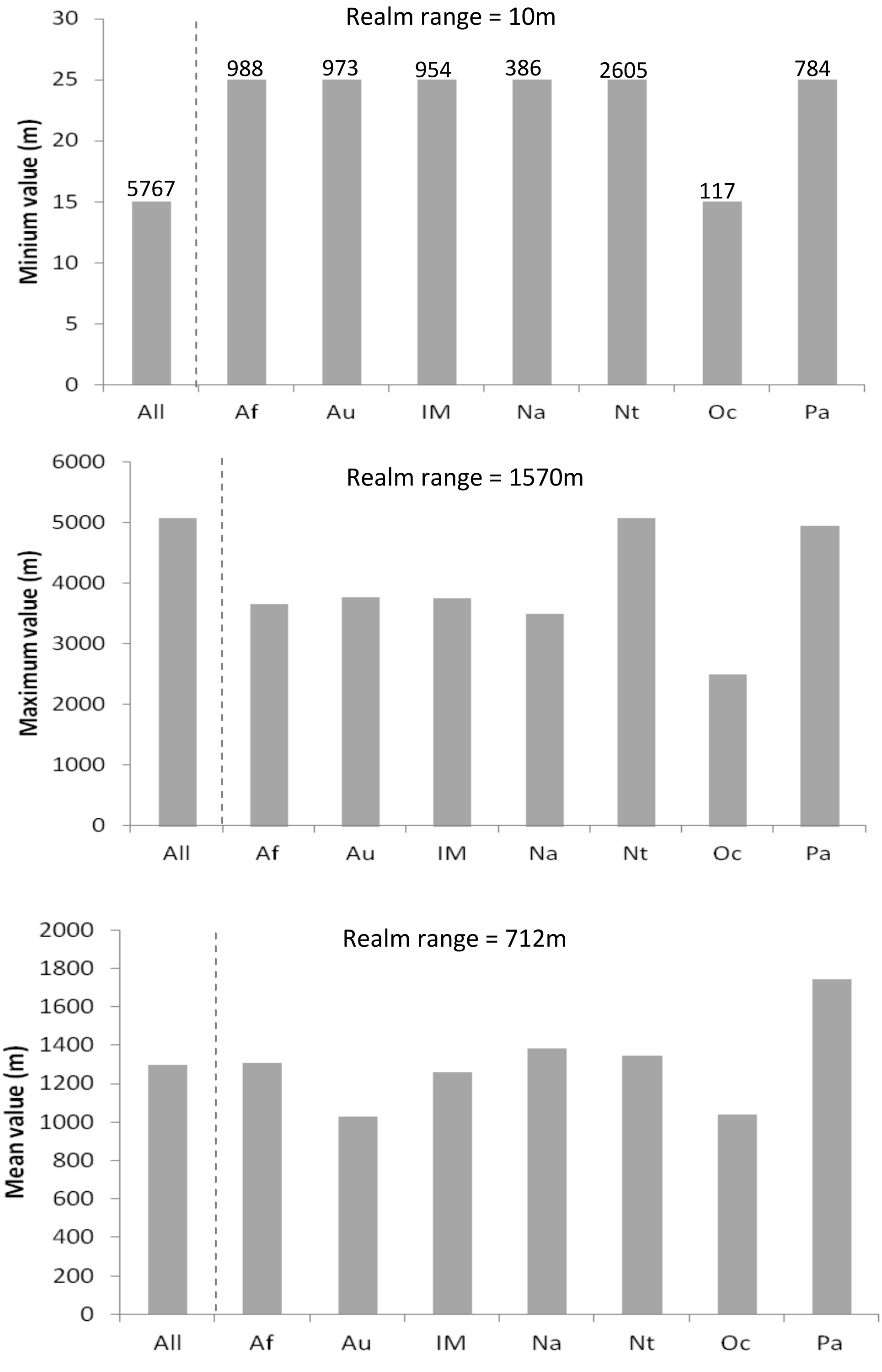


Figure 3.5 Minimum, maximum and mean values of avian species-level elevational midpoint elevation for the global dataset (All) and individual biogeographic realms. Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001). Sample sizes are located at the top of each column in the minimum value plot.

assumption for this study, as both *x* and *y* are subject to natural variation and measurement error, which in turn would lead to an underestimation of the slope of the linear relationship – especially when the correlation coefficient is less than around 0.98 (Sokal & Rohlf 2012). In contrast, 'Model II' regression techniques assume measurement error on both axes and are a less biased line-fitting technique than OLS regression. However, there is some debate concerning the justification of choosing 'Model II' regressions based on the presence of measurement error in *x* (e.g. Warton *et al.* 2006; Price & Phillimore 2007; Smith 2009). Nevertheless, if the statistic of primary interest is the slope (β), as in this study, then 'Model II' is usually more appropriate than OLS regressions (Warton *et al.* 2006).

There are two main types of 'Model II' regression, namely major axis (MA) and reduced major axis (RMA), also known as standardised major axis (SMA) regressions. For an overview and review of these methods, along with 'Model I' OLS regression, see Warton *et al.* (2006). There has been a longstanding and largely unresolved debate about which is the more appropriate line-fitting technique – MA or RMA? However, for the purposes of this research, RMA was selected. RMA is the preferred line-fitting technique of Warton *et al*. (2006). The authors state that they have not yet encountered a situation where use of MA instead of RMA led to a qualitatively different interpretation of results, and believe that such an instance would be exceptional. Yet, they emphasise the importance of quoting the line-fitting method used, as different techniques estimate (slightly) different things about the data, so a slope estimate needs to be interpreted in the context of the method used to estimate it.

Specifically, RMA regressions were calculated within the R package 'Standardised Major Axis Estimation and Testing Routines' ('SMATR', Falster *et al.* 2003).

Controlling for the confounding effect of body size: One well-known confounding variable that can lead to misleading results in comparative studies is difference in body size between taxa. Therefore, in order to identify unbiased bivariate relationships between avian traits and elevational distribution, body weight was first removed as a potential confounding variable, where appropriate, through allometric analysis. Specifically, RMA regressions were conducted between body weight and each morphological, life-history and elevational distribution study variable (Table 3.2). Residual values were calculated where a strongly significant relationship was found ($p < 0.01$). These relative values were used in all further bivariate analyses (except where explicitly stated). The significance and strength of the relationship between clutch size and body weight is negligible, and therefore clutch size was studied in its raw form. It is appreciated that taking an average ('common') slope among all slopes at the family level is a more rigorous method of obtaining residuals than the single slope method used here (Bennett 1986; Harvey & Pagel 1991). However, it could not be used in this study, due to significant heterogeneity of slopes, identified via maximum-likelihood tests. This was found to be the case even for study variables known to have a strong allometric component like egg weight, and was likely due to the large sample sizes being used in this study, that resulted in hundreds of heterogenous regression slopes.

It is important to note that a correlation coefficient does not indicate the direction of a relationship, and it may well be that the variable on the y-axis causes differences in body size rather than the opposite relationship.

3.7.2 Multivariate associations

Investigating relationships in a multiple regression framework allows one to see if significant relationships identified at the bivariate level are robust when controlling for covariance of other (potentially confounding) predictor variables. It can therefore detect more complex

Table 3.2 Pearson correlation coefficients (*r*) between avian traits and body weight, using the global species-level dataset.

Study variable	***n***	***r***	***p-value***
Morphological			
Sexual dimorphism	4044	– 0.05	<0.001
Wing length	5051	0.94	<0.001
Tarsus length	4693	0.83	<0.001
Culmen length	4642	0.74	<0.001
Reproduction			
Clutch size	6359	0.03	0.036
Annual fecundity	2182	– 0.31	<0.001
Egg weight	3368	0.97	<0.001
Development			
Incubation period	2975	0.78	<0.001
Fledging time	2578	0.78	<0.001
Age at first breeding	1020	0.64	<0.001
Survival			
Adult survival	445	0.52	<0.001
Geographical			
Maximum elevation	6376	– 0.07	<0.001
Elevational range	5017	– 0.04	0.005
Elevational midpoint	5017	– 0.13	<0.001

n = correlation sample size. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed). Wing aspect ratio is not included because it is already a residual.

relationships than bivariate analyses alone, although it requires that the value of every predictor is known for each species analysed – therefore sample sizes are often reduced. Specifically, for this research, multivariate associations were investigated using stepwise multiple regressions (α-to-enter/remove = 0.05). The stepwise method was selected (as opposed to either the forwards or backwards strategy) in order to prevent the introduction and retention of uninformative or spurious variables in a given model. This technique sequentially adds significant predictor variables to a model, controlling at each step for variables already included. It also removes any predictors in the model which, with the addition of new predictors, fall below the chosen level of significance (Sokal & Rohlf 2012). In this way, the best fit from any combination of the variables will be made. In order to minimise multicollinearity, multiple regression models were built ensuring that no more than one variable from each trait cluster (i.e. morphological, reproductive, developmental, survival, niche breadth) were included per model. To explicitly test for the presence of multicollinearity, variance inflation factors (VIFs) were calculated for each model. All VIFs calculated were <5.00, indicating successful minimisation of multicollinearity (O'Brien 2007).

3.8 Representativeness of the global dataset

As discussed in Section 3.2.3, a major problem with large-scale species-level trait databases is that it is rarely the case that data for each variable are available for every species, with data typically missing in a non-random manner. This section discusses the representativeness of the global dataset used in this research, in terms of: (a) study variables, (b) geography, and (c) taxonomy.

3.8.1 Study variable representation

Table 3.3 shows the representation of each study variable in the global dataset with respect to the number of species and families with available data.

Species level: Geographical range is by far the best represented study variable in the full dataset. In fact, all six geographical variables have relatively high data representation, i.e. >60% of all bird species. Regarding the non-geographical variables, only body weight and clutch size have representation above 60%, with the morphological variables best represented out of the five non-geographical variable categories. However, data availability for sexual dimorphism is less than half that for body weight, which compared to other avian traits, is much easier to measure in the wild. This is due to the lack of species with reliable adult body weight data for both females and males. Similarly, the number of species with data for annual fecundity is much lower than that for clutch size. This is likely due to the fact

Table 3.3 Species- and family-level representation of each study variable in the global dataset. *n* gives the number of species/families for which data on each study variable was available. '% total' gives the percentage of all species/families in the dataset for which data on each study variable was available (highlighted in bold if ≥50%). These values were calculated for the full dataset and for species/families that possess data on elevational range.

	Species				**Family**			
	Full dataset *n* **= 9412**		**Elevational range** *n* **= 5767**		**Full dataset** *n* **= 144**		**Elevational range** *n* **= 139**	
Variable	***n***	**% total**	***n***	**% total**	***n***	**% total**	***N***	**% total**
MORPHOLOGICAL								
Body weight	8152	**86.6**	5017	**87.0**	144	**100.0**	139	**100.0**
Sexual dimorphism	4044	43.0	2322	40.3	128	**88.9**	123	**88.5**
Wing length	5566	**59.1**	3182	**55.2**	129	**89.6**	124	**89.2**
Wing-aspect ratio	5051	**53.7**	2871	49.8	129	**89.6**	124	**89.2**
Tarsus length	5135	**54.6**	2925	**50.7**	126	**87.5**	121	**87.1**
Culmen length	5081	**54.0**	2929	**50.8**	128	**88.9**	124	**89.2**
REPRODUCTIVE								
Clutch size	6873	**73.0**	4049	**70.2**	143	**99.3**	138	**99.3**
Annual fecundity	2216	23.5	1068	18.5	122	**84.7**	117	**84.2**
Egg weight	3415	36.3	1856	32.2	137	**95.1**	133	**95.7**
DEVELOPMENT								
Incubation time	3050	32.4	1642	28.5	131	**91.0**	126	**90.6**
Fledging time	2631	28.0	1370	23.8	125	**86.8**	121	**87.1**
Age at first breeding	1028	10.9	491	8.5	100	**69.4**	95	**68.3**
SURVIVAL								
Adult survival	448	4.8	220	3.8	66	45.8	65	46.8
ECOLOGICAL								
Diet breadth	3435	36.5	2099	36.4	113	**78.5**	111	**79.9**
Habitat breadth	4029	42.8	2497	43.3	122	**84.7**	119	**85.6**
GEOGRAPHIC								
Geographical range	9243	**98.2**	5655	**98.1**	144	**100.0**	139	**100.0**
Raw mean latitude	7506	**79.7**	4609	**79.9**	141	**97.9**	137	**98.6**
Abs. mean latitude	7506	**79.7**	4609	**79.9**	141	**97.9**	137	**98.6**
Maximum elevation	7284	**77.4**	5767	**100.0**	140	**97.2**	139	**100.0**
Elevational range	5767	**61.3**	5767	**100.0**	139	**96.5**	139	**100.0**
Elevational midpoint	5767	**61.3**	5767	**100.0**	139	**96.5**	139	**100.0**

that broods per year are poorly known for many tropical species. Adult survival is by far the worst represented study variable in the dataset, with <5% of species possessing data on it.

However, this is not surprising given the difficulty in obtaining a reliable measure of it because it is dependent on long-term mark-recapture population studies. In addition, adult survival values were excluded from the dataset for species either receiving or having recently received considerable conservation action. The global representativeness and generality of the results obtained for adult survival, and also for age at first breeding has to be questioned, with species from tropical regions particularly under-represented.

The term 'Wallacean shortfall' (Lomolino & Heaney 2004), refers to our inadequate knowledge of the geographical distributions of most species. However, with respect to birds (and most likely other terrestrial taxa), elevational distribution is far less understood than planimetric distribution. This is shown within the study dataset, where 98.2% of species have geographical range data, yet only 61.3% have data on elevational range limits. In addition, more species in the dataset have maximum elevation data than for either elevational range or elevational midpoint. This was due to the fact that the sources used to input data would more often explicitly state maximum elevational limits than minimum elevational limits. It is also important to stress that, regardless of the amount of life-history data contained within the dataset for a given species, the overall limiting factor as to whether a species was included in analyses for this thesis was whether or not elevational range data (greater than zero meters) was available.

A final point to make is that known elevational limits could be considerably different to actual elevational limits for a number of bird species – particularly those that are understudied, cryptic and live in remote locations.

Family level: Family-level representation for all study variables is very high, except for adult survival, which is the only trait represented by <50% of families. However, a degree of caution is needed because the comparatively lower species-level representation for some of the study variables indicates that within family sample sizes may be quite low and therefore not truly representative of the family in question. For example, annual fecundity has a relatively low level of representation at the species level (23.5%), but a very high level of representation at the family level (84.7%).

3.8.2 Geographic representation

When the GADB was first created and used (Bennett 1986; Bennett & Owens 2002), the dataset was heavily geographically biased with respect to temperate species, due to the lack of studies conducted within the tropics at the time. Although the GADB in its current state is certainly more geographically representative than earlier versions, there is still an overall bias towards temperate regions and species. This trend of species being best studied and understood within Europe and North America, while more diverse tropical regions, particularly Asia and Africa, are left underrepresented, is seen not only in birds, but across taxa (Beck *et al.* 2012).

Biogeographic realm representation of the three elevational distribution study variables (maximum, range and midpoint), are presented in Table 3.4. To summarise, all realms contained elevational distribution data for more than 50% of the species inhabiting them. The least represented realms with respect to maximum elevation data are Oceania and the Nearctic, whereas for elevational range/midpoint data, they are Oceania and the Afrotropics. The best represented realms with respect to all three measures of elevational distribution are the Neotropics and Indo-Malay. This is surprising considering the overall study and knowledge bias towards the temperate regions of the Northern Hemisphere. Nevertheless, it is reassuring that the elevational distribution data in the GADB is geographically representative.

Table 3.4 Representation of data on elevational distribution (maximum, range and midpoint) for bird species in the global dataset and each biogeographic realm (Olson *et al.* 2001). *n* gives the number of species for which data on elevational distribution was available. 'missing' gives the number of species for which data on elevational distribution was not available. '% total' gives the percentage of all species in the global/realm dataset for which data on elevational distribution was available.

	Maximum elevation			**Elevational range/midpoint**		
	n	**missing**	**% total**	***n***	**missing**	**% total**
Global	7284	2128	77.4	5767	3645	61.3
Afrotropical	1353	565	70.5	988	930	51.5
Australasia	1162	520	69.1	973	709	57.8
Indo-Malay	1314	270	83.0	954	630	60.2
Nearctic	446	279	61.5	386	339	53.2
Neotropical	3129	404	88.6	2605	928	73.7
Oceania	128	103	55.4	117	114	50.6
Palearctic	1060	412	72.0	688	688	53.3

3.8.3 Taxonomic representation

Focusing on the representation of elevational distribution data within taxonomic orders, Anseriformes (ducks and geese) contain the lowest proportion of species with elevational distribution data, followed by Ciconiiformes (comprising 30 families). Other orders with relatively poor representation of elevational range/midpoint data (i.e. <50%), include Bucerotiformes (hornbills), Cucliformes (cuckoos) and Tinamiformes (tinamous). The orders with the best representation of elevational distribution data (i.e. >90%) were the Craciformes (guans, chachalacas, curassows and megapodes), Musophagiformes (turacos and plantain-eaters), Trochiliformes (hummingbirds) and Turniciformes (button quails). See Table A3.2 for the summary statistics and representation levels of elevational distribution with respect to all 23 avian orders. Overall, the representativeness of elevational distribution data across orders is high, with no obvious bias.

Despite identified and inherent shortcomings regarding the representativeness of the dataset, these data limitations are currently unavoidable caveats for a global-scale view of the research questions addressed in this thesis. Birds remain, by far, the best studied taxon and therefore present the least taxonomic and geographical bias, i.e. birds provide a best-case study system.

3.9 Appendix: Supplementary figures and tables

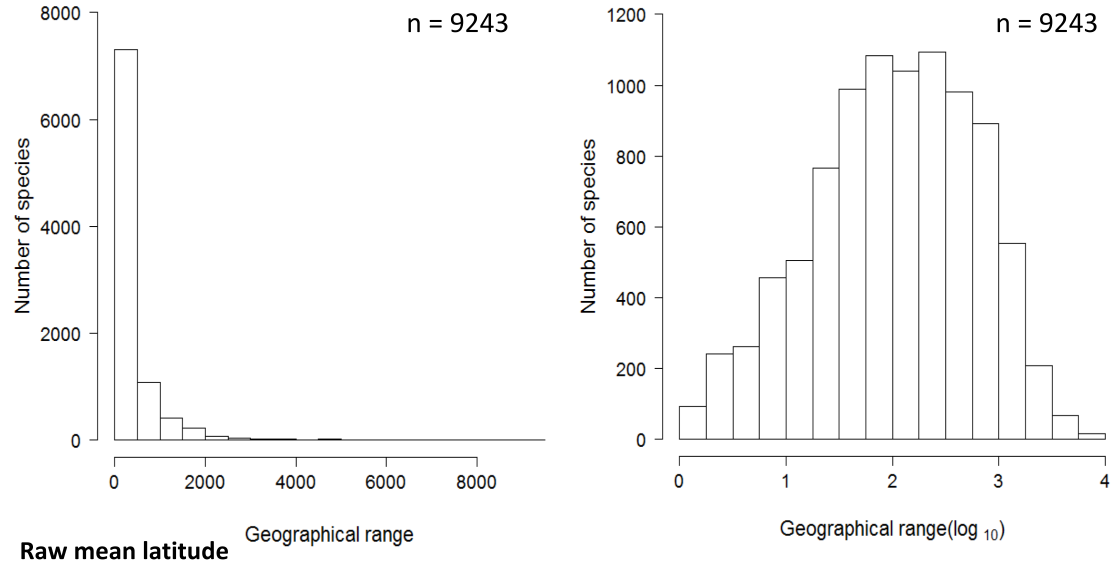
Table A3.1 Two-level habitat classification used to derive the study variable ‘habitat breadth’, following the *IUCN Red List Habitats Authority File (Version 3.0)*. Habitat breadth refers to the number of Level 2 habitats typically utilised per species.

Habitat: Level 1	Habitat: Level 2	Habitat: Level 1	Habitat: Level 2
01. FOREST		3.8	Mediterranean-type
1.1	Boreal	**04. GRASSLAND**	
1.2	Subarctic	4.1	Tundra
1.3	Subantarctic	4.2	Subarctic
1.4	Temperate	4.3	Subantarctic
1.5	Subtropical/tropical dry	4.4	Temperate
1.6	Subtropical/tropical moist lowland	4.5	Subtropical/tropical (lowland) dry
1.7	Subtropical/tropical mangrove	4.6	Subtropical/tropical (lowland) seasonally wet/flooded
1.8	Subtropical/tropical swamp	4.7	Subtropical/tropical high altitude
1.9	Subtropical/tropical moist montane	**05. WETLANDS (INLAND)**	
02. SAVANNA		5.1	Rivers, streams creaks – permanent
2.1	Dry	5.2	Rivers, streams, creaks –seasonal/intermittent/irregular
2.2	Moist	5.3	Shrub dominated wetlands
03. SHRUBLAND		5.4	Bogs, marshes, swamps, fens, peatlands
3.1	Subarctic	5.5	Freshwater lakes (>8 ha) – permanent
3.2	Subantarctic	5.6	Freshwater lakes (>8 ha) – seasonal/intermittent
3.3	Boreal	5.7	Freshwater marshes/pools (< 8ha) – permanent
3.4	Temperate	5.8	Freshwater marshes/pools (<8 ha) – seasonal/intermittent
3.5	Subtropical/tropical (lowland) dry	5.9	Freshwater springs, oases
3.6	Subtropical/tropical (lowland) moist	5.10	Tundra wetlands
3.7	Subtropical/tropical high altitude	5.11	Alpine wetlands

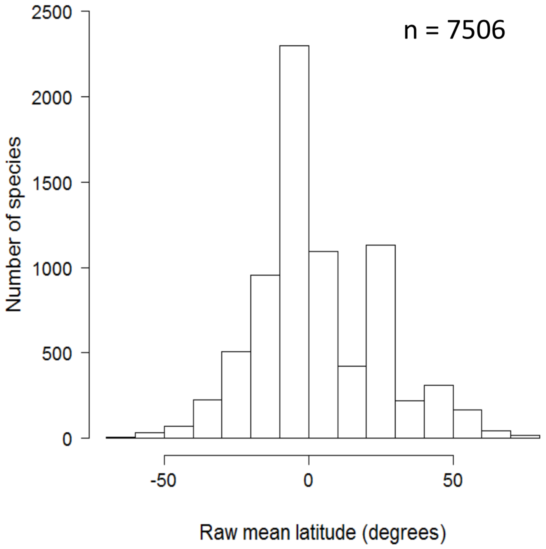
Table A3.1 Continued.

Habitat: Level 1	Habitat: Level 2	Habitat: Level 1	Habitat: Level 2
5.12	Geothermal wetlands	10.3	Estuarine waters
5.13	Inland deltas – permanent	10.4	Intertidal mud, sand/salt flats
5.14	Saline, brackish/alkaline lakes – permanent	10.5	Intertidal marshes
5.15	Saline brackish/alkaline lakes, flats – seasonal/intermittent	10.6	Coastal brackish/saline lagoons
5.16	Saline brackish/alkaline marshes/pools – permanent	10.7	Coastal freshwater lagoons
5.17	Saline brackish/alkaline marshes/pools – seasonal/intermittent	**11. ARTIFICIAL TERRESTRIAL**	
06. ROCKY AREAS		11.1	Arable land
6.1	Inland cliffs/mountains	11.2	Pastureland
6.2	Talus/feldmark	11.3	Plantations
07. CAVES/SUBTERRANEAN		11.4	Rural gardens
7.1	Caves	11.5	Urban areas
7.2	Other subterranean habitats	11.6	Subtropical/tropical heavily degraded former forest
08. DESERT		**12. ARTIFICIAL AQUATIC**	
8.1	Hot desert	12.1	Water storage areas (>8ha)
8.2	Temperate desert	12.2	Ponds (<8ha)
8.3	Cold desert	12.3	Aquaculture ponds
8.4	Semi-desert	12.4	Salt exploitation sites
09. SEA		12.5	Open excavations
9.1	Open sea	12.6	Wastewater treatment areas
9.2	Shallow sea	12.7	Irrigated land
9.3	Subtidal aquatic beds	12.8	Seasonal flooded agricultural lands
9.4	Coral reefs	12.9	Canals, channels, drainage ditches
10. COASTLINE		**13. INTRODUCED VEGETATION**	
10.1	Rocky shores	**14. OTHER HABITAT**	
10.2	Sand, shingle, pebble shores		

Geographical range



Raw mean latitude



Absolute mean latitude

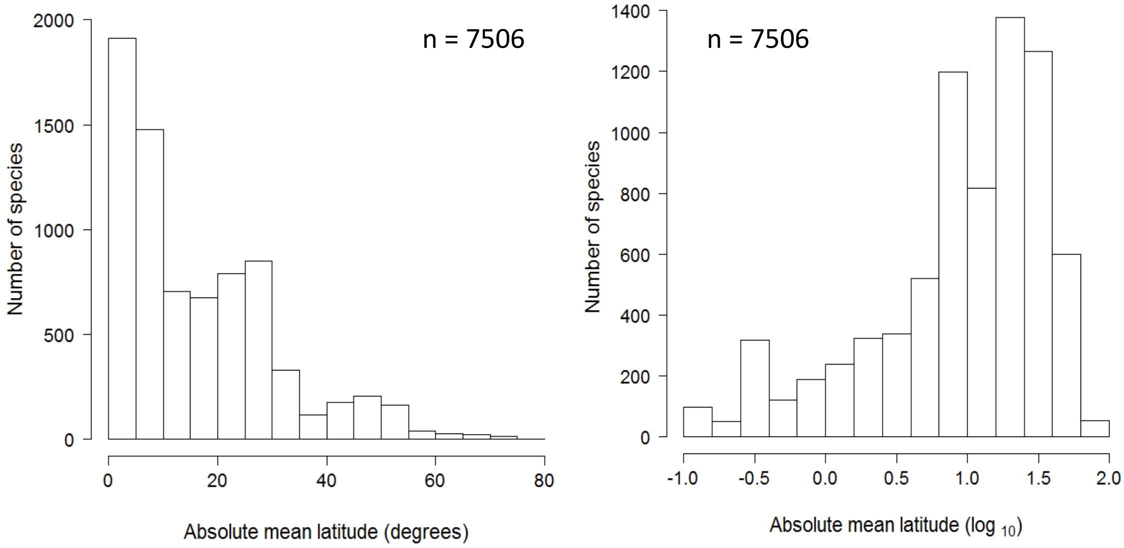
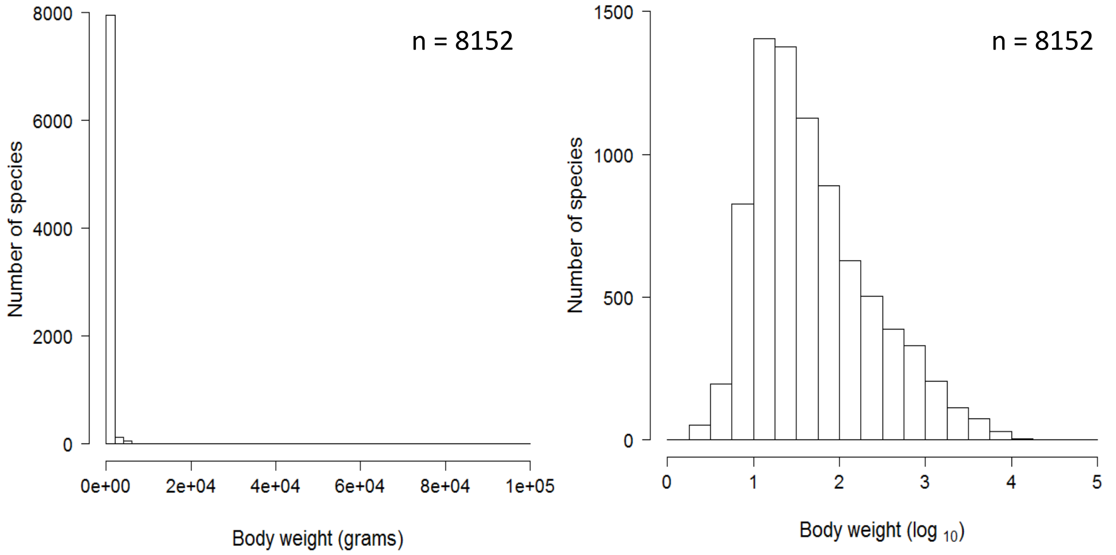
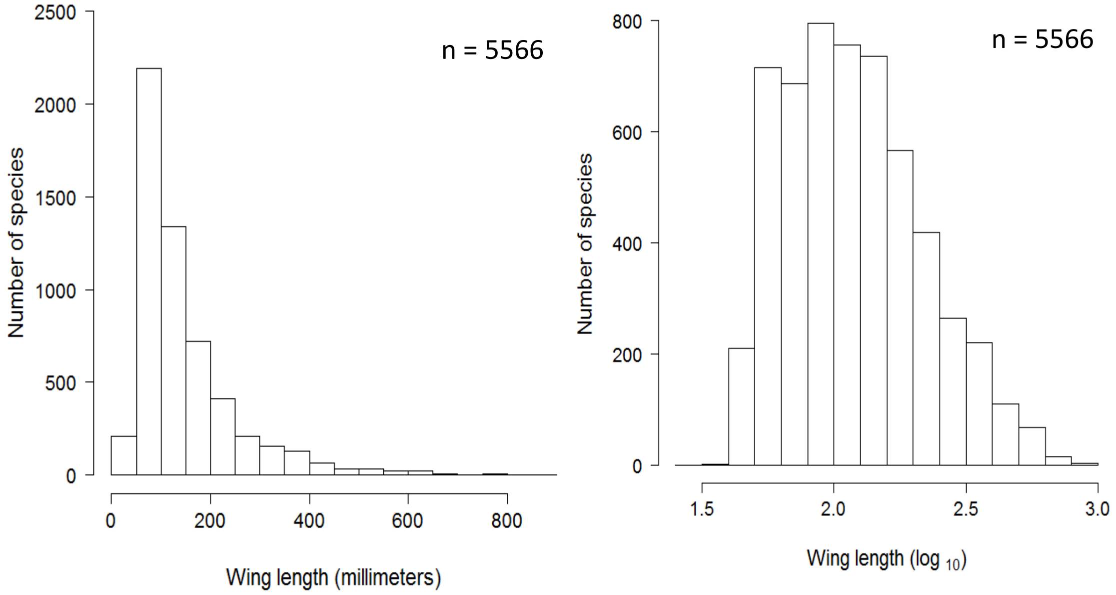


Figure A3.1 Global species-level frequency distribution histograms of the avian non-elevational distribution study variables before (left-hand side) and after (right-hand side) transformation.

Body weight



Wing length



Tarsus length

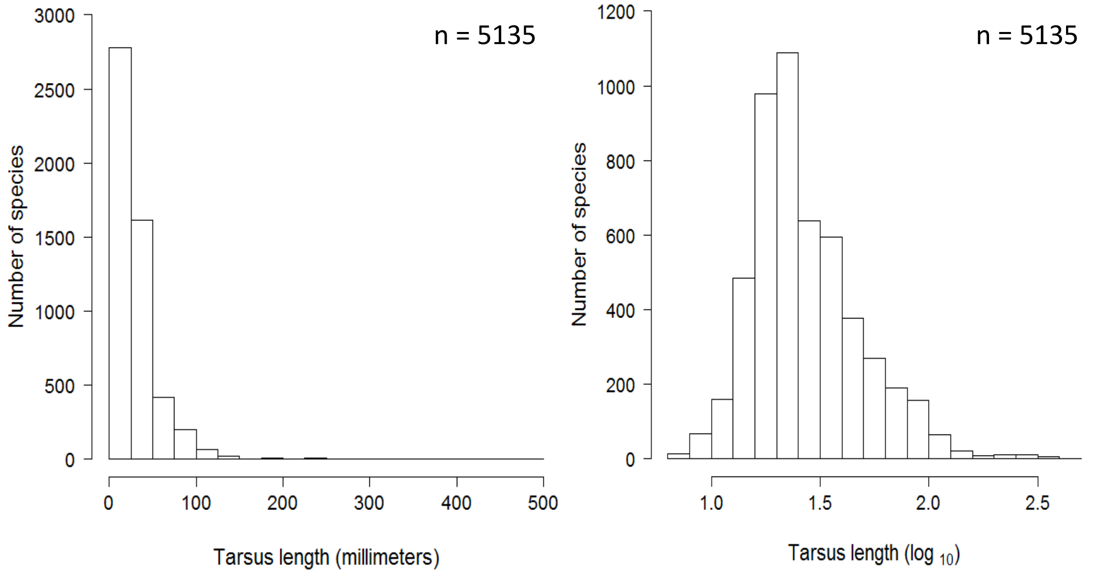
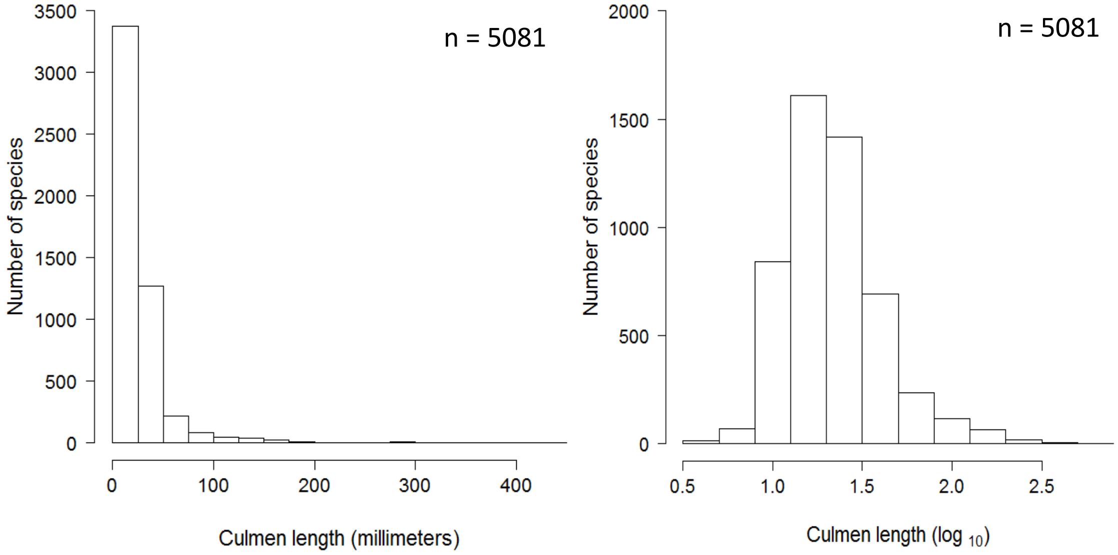
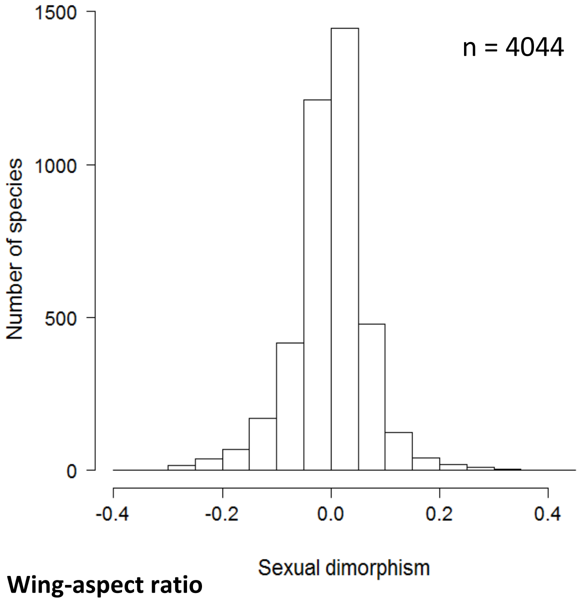


Figure A3.1 Continued.

Culmen length



Sexual dimorphism



Wing-aspect ratio

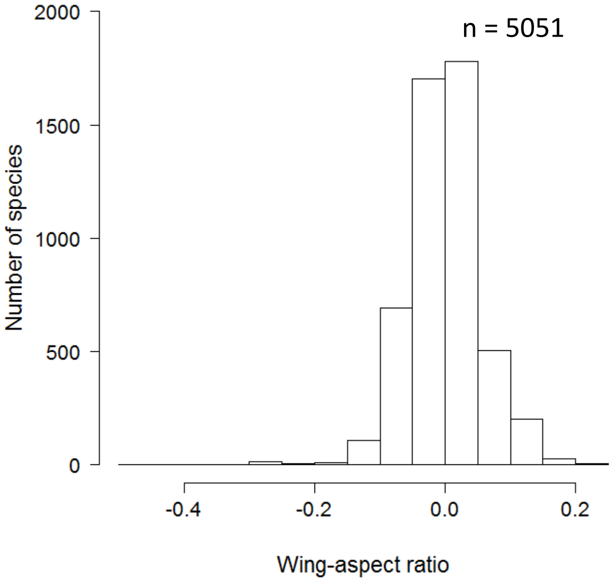
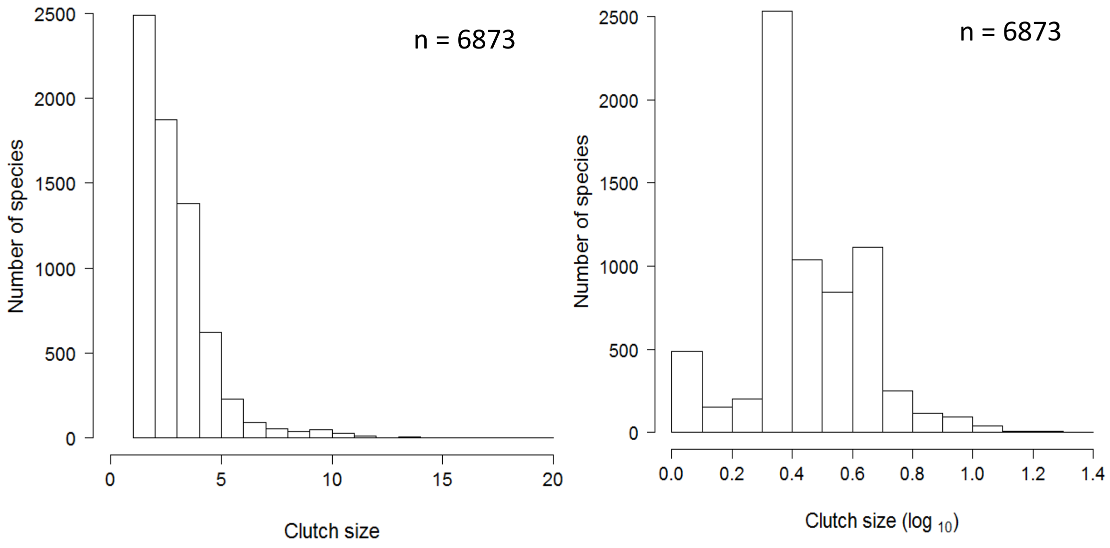
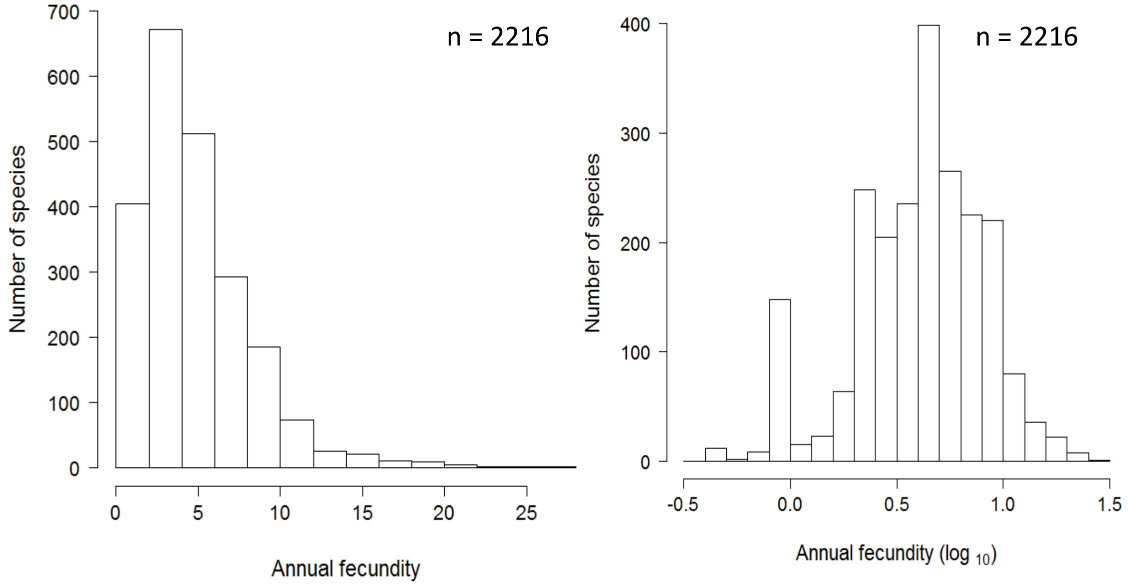


Figure A3.1 Continued.

Clutch size



Annual fecundity



Egg weight

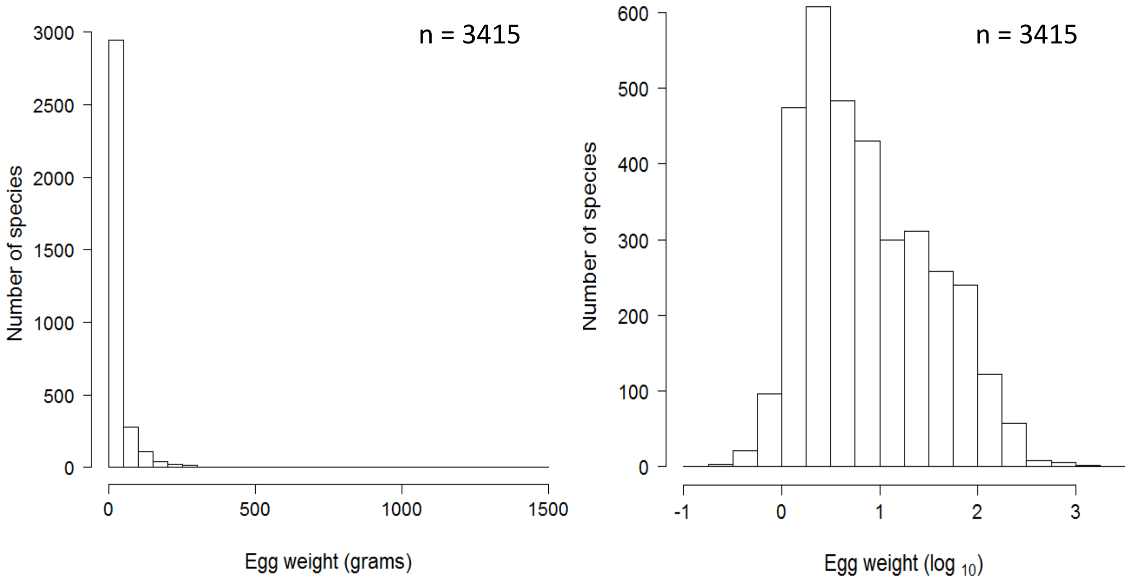
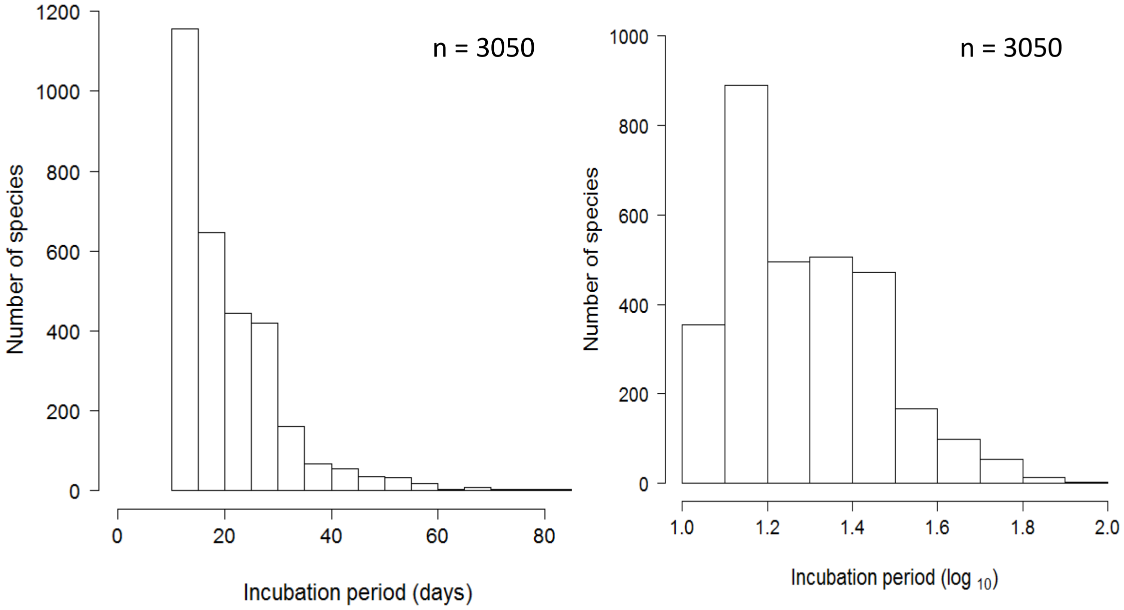
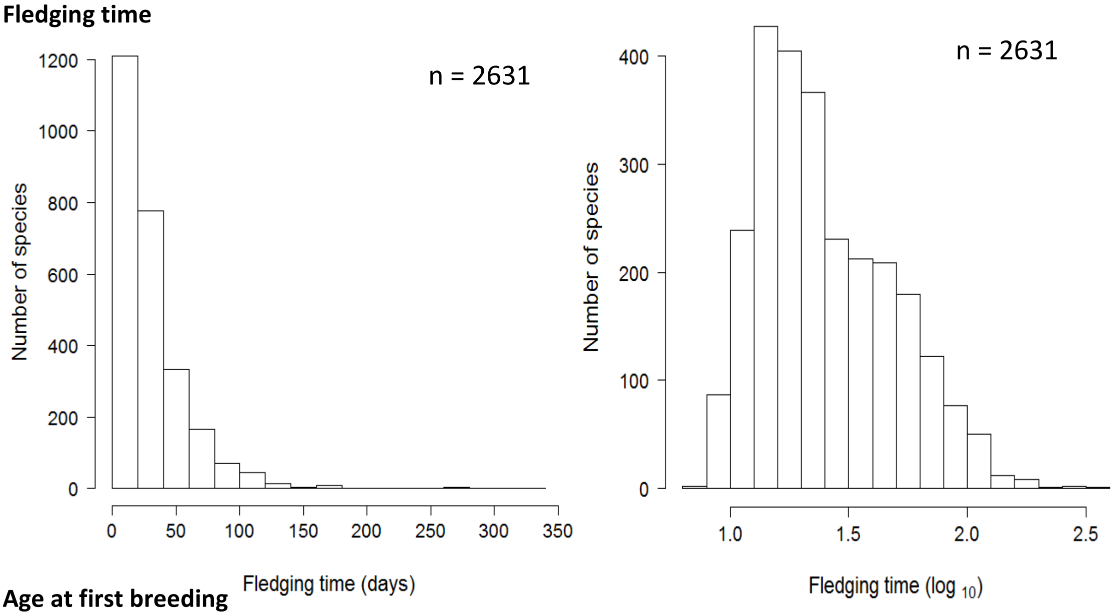


Figure A3.1 Continued.

Incubation period



Fledging time



Age at first breeding

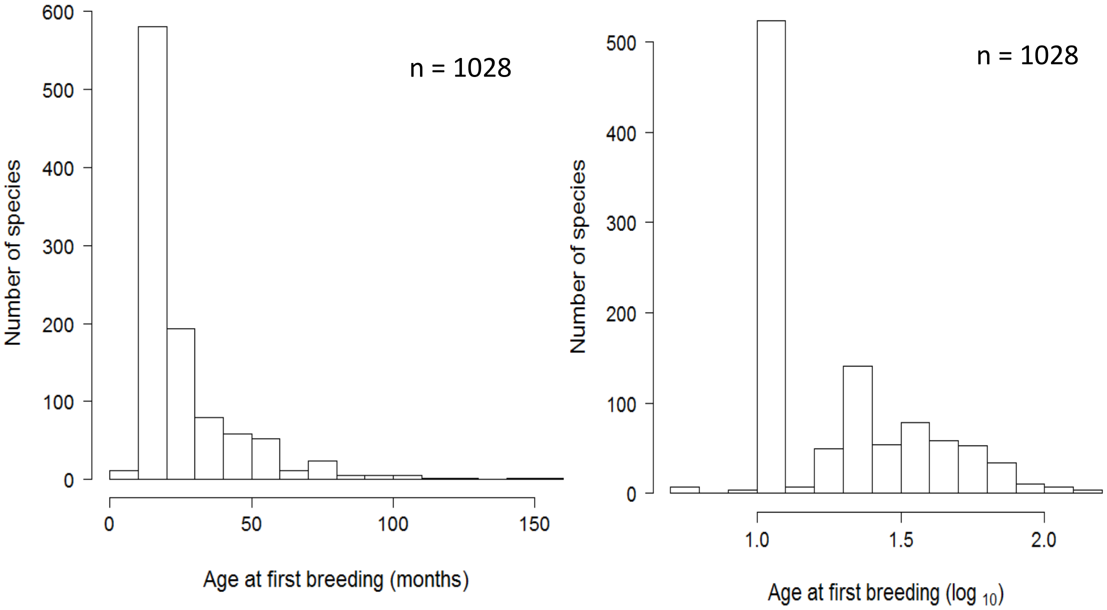
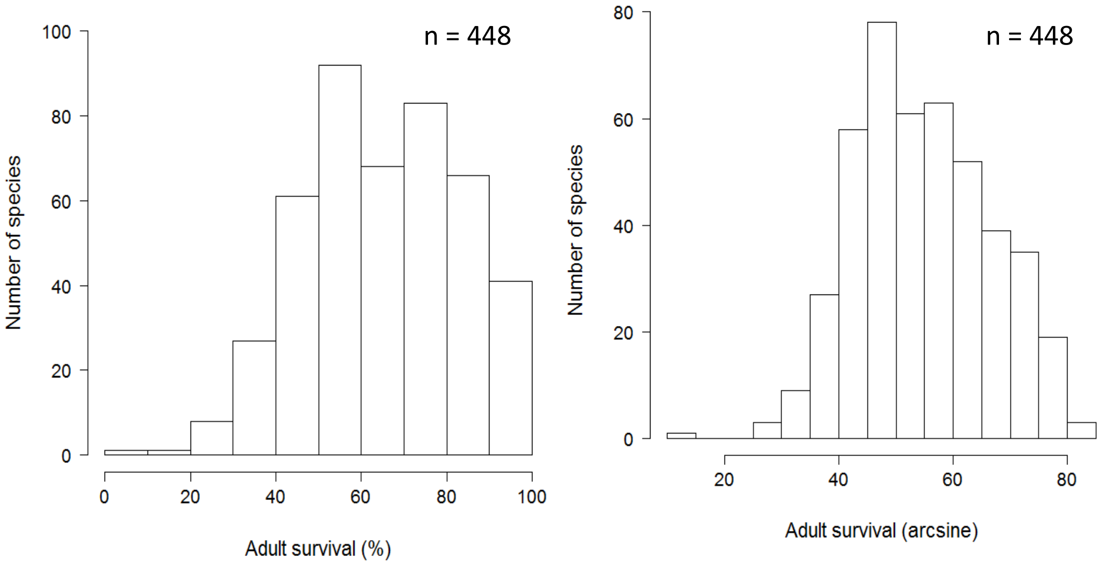
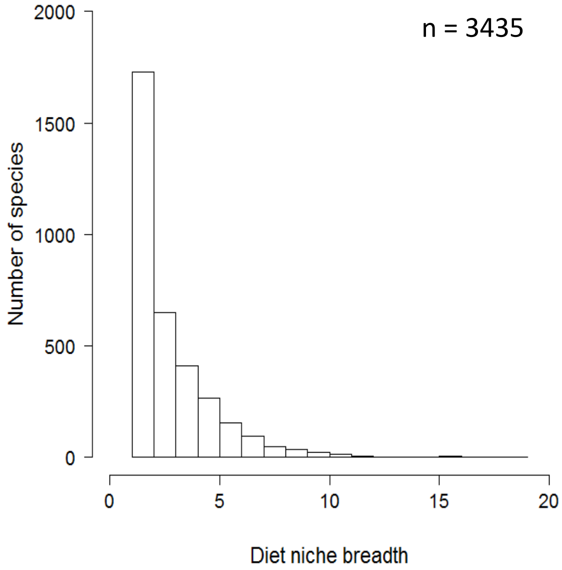


Figure A3.1 Continued.

Adult survival



Diet breadth



Habitat breadth

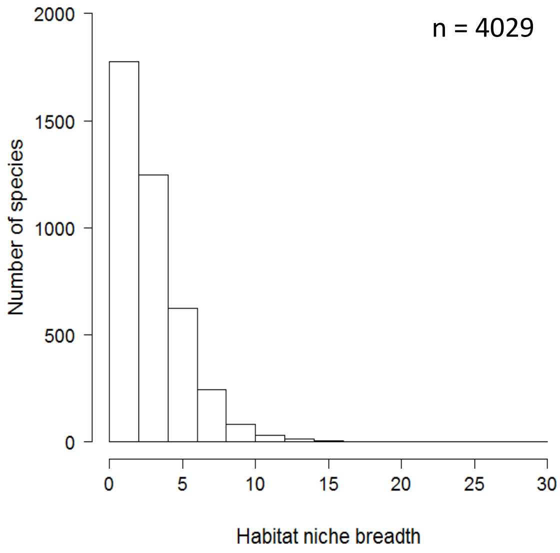


Figure A3.1 Continued.

Table A3.2 Species-level summary statistics (minimum, mean, maximum), sample sizes and representation of the three elevational distribution study variables (maximum, range and midpoint), within avian orders for the global dataset. *n* gives the number of species for which data on elevational distribution was available. 'Missing' gives the number of species for which data on elevational distribution was not available. '% total' gives the percentage of all species in the order for which data on elevational distribution was available.

	Anseriformes			**Apodiformes**			**Bucerotiformes**		
	Max.	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**
Min.	200	200	100	450	400	225	200	200	100
Mean	2682	2339	1397	2276	2101	1265	1610	1122	571
Max.	5000	5000	3900	4575	4500	3038	4300	3257	1629
N	39	37	37	70	58	58	40	16	16
Missing	114	116	116	26	38	38	17	41	41
% total	25.5	24	24	72.9	60	60	70	28	28

	Ciconiiformes			**Coliiformes**			**Columbiformes**		
	Max.	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**
Min.	33	33	17	1400	2000	1000	80	80	40
Mean	2086	1897	1065	2075	2300	1150	1785	1536	997
Max.	6000	5500	3750	2800	2800	1400	5500	4700	4000
n	386	319	319	4	3	3	231	159	159
Missing	524	591	591	2	3	3	70	142	142
% total	42	35	35	67	50	50	77	53	53

	Coraciformes			**Craciformes**			**Cucliformes**		
	Max.	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**
Min.	100	100	50	50	50	25	100	100	50
Mean	1601	1551	833	1560	1378	871	1775	1608	904
Max.	5000	5000	2500	3900	3000	2700	4500	3550	2725
n	105	86	86	65	65	65	108	65	65
Missing	42	61	61	4	4	4	32	75	75
% total	71	59	59	94	94	94	77	46	46

	Galbuliformes			**Galliformes**			**Gruiformes**		
	Max.	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**
Min.	100	100	50	150	150	75	30	30	15
Mean	1284	1230	693	2378	1725	1519	2106	1912	1127
Max.	2900	2500	1825	5800	4500	4400	6540	4200	5070
n	44	37	37	189	187	187	116	107	107
Missing	7	14	14	22	24	24	66	75	75
% total	86	73	73	90	89	89	64	59	59

Table A3.2 Continued.

	Musophagiformes			**Passeriformes**			**Piciformes**		
	Max.	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**
Min.	1000	610	500	30	30	15	100	100	50
Mean	2191	1776	1317	2131	1745	1393	2028	1841	1165
Max.	3600	2700	2800	6000	6000	4950	5000	4000	3000
N	22	21	21	4654	3559	3559	308	199	199
Missing	1	2	2	985	2080	2080	39	148	148
% total	96	91	91	83	63	63	89	57	57

	Psittaciformes			**Strigiformes**			**Struthioniformes**		
	Max.	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**
Min.	30	30	15	210	210	105	500	500	250
Mean	1579	1305	913	2006	1679	1196	1880	1975	988
Max.	6000	4500	3750	5000	5000	3500	4500	4500	2250
n	303	293	293	207	184	184	10	8	8
Missing	46	56	56	86	109	109	1	3	3
% total	87	84	84	71	63	63	91	73	73

	Tinamiformes			**Trochiliformes**			**Trogoniformes**		
	Max.	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**
Min.	200	200	100	100	20	50	700	600	350
Mean	2233	1321	1677	2178	1394	1482	2053	1808	1238
Max.	5300	3050	4650	5200	3600	4350	3600	3500	2400
n	30	21	21	294	291	291	36	29	29
Missing	16	25	25	24	27	27	3	10	10
% total	65	46	46	92	92	92	92	74	74

	Turniciformes			**Upupiformes**		
	Max.	**Range**	**Mid.**	**Max.**	**Range**	**Mid.**
Min.	220	220	110	1500	1500	750
Mean	1521	1521	761	2125	2125	1063
Max.	2500	2500	1250	3200	3200	1600
n	15	15	15	8	8	8
Missing	0	0	0	1	1	1
% total	100	100	100	89	89	89

CHAPTER FOUR

Global biogeography of avian traits: an elevational perspective

4.1 Abstract

Understanding how and why life-history and ecological strategies vary spatially at the global scale is central to many fundamental questions in biogeography, ecology and conservation biology. Studies to date have focused on the relationships between life-history and ecological traits with either latitude or geographical range. Research examining elevational variation in traits is comparatively scarce, and both taxonomically and geographically restricted. This is despite the known global importance of mountainous regions for terrestrial biodiversity. Here, the relationships between elevational distribution and a suite of morphological, life-history and ecological (specifically niche-breadth) traits are investigated within an entire taxonomic class (Aves), using a global species-level dataset. Elevational distribution (range, maximum and midpoint) was found to be positively associated with reproduction and niche breadth, whilst being negatively associated with morphology, growth and survival. These patterns remained robust at the family level, for species within biogeographic realms and largely across phylogenetically independent contrasts. Findings from previous restricted studies of trait variation with elevation were not supported by the global analysis performed here. Instead, the relationships identified seem to mirror known latitudinal and geographical range size patterns. Fast life histories at high elevations may therefore result from exposure to more harsh seasonal environments compared to lowland birds.

4.2 Introduction

Recent global studies of geographical range sizes, utilising a grid-cell approach, have shown that major mountain chains, predominately within the tropics, are the richest areas for terrestrial species richness (e.g. Orme *et al.* 2005; Davies *et al*. 2007; Jenkins *et al.* 2013), and are therefore of key biodiversity and conservation value. Yet, the reasons for this distribution are poorly understood, as to date, scientists possess limited understanding of the evolutionary, environmental and ecological factors that promote hotspots of diversity associated with mountainous regions and elevational variation. This is due primarily to a lack of focused large-scale studies on mountain systems and elevational gradients (however, for birds, see McCain 2009a), and is in stark contrast to the considerable knowledge accrued from numerous studies investigating latitudinal variation in diversity (e.g. Rahbek & Graves 2001; Hawkins *et al.* 2003a,b; Storch *et al*. 2006; Davies *et al*. 2007; Hawkins *et al*. 2007).

Although patterns and underlying processes of both species diversity and co-occurrence have traditionally and largely been studied from a taxonomic perspective, there has been a resurgence of interest over the past 30 years in understanding patterns in the distribution of the traits those taxa possess (Section 2.1). Understanding how and why life-history and ecological strategies vary spatially at the global scale is central to many fundamental questions in biogeography, ecology and conservation biology, including: why organisms live where they do, and how they are responding, and could respond in the future, to anthropogenically induced environmental change.

Life-history studies have been conducted for decades at a variety of spatial scales, primarily to understand adaptation and the evolution of trait diversity, but also to investigate allometry, and patterns of trait covariation in order to examine trade-offs (e.g. Bennett & Owens 2002 and references within). However, until recently, such studies at the global scale have lacked an explicit environmental focus and robust analytical framework. With the increasing availability of morphological, life-history (hereafter collectively referred to as life-history) and ecological data being compiled for whole taxonomic groups, combined with the advent of high-quality satellite data and spatially-explicit models, the first global studies on spatial trait variation are starting to be undertaken for well-studied taxa, such as plants (e.g. Moles *et al.* 2007, 2009; Swenson & Enquist 2007) and birds (e.g. Jetz *et al*. 2008a; Olson *et al*. 2009).

Trait biogeography was reviewed and current knowledge gaps identified in Section 2.1. As with species diversity studies, trait biogeography research to date has focused predominantly on the latitudinal distribution of traits, or their variation in relation to geographical range size (Sections 2.1.4–2.1.7). In some studies of trait variation, latitude and elevation have been combined into a single variable, as both are considered suitable surrogates of temperature (see Pincheira-Donoso *et al.* 2008). However, latitudinal and elevational gradients are known to differ from each other in relation to a number of other climatic and non-climatic factors, e.g. land area, atmospheric pressure and radiation (Körner 2007). In addition, the frequent use of latitude as a climatic surrogate is clearly inaccurate with respect to high elevations, e.g. low latitude climate is not comparable to climates at high tropical elevations. Overall, it is therefore incorrect to assume that relationships found with respect to latitude or geographical range are mirrored by those of elevation or elevational range - complementary studies focusing on both dimensions are necessary.

A few plant studies have investigated elevational variation in single traits at the global scale, e.g. for seed size (Moles *et al.* 2007), wood density (Swenson & Enquist 2007) and plant height (Moles *et al.* 2009). However, for animals, research concerning variation in life-history and ecological traits with elevational distribution are scarce, taxonomically and geographically restricted, predominantly intraspecific, and focused on either one (typically body size) or a few traits in isolation (Sections 2.1.4–2.1.7). Consequently, their results are often heterogeneous, ambiguous, and preclude any potential general relationships from being identified. A global assessment of the role of elevational distribution in determining variation in life-history and ecological traits is therefore required.

In this study, I addressed this important knowledge gap, using birds as a model system. Utilising a global avian species-level dataset and a comparative approach, the presence, direction and strength of bivariate interrelationships between elevational distributions (range, maximum and midpoint) and a complementary suite of life-history (morphological, reproductive, developmental, survival) and ecological (niche-breadth) traits were assessed. Specifically, this study aimed to answer the following questions:

1) How do life-history and ecological traits vary with respect to elevational distribution across species at the global scale?
2) Are relationships identified at the global species level maintained across families, for species within biogeographic realms, or across phylogenetically independent contrasts?
3) How does trait variation with respect to elevation at the global scale support or differ from previous, yet restricted, elevational studies?
4) How does trait variation with respect to elevational distribution support or differ from both known latitudinal and geographical range patterns?

Overall, the null hypothesis that no relationship exists between variation in these traits and elevational distribution was tested.

4.3 Materials and methods

The overall methodology and details on the materials used are described and justified in full in Chapter 3.

4.3.1 Study variables

To examine bivariate relationships between elevational distribution (range, maximum and midpoint) and both life history and ecology in birds at the global scale, the following complementary species-typical traits were selected, reflecting: (a) morphology (body weight, wing length, tarsus length, culmen length), (b) reproduction (clutch size, annual fecundity, egg weight), (c) development (incubation period, fledging time, age at first breeding), (d) survival (adult survival), and (e) niche breadth (diet breadth, habitat breadth) – see Section

3.3 for a concise overview of each study variable. To better comply with the assumptions of normality, all study variables were $\log_{10}$ transformed prior to analysis, except adult survival which was arcsine transformed, and both diet breadth and habitat breadth, which were untransformed (Section 3.4).

This study principally investigates global patterns and the generality of relationships between elevational distribution and avian traits, which have previously only been examined within restricted geographical regions, and either intraspecifically or within small groups of closely-related species. Accordingly, the maximum sample sizes available for each study variable were used, in order to maximise statistical power and both taxonomic and geographic coverage. Use of a full array of complete data for all variables would considerably reduce the sample sizes and produce results that would be less taxonomically and globally representative.

4.3.2 Statistical analyses

Bivariate linear regressions: In order to identify unbiased bivariate relationships between elevational distribution and avian life-history and niche-breadth traits (hereafter traits), body weight was first removed as a potential confounding variable, where appropriate, through allometric analysis (Section 3.7.1). Specifically, relative trait and elevational distribution values were used throughout, except for $\log_{10}$ body weight, $\log_{10}$ clutch size, diet breadth and habitat breadth (which remained in their absolute form).

Reduced Major Axis (RMA) bivariate linear regressions were performed between each of the three measures of elevational distribution and the traits at the global scale, firstly across species and then across families. To test for any regional similarities or differences in the global patterns found, bivariate regressions were also conducted for breeding bird species found within each of the biogeographic realms delimited by Olson *et al*. (2001): Nearctic, Palearctic, Neotropical, Afrotropical, Indo-Malay, Australasia and Oceania (excluding Antarctica due to small sample sizes). Finally, in order to account for variation in the degree of common phylogenetic association, the bivariate relationships were additionally assessed using phylogenetically independent contrasts (PICs) – see Section 3.5.3. Across PICs, all measures of elevational distribution and traits were analysed in their non-residual form.

Elevational bands: Mean species-level trait values with respect to discrete elevational bands were derived, at the global level, using the UNEP-WCMC (2002) ‘Mountains of the World’ map first developed by Kapos *et al.* (2000). This classification scheme recognises seven quantitatively-defined mountain bands (Table 1.1; summarised by UNEP-WCMC 2002). It was chosen based on its fine-resolution (1 km) and use of consistent objective definitions of mountain classes based on elevation, slope and local relief. For the purposes of this analysis, species were placed into: (a) one of six bands based on their elevational midpoint, and (b) one of seven bands based on their maximum elevation. The difference in the number of elevational bands used for the two methods is based on species sample sizes within each band, and their respective distribution across the bands. Specifically, the midpoint method used the following elevational bands: (1) = <300m, (2) = ≥300 & <1000m, (3) = ≥1000 & <1500m, (4) = ≥1500 & <2500m, (5) = ≥2500 & <3500m, (6) = ≥3500m. Whereas the elevational bands used in the maximum elevation method were: (1) = <300m, (2) = ≥300 & <1000m, (3) = ≥1000 & <1500m, (4) = ≥1500 & <2500m, (5) = ≥2500 & <3500m, (6) = ≥3500 & <4500m, (7) = ≥4500m. For a breakdown of sample sizes within each elevational band for both methods, see Fig. A4.1a,b. One-way ANOVAs were performed to identify significant differences across elevational bands for each trait, along with associated post-hoc tests.

4.4 Results

4.4.1 Bivariate linear regressions

The global species-level and family-level bivariate relationships between elevational distribution (range, maximum and midpoint) and avian traits are presented in Tables 4.1a and 4.1b respectively. Table 4.2 provides a summary of the direction of the significant relationships found for species within individual biogeographic realms (see Tables A4.1-3 for corresponding within-realm correlation coefficients and significance levels).

Morphological: Across species globally, adult body weight was found to decline with an increase in all three measures of elevational distribution, with the strongest correlation occurring between body weight and elevational midpoint. This negative relationship was maintained at the family level, but only significantly so for elevational midpoint (Fig. 4.1a). Within individual biogeographic realms, negative relationships between body weight and elevational distribution were dominant, except within the Afrotropical subset, where a positive relationship was identified across all measures of elevational distribution. Significant relationships were not found within the Neotropical (elevational range and maximum elevation), Oceania (elevational range) and Palearctic (maximum elevation and elevational midpoint) realms. Across PICs, the relationship between elevational distribution and body weight varied (Table A4.4). Specifically, variation in body weight was found to be positively associated with elevational range (Table A4.4a), unrelated to maximum elevation (Table A4.4b), and either unrelated (Ericson tree) or negatively related (Hackett tree) to elevational midpoint (Table A4.4c).

Table 4.1 Pearson correlation coefficients (*r*) between avian traits and elevational distribution at the global scale, for (a) species-level relationships and (b) family-level relationships.

(a) Species-level	Elevational range		Maximum elevation		Elevational midpoint	
	n	*r*	*n*	*r*	*n*	*r*
Morphological						
Body weight	5017	– 0.04**	6376	– 0.07***	5017	– 0.13***
Wing length	2871	– 0.07***	3678	– 0.07***	2871	– 0.13***
Tarsus length	2656	– 0.11***	3416	– 0.10***	2656	– 0.06***
Culmen length	2661	– 0.30***	3427	– 0.28***	2661	– 0.31***
Reproduction						
Clutch size	3749	0.22***	4785	0.16***	3749	0.17***
Annual fecundity	1048	0.59***	1304	0.55***	1048	0.57***
Egg weight	1829	– 0.23***	2366	– 0.24***	1829	– 0.23***
Development						
Incubation period	1600	– 0.39***	2007	– 0.38***	1600	– 0.37***
Fledging time	1338	– 0.32***	1708	– 0.31***	1338	– 0.29***
Age at first breeding	485	– 0.52***	589	– 0.52***	485	– 0.53***
Survival						
Adult survival	217	– 0.56***	260	– 0.51***	217	– 0.55***
Niche breadth						
Diet breadth	1926	0.41***	2406	0.37***	1926	0.33***
Habitat breadth	2178	0.28***	2702	0.15***	2178	0.07***

(b) Family-level	Elevational range		Maximum elevation		Elevational midpoint	
	n	*r*	*n*	*r*	*n*	*r*
Morphological						
Body weight	139	– 0.05	140	– 0.14	139	– 0.19*
Wing length	124	– 0.21*	125	– 0.21*	124	– 0.22*
Tarsus length	124	0.15	122	0.14	124	0.15
Culmen length	117	– 0.32***	125	– 0.32***	117	– 0.37***
Reproduction						
Clutch size	138	0.30***	139	0.27***	138	0.28***
Annual fecundity	117	0.66***	118	0.63***	117	0.62***
Egg weight	133	– 0.31***	134	– 0.31***	133	– 0.28***
Development						
Incubation period	126	– 0.50***	127	– 0.50***	126	– 0.48***
Fledging time	121	– 0.41***	122	– 0.42***	121	– 0.40***
Age at first breeding	95	– 0.62***	96	– 0.63***	95	– 0.63***
Survival						
Adult survival	65	– 0.57***	66	– 0.58***	65	– 0.59***
Niche breadth						
Diet breadth	111	0.67***	111	0.64***	111	0.63***
Habitat breadth	119	0.42***	119	0.40***	119	0.37***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. n = correlation sample size. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative elevational distribution used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed).

Table 4.2 Strength and direction of Pearson correlation coefficients for species-level relationships between avian traits and elevational distribution within biogeographic realms.

	Elevational range							**Maximum elevation**							**Elevational midpoint**						
	Af	Au	IM	Na	Nt	Oc	Pa	Af	Au	IM	Na	Nt	Oc	Pa	Af	Au	IM	Na	Nt	Oc	Pa
Morphological																					
Body weight	++	– –	– –	– –	*NS*	*NS*	– –	++	– –	– –	– –	*NS*	–	*NS*	++	– –	– –	– –	– –	– –	*NS*
Wing length	*NS*	++	*NS*	– –	– –	*NS*	– –	*NS*	+	*NS*	– –	– –	*NS*	– –	–	*NS*	*NS*	– –	– –	*NS*	– –
Tarsus length	– –	*NS*	*NS*	*NS*	*NS*	*NS*	– –	– –	*NS*	*NS*	*NS*	*NS*	*NS*	– –	–	*NS*	*NS*	*NS*	*NS*	*NS*	– –
Culmen length	– –	– –	– –	*NS*	– –	*NS*	– –	– –	– –	– –	*NS*	– –	*NS*	– –	– –	– –	– –	*NS*	– –	*NS*	– –
Reproduction																					
Clutch size	++	+	*NS*	++	++	++	++	++	*NS*	*NS*	++	++	++	*NS*	++	*NS*	*NS*	++	++	++	*NS*
Annual fecundity	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
Egg weight	– –	– –	– –	– –	–	*NS*	– –	– –	– –	– –	– –	– –	–	– –	– –	– –	– –	– –	–	–	– –
Development																					
Incubation period	– –	– –	– –	– –	– –	–	– –	– –	– –	– –	– –	– –	–	– –	– –	– –	– –	– –	– –	–	– –
Fledging time	– –	– –	– –	– –	– –	–	– –	– –	– –	– –	– –	– –	–	– –	– –	– –	– –	– –	– –	–	– –
Age at first breeding	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –
Survival																					
Adult survival	– –	– –	–	– –	– –	– –	– –	– –	– –	– –	– –	– –	–	– –	– –	– –	–	– –	– –	–	– –
Niche breadth																					
Diet breadth	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	+	++
Habitat breadth	++	++	++	++	++	++	*NS*	++	++	++	++	++	++	*NS*	++	++	+	++	+	++	*NS*

–/+ negative/positive correlation (*P* <0.05). – – /++ correlation remains significant under Bonferroni correction of the α-level (*P* <0.05/7 = 0.007). *NS*: Correlation not significant. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative elevational distribution used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). Biogeographic realms: Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001). See Tables A4.1-3 for corresponding within-realm correlation coefficients.

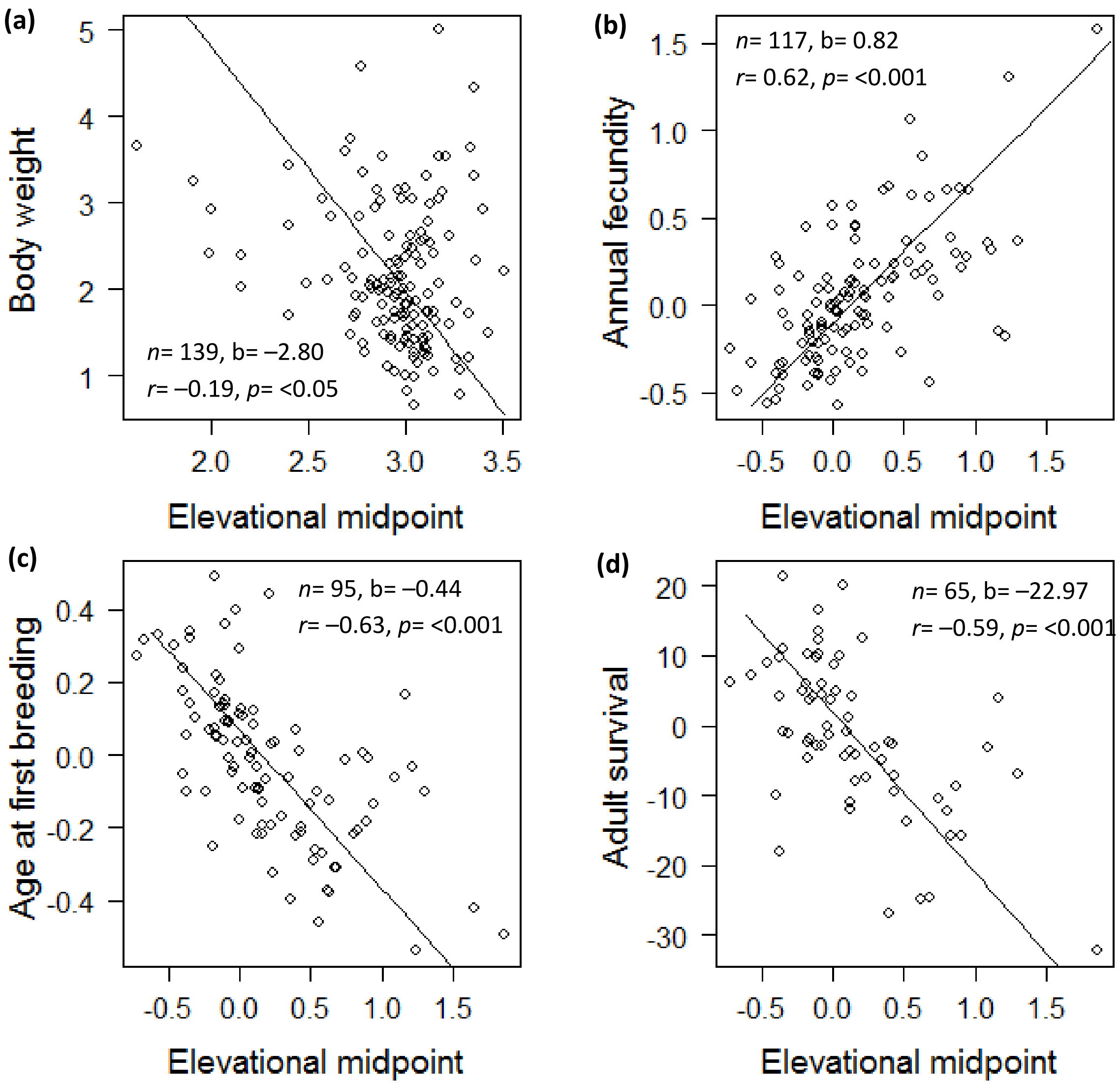


Figure 4.1 Global family-level relationships between avian elevational midpoint and (a) body weight (grams), (b) annual fecundity, (c) age at first breeding (months), (d) adult survival. Relative values used, except for plot (a). Study variables $\log_{10}$ transformed except adult survival (arcsine transformed). RMA linear regressions were used to produce lines of best fit and slope estimates.

Wing length, tarsus length and culmen length were all significantly negatively correlated with elevational distribution at the global species level, with the relationships strongest for culmen length. At the global family-level, significant (negative) correlations were found only for wing length and culmen length against elevational distribution, and were once again strongest for culmen length. Within individual biogeographic realms, all significant correlations were negative in direction for all three morphological traits against elevational distribution, except for a positive relationship identified between wing length and both elevational range and maximum elevation within the Australasia subset. Across biogeographic realms, non-significant relationships with elevational distribution were found for all three morphological traits. However, the greatest number of non-significant relationships were found between tarsus length and elevational distribution, with significant relationships only identified for the Afrotropical and Palearctic realms. Across PICs, the majority of significant relationships between elevational distribution and the three non-body weight morphological traits were positive in direction (Table A4.4). Specifically, variation in wing length, tarsus length and culmen length were consistently positively associated with elevational range (Table A4.4a) and maximum elevation (Table A4.4b), although not significantly so with respect to culmen length and maximum elevation. Variation in both wing length and tarsus length with respect to elevational midpoint was significantly positive in direction using the Ericson tree to derive PICs from, but significantly negative when using the Hackett tree (Table A4.4c). Variation in culmen length was not related to elevational midpoint across PICs (Table A4.4c).

Reproductive: A positive relationship was found between clutch size and elevational distribution across both species and families globally. Within individual biogeographic realms, the positive relationship was maintained. However, significant relationships were not found within the Indo-Malay (all measures of elevational distribution), Australasia (maximum elevation and elevational midpoint) and Palearctic (maximum elevation and elevational midpoint) realms. Annual fecundity increased significantly with an increase in elevational distribution across species, families (Fig. 4.1b) and within all biogeographic realms. Across PICs, variation in both clutch size and annual fecundity were also found to be positively associated with elevational distribution (Table A4.4), however, with respect to elevational midpoint, the relationship was relatively weak (Table A4.4c). A negative relationship was found between egg weight and elevational distribution across species, families and within all biogeographic realms (except against elevational range within the Oceania realm), but not across PICs (Table A4.4).

Developmental: For all three developmental traits investigated (incubation period, fledging time and age at first breeding), a negative relationship was found with respect to elevational distribution. This association was strongest for age at first breeding, followed by incubation period and fledging time, at both the species and family level globally (Fig. 4.1c). This negative relationship was maintained within all biogeographic realms. Across PICs, both incubation period and fledging time were found to be negatively associated with elevational distribution (Table A4.4). Age at first breeding was instead found to be positively associated with elevational range (Hackett tree only), maximum elevation, and elevational midpoint (Ericson tree only).

Survival: Adult survival declined significantly with an increase in elevational distribution across species, families (Fig. 4.1d) and within all biogeographic realms. Across PICs, adult survival varied significantly and in a negative direction with elevational range and maximum elevation (Hackett tree only), and was unrelated to elevational midpoint (Table A4.4).

Niche breadth: At the global level, across both species and families, diet breadth and habitat breadth were found to increase with increasing elevational distribution. These elevational relationships were strongest with respect to diet breadth, and strongest for elevational range (for both diet breadth and habitat breadth). Across biogeographic realms, this significant positive relationship was maintained for both measures of niche breadth, except between habitat breadth and elevational distribution within the Palearctic subset, where no significant trends were identified. Across PICs, both measures of niche breadth were found to be positively associated with elevational range and maximum elevation (Table A4.4a,b). Diet breadth was found to vary significantly with elevational midpoint, although in a negative direction with respect to the Ericson tree derived PICs and in a positive direction with the Hackett tree; habitat breadth did not vary significantly with elevational midpoint (Table A4.4c).

4.4.2 Elevational bands

For clarity of presentation and interpretation, only the most informative and significant plots from each trait category were selected for presentation and discussion in this study, i.e. two representing morphology, reproduction, development and niche breadth. Adult survival could not be analysed via one-way ANOVA due to small sample sizes across the elevational bands, for both methods.

Elevational midpoint method: Mean body weight declined significantly with each increasing elevational band, except for the highest elevational band (≥3500m), where a noticeable and significant peak in body weight was found (Fig. 4.2a). Conversely, mean tarsus length increased with increasing elevational band, except for the highest elevational band (≥3500m), where a noticeable yet non-significant drop in tarsus length was observed (Fig. 4.2b). An overall increase in mean clutch size (Fig. 4.2c), and an overall decrease in mean egg weight (Fig. 4.2d) were found with increasing elevational band. Both mean incubation period (Fig. 4.2e) and mean age at first breeding (Fig. 4.2f) declined with increasing elevational band, although the trend with age at first breeding was not found to be significant. No significant relationship was found between mean diet breadth and increasing elevation (Fig. 4.2g), whereas habitat breadth displayed a significant unimodal relationship (Fig. 4.2h).

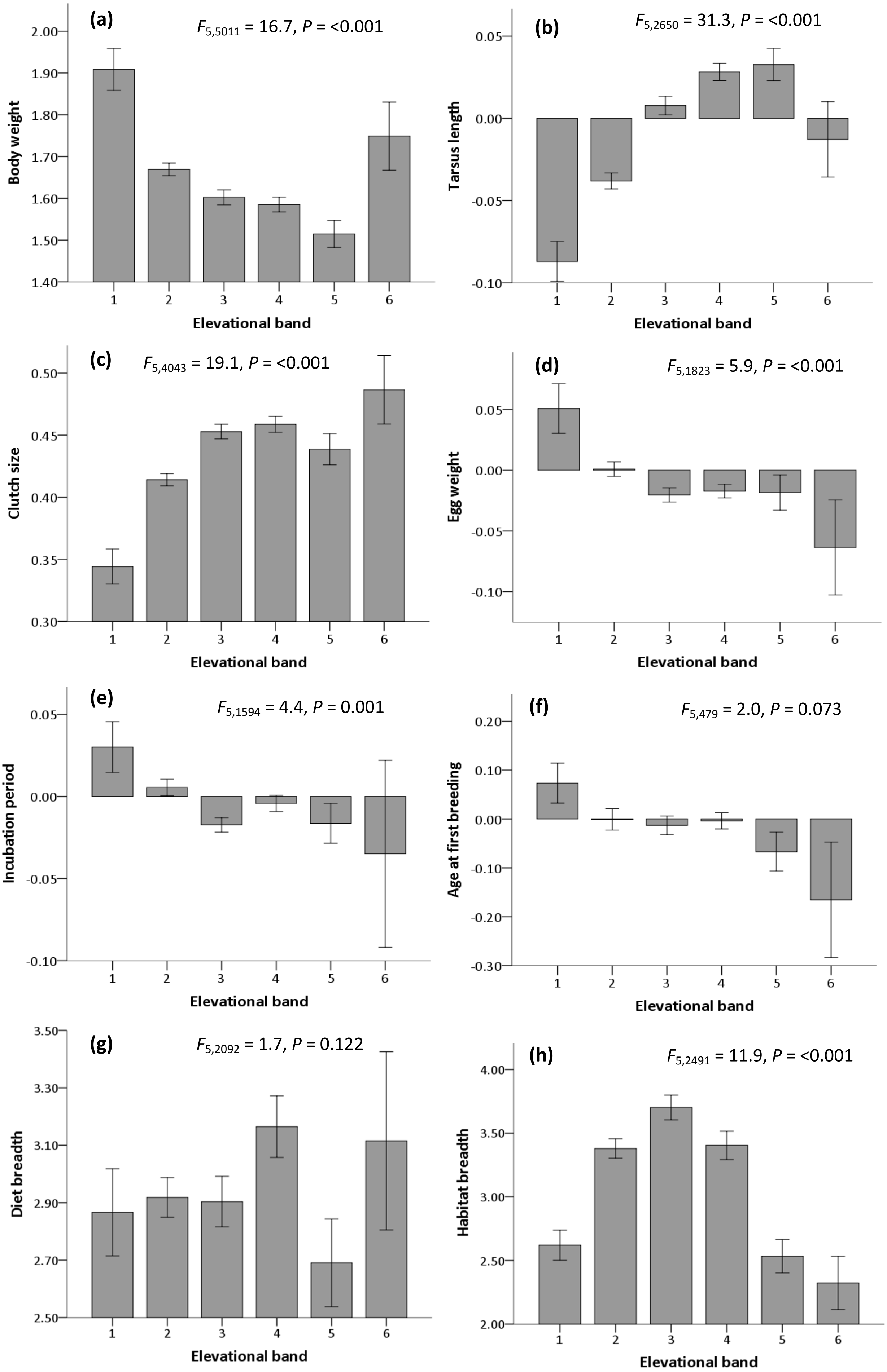

(a)
$F_{5,5011}$ = 16.7, P = <0.001
Body weight
2.00
1.90
1.80
1.70
1.60
1.50
1.40
1
2
3
4
5
6
Elevational band
(b)
$F_{5,2650}$ = 31.3, P = <0.001
Tarsus length
0.05
0.00
-0.05
-0.10
Elevational band
(c)
$F_{5,4043}$ = 19.1, P = <0.001
Clutch size
0.50
0.45
0.40
0.35
0.30
Elevational band
(d)
$F_{5,1823}$ = 5.9, P = <0.001
Egg weight
0.05
0.00
-0.05
-0.10
Elevational band
(e)
$F_{5,1594}$ = 4.4, P = 0.001
Incubation period
0.05
0.00
-0.05
-0.10
Elevational band
(f)
$F_{5,479}$ = 2.0, P = 0.073
Age at first breeding
0.20
0.10
0.00
-0.10
-0.20
-0.30
Elevational band
(g)
$F_{5,2092}$ = 1.7, P = 0.122
Diet breadth
3.50
3.30
3.10
2.90
2.70
2.50
Elevational band
(h)
$F_{5,2491}$ = 11.9, P = <0.001
Habitat breadth
4.00
3.50
3.00
2.50
2.00
Elevational band

Figure 4.2 *(previous page)* Mean (±1SE) species-level avian trait values with respect to discrete elevational bands (UNEP-WCMC 2002) at the global scale. All species with their elevational midpoint in the same band were pooled. Full ANOVA statistics reported. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Study variables log10 transformed except diet/habitat breadth (untransformed). (a) body weight (grams), (b) tarsus length (millimetres), (c) clutch size, (d) egg weight (grams), (e) incubation period (days), (f) age at first breeding (months), (g) diet breadth, (h) habitat breadth. Elevational bands: (1) = <300m, (2) = ≥300 & <1000m, (3) = ≥1000 & <1500m, (4) = ≥1500 & <2500m, (5) = ≥2500 & <3500m, (6) = ≥3500m.

Maximum elevation method: Using the maximum elevation method, qualitatively similar patterns were found to those using elevational midpoint for body weight, tarsus length, clutch size, egg weight, incubation period and age at first breeding (Fig. 4.3a-f). Fig. 4.4 depicts a map of the world displaying the global variation in avian clutch size with respect to discrete elevational bands (UNEP-WCMC 2002). A clear incremental increase in clutch size with each successively higher elevational band can be seen (see also Fig. 4.3c), with noticeable extensive peaks across the length of the Andes and the Himalayas. Different patterns to those identified using the elevational midpoint method were found for both measures of niche breadth. Specifically, both diet breadth (Fig. 4.3g) and habitat breadth (Fig. 4.3h) were found to significantly increase with increasing elevational band.

4.5 Discussion

4.5.1 Life-history variation with elevational midpoint and maximum elevation

Previous studies have typically concluded that birds shift in life history from a high reproductive strategy at low elevations to a high survival strategy at high elevations (e.g. Krementz & Handford 1984; Badyaev 1997b; Badyaev & Ghalambor 2001; Bears *et al.* 2009). However, the results from this research on a global scale show the opposite pattern, suggesting that the trends documented in previous taxonomically and geographically restricted studies are not supported by a broad analysis across species at the global scale (Table 4.1a). Specifically, after controlling for the confounding effects of body size, both elevational midpoint and maximum elevation (measures of mean elevational 'height' of a species' elevational range and physiological tolerance respectively) were shown to be positively associated with reproductive output (clutch size and annual fecundity), and negatively associated with traits concerning size (body weight, wing length, tarsus length and culmen length), egg weight, development (incubation period, fledging time and age at first breeding) and survival (adult survival). These trends were maintained at the family level (Table 4.1b) and generally for species within individual biogeographic realms (Table 4.2).

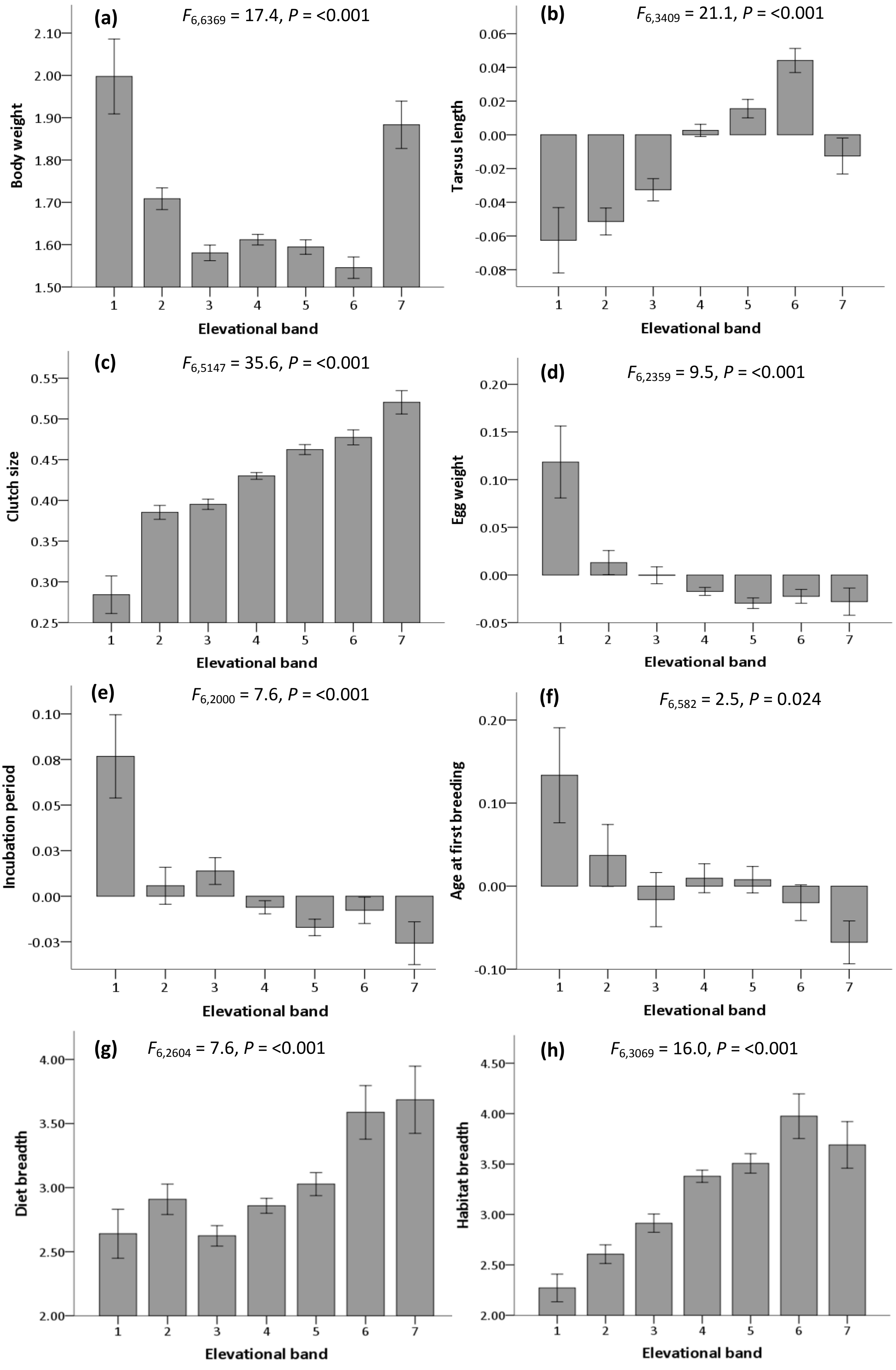

(a)
$F_{6,6369}$ = 17.4, P = <0.001
Body weight
2.10
2.00
1.90
1.80
1.70
1.60
1.50
1 2 3 4 5 6 7
Elevational band
(b)
$F_{6,3409}$ = 21.1, P = <0.001
Tarsus length
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
1 2 3 4 5 6 7
Elevational band
(c)
$F_{6,5147}$ = 35.6, P = <0.001
Clutch size
0.55
0.50
0.45
0.40
0.35
0.30
0.25
1 2 3 4 5 6 7
Elevational band
(d)
$F_{6,2359}$ = 9.5, P = <0.001
Egg weight
0.20
0.15
0.10
0.05
0.00
-0.05
1 2 3 4 5 6 7
Elevational band
(e)
$F_{6,2000}$ = 7.6, P = <0.001
Incubation period
0.10
0.08
0.05
0.03
0.00
-0.03
1 2 3 4 5 6 7
Elevational band
(f)
$F_{6,582}$ = 2.5, P = 0.024
Age at first breeding
0.20
0.10
0.00
-0.10
1 2 3 4 5 6 7
Elevational band
(g)
$F_{6,2604}$ = 7.6, P = <0.001
Diet breadth
4.00
3.50
3.00
2.50
2.00
1 2 3 4 5 6 7
Elevational band
(h)
$F_{6,3069}$ = 16.0, P = <0.001
Habitat breadth
4.50
4.00
3.50
3.00
2.50
2.00
1 2 3 4 5 6 7
Elevational band

Figure 4.3 *(previous page)* Mean (±1SE) species-level avian trait values with respect to discrete elevational bands (UNEP-WCMC 2002) at the global scale. All species with their maximum elevation in the same band were pooled. Full ANOVA statistics reported. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Study variables log10 transformed except diet/habitat breadth (untransformed). (a) body weight (grams), (b) tarsus length (millimetres), (c) clutch size, (d) egg weight (grams), (e) incubation period (days), (f) age at first breeding (months), (g) diet breadth, (h) habitat breadth. Elevational bands: (1) = <300m, (2) = ≥300 & <1000m, (3) = ≥1000 & <1500m, (4) = ≥1500 & <2500m, (5) = ≥2500 & <3500m, (6) = ≥3500 & <4500m, (7) ≥4500m.

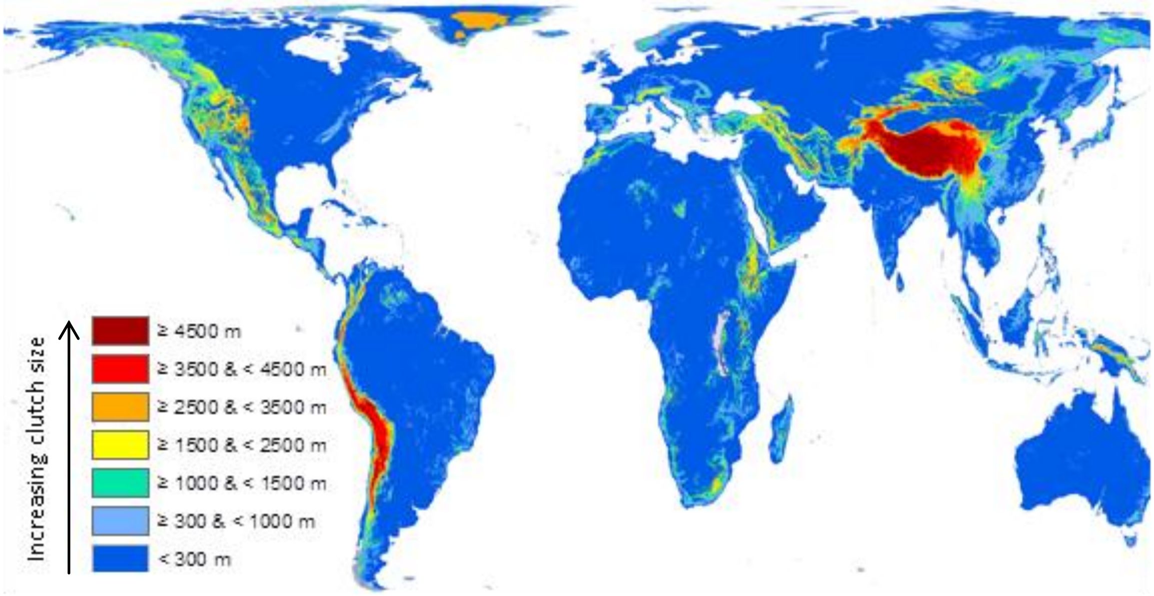


Figure 4.4 Global variation in species-level avian clutch size ($\log_{10}$ transformed) with respect to discrete elevational bands (UNEP-WCMC 2002). All species with their maximum elevational limit in the same band were pooled to obtain mean clutch size for each elevational band. Mean clutch size: (<300m) n = 92, $\bar{x}$ = 0.28; (≥300 & <1000m) n = 533, $\bar{x}$ = 0.39; (≥1000 & <1500m) n = 796, $\bar{x}$ = 0.40; (≥1500 & <2500m) n = 1947, $\bar{x}$ = 0.43; (≥2500 & <3500m) n = 1083, $\bar{x}$ = 0.46; (≥3500 & <4500m) n = 490, $\bar{x}$ = 0.48; (≥4500m) n = 203, $\bar{x}$ = 0.52. ANOVA statistics: $F_{6,5147}$ = 35.6, P = <0.001. Map produced in ArcMap version 10.0 (ESRI 2011), using a Berhmann equal-area projection and the freely downloadable UNEP-WCMC (2002) 'Mountains of the World' raster dataset (http://www.unep-wcmc.org/mountains-and-tree-cover-in-mountain-regions-2002_724.html).

The main patterns (i.e. reproduction versus development) also remained robust when controlling for the effects of phylogeny (Table A4.4b,c). In other words, across all units and subsets studied, strong evidence was found for bird species with higher elevational midpoints and higher maximum elevations to possess traits consistent with a fast life history, and vice versa. Consequently, the null hypothesis that no relationship exists between variation in these traits and both elevational midpoint and maximum elevation can be conclusively rejected.

Concerning adult body weight variation with respect to elevational distribution, no overarching evidence was found for an elevational equivalent of the classic Bergmann's Rule (1847), which predicts increasing body size towards higher (i.e. colder) elevations – in fact, a predominantly negative trend was found instead. Although a few studies have found supporting evidence for Bergmann's rule with respect to elevation (e.g. Blackburn & Ruggiero 2001; Altshuler *et al.* 2004), body weight is a complex trait to study in terms of large-scale biogeography. Contradictory relationships with respect to elevation have been found for different groups of birds (e.g. Kennedy *et al.* 2012), and ambiguous trends found across taxa (Section 2.1.4). In fact, Blackburn & Ruggiero (2001) reported that elevation explained only a few percent of the variation in body weight of Andean passerines, with just under a third of all genera studied showing a negative relationship between body weight and elevational midpoint – counter to their expectation, but mirroring the results in this study both at the global scale and for breeding birds of the Neotropics (Table 4.2).

Body weight has the largest sample size out of all the avian traits investigated. As such, the results at the global level are a robust representation of the general relationship between body weight and elevation in birds (Table 4.1a). At the family level, the significance of the negative relationship declined (Table 4.1b), which, apart from a reduced sample size, is likely due to the fact that species weights within some families can vary by orders of magnitude. For example, the species in this dataset for the Accipitridae family (hawks, eagles, Old World vultures) range in body size from just over 90g (*Gampsonyx swainsonii*: Pearl kite) up to 10kg (*Aegypius monachus*: Cinereous vulture). In fact, the negative relationship was also found to weaken when using PICs as the study unit (Table 4.1b,c), with a significant correlation found only with respect to elevational midpoint using the Hackett tree. This suggests that phylogenetic effects influence the species-level relationships found, and also imply that the relationship is taxonomically heterogeneous, and so complex to interpret.

Regarding biogeographic realms, the positive relationship found between body weight and elevational distribution within the Afrotropics is intriguing (Table 4.2) – why is it the only realm to display such a trend? When comparing mean body weight between species with elevational midpoints <1000m and species with elevational midpoints ≥2500m within individual realms, only the species within the Afrotropical realm have a much greater body weight at higher elevations than in the lowlands (Table A4.5). The lack of a significant relationship between body weight and elevation within the Palearctic realm implies that both small and large bodied species are found across the elevational gradient, similar to the recent findings of Kennedy *et al.* (2012) for bird species of the Himalayas. Clearly further investigation is required to reveal the underlying causes for such differences between biogeographic realms. For example, geographic variation in the history and extent of anthropogenic extinction filters may be relevant, especially those where extinctions are related to body size, e.g. hunting (Balmford 1996).

When looking at the global species-level relationships between body weight and elevational distribution using elevational bands, a distinct peak in the highest band (elevational midpoint method ≥3500m or maximum elevation method ≥4500m) was found (Figs. 4.2a,4.3a). This peak is predominantly due to a number of large-bodied species being endemic to high-elevation areas, including certain species of Galliformes (e.g. *Lophophorus lhuysii*: Chinese monal*, Crossoptilon harmani*: Tibetan-eared pheasant), Rallidae (e.g. *Fulica gigantean*: Giant coot; *Fulica cornuta*: Horned coot), Tinamiformes (e.g. *Tinamotis pentlandii*: Puna tinamou, *Nothoprocta ornata*: Ornate tinamou) and Anatidae (e.g. *Chloephaga melanoptera*: Andean goose). Nevertheless, it is important to note that some very small species possess a very high elevational midpoint, such as certain members of the Trochilidae family (e.g. *Oreotrochilus chimborazo*: Ecuadorian hillstar, *Chalcostigma olivaceum*: Olivaceous thornbill). It is therefore likely that the lower elevational bands are dominated by small-bodied passerines, which may also partially explain the general lack of a significant relationship found when controlling for phylogeny.

The three other morphological traits studied here (wing length, tarsus length and culmen length) were found to decline with increasing elevational midpoint and maximum elevation (Table 4.1a). This, in turn, provides potential evidence for Allen's rule (Allen 1877), which proposes that the appendages of endotherms are smaller, relative to body size, in colder climates (i.e. higher latitudes and elevations) in order to reduce thermoregulatory costs. Although a neglected ecogeographic rule (Section 2.1.5), it has been studied for birds previously (e.g. Symonds & Tattersall 2010). For approximately 200 species, they found a strongly significant negative relationship between bill length and elevation, whereas support for Allen's rule in leg morphology was weaker – mirroring the results of this larger-scale study at both the species and family level, and across biogeographic realms (Tables 4.1,4.2). The finding that tarsus length is less strongly related to elevation than culmen length, suggests that bird bills may be more susceptible to thermoregulatory constraints, and that other confounding selection pressures might be of greater influence for leg length. In fact, Kennedy *et al.* (2012) proposed that the positive relationship they found between elevation and tarsus length in Himalayan core Corvoidea (contradictory to Allen's rule) likely reflects adaptations to foraging for food. A possible physiological explanation lies in the fact that many birds can control the loss and retention of heat through their legs via a counter-current heat exchange system and shunt vessels (Steen & Steen 1965) – yet, no conclusive evidence has been found for such an arrangement in beaks (Symonds & Tattersall 2010). In addition, the frequency with which legs are covered by feathers may partially explain why they could be less important in heat exchange than the bill (Greenburg *et al.* 2012). Nevertheless, it is also possible that factors other than temperature are contributing to the variation in bill length with respect to elevation, e.g. food type, food size and phylogeny – across PICs, no significant relationship was found between culmen length and either maximum elevation or elevational midpoint (Table A4.4). Another interesting result was that the overall negative trend in tarsus length found via bivariate regression analysis was the opposite of that found with respect to elevational bands ordered by both elevational midpoint and maximum elevation (Figs. 4.2b,4.3b). In addition, across PICs, a negative trend between elevational midpoint and tarsus length was found using the Hackett tree, but not with the Ericson tree or with respect to maximum elevation (Table A4.4b,c). Once again, this highlights the complex relationship between leg length variation and elevation, which needs further investigation.

Interpreting spatial patterns in wing length is problematic (Section 2.1.5). For example, wing length has been advocated and used as a proxy of body size (e.g. Gosler *et al.* 1998), creating a conflict between the predictions of Bergmann's rule and Allen's rule (see Salewski *et al.* 2010). Across species, the only significant contradictory relationship to the general pattern found was a positive relationship between wing length and maximum elevation for Australasian species (Table 4.2). Such a trend cannot simply be explained as occurring due to an increase in body size with elevation, as in fact the opposite trend was found. This relationship needs to be further investigated in the future by incorporating divergent selection pressures as potential explanatory variables, including: flight ability, migratory behaviour, microhabitat selection and foraging ecology. Also, across PICs at the global scale, the relationship is not clear, with both negative and positive trends identified with respect to elevation depending on the phylogenetic tree used (Table A4.4c).

An elevational equivalent of Lack's rule (Lack 1947) – the tendency for clutch size to increase with latitude – was clearly evident across species, families and PICs. Clutch size, which is central to avian reproductive effort, is one of the best recorded animal life-history traits. Consequently its spatial variation, although biased with respect to latitude, has been extensively studied – including at the global-scale (Jetz *et al.* 2008a). In their study, Jetz *et al.* (2008a) used a grid-cell approach to investigate and map clutch size variation at the two-dimensional geographic level. The map produced here (Fig. 4.4) uses species-level data and provides additional information, by enabling visualisation of clutch size variation in the third-dimension, i.e. elevation. As with body weight, the sample size for clutch size in this study is large and therefore the positive relationship found is likely to be an accurate representation of the global trend. This finding, in combination with the robust and consistent positive trend in annual fecundity with increasing elevation, provides convincing evidence for an overall increase in annual reproductive output with elevation. The trade-off between clutch size and egg weight has long been known and widely discussed (e.g. Lack 1967; Blackburn 1991), and such a trade-off was also found in these results, across species and families – as reproductive output (clutch size and annual fecundity) increases with elevation, egg weight decreases with elevation. However, it should be highlighted that when controlling for phylogenetic non-independence, egg weight was instead found to be unrelated to both maximum elevation and elevational midpoint (Table A4.4b,c). Egg weight is highly positively correlated with body weight (Table 3.2), which, as discussed above, was found to be only weakly negatively related to elevation, across PICs, and could partially explain this finding.

The trade-off between avian fecundity and survival found in previous avian studies with respect to elevation (Section 2.1.6), has typically been attributed to greater environmental harshness/variability at higher elevations, which in turn constrains the reproductive output of high-elevation birds, such that they have reduced fecundity, but consequently allocate more energy into each offspring (Badyaev & Ghalambor 2001). Conversely, this study finds evidence for high-elevation bird species possessing faster life histories than low-elevation species. In fact, the relationships identified closely mirror those found in latitudinal studies (Section 2.1.6), where considerable evidence exists for tropical species having slower life histories compared to temperate species (e.g. Russell *et al.* 2004; Møller 2007; Wiersma *et al.* 2007; McNamara *et al.* 2008; Jetz *et al*. 2008, however, see Geffen & Yom-Tov 2000). Both tropical and lowland regions experience less pronounced seasonality and more stable temperature regimes than temperate and high-elevation regions (Janzen 1967; MacArthur 1972; Ghalambor 2006). It is therefore possible that variation in life-history strategies for bird species along elevational gradients can potentially be explained, in part, by similar processes applied to life-history variation along latitudinal gradients. For instance, the classic life-history theory of Ashmole (1963) proposed that a high level of seasonality in resources in temperate regions brings about high winter adult mortality among birds. This in turn reduces population densities, resulting in increased individual resource availability during the short but highly productive growing/breeding season, consequently favouring the evolution of higher reproductive rates. This hypothesis is supported by a number of empirical and simulated studies (e.g. Ricklefs 1980; Jetz *et al.* 2008a; McNamara *et al.* 2008; Griebeler *et al.* 2010). Finally, it is important to note that, across PICs, both the overall conflicting positive relationship between age at first breeding and elevation, and lack of a negative relationship between adult survival and elevation, are likely due to small sample sizes.

4.5.2 Life history variation with elevational range

As with both elevational midpoint and maximum elevation, evidence was found for bird species with larger elevational ranges to possess traits consistent with a fast life history, and vice versa – across species, families, phylogenetically independent contrasts, and within individual biogeographic realms. Consequently, the null hypothesis that no relationship exists between variation in these traits and elevational range can be convincingly rejected.

Research on life-history variation with respect to elevational range, across taxa, is conspicuously scarce in comparison to studies investigating life-history relationships with geographical range, and are even limited in comparison to the small number of studies concerning trait variation in relation to elevational gradients (Sections 2.1.4–2.1.7). Focusing on the traits included in this research, only body weight and its relationship with elevational range has been analysed in previous work (e.g. Blackburn & Ruggiero 2001; McCain 2006), with no significant trends found for Andean passerines or Costa Rican rodents respectively. Although this contradicts with the overall negative relationship I found at the global level across species, it mirrors the non-significant relationship identified here for species within the Neotropical realm and across families, i.e. small and large elevational ranges occur across all body sizes. Interestingly, although utilising a grid-cell approach and deriving elevational range (a proxy for habitat heterogeneity) from digital elevation models, Olson *et al.* (2009) found large body size to be related to low elevational range across bird species globally, supporting the results of this study. Based on geographical range size patterns, confusion has existed over the interspecific relationship between range size and body size, with positive, negative, triangular and non-significant trends found (Section 2.1.4). Laube *et al.* (2013) suggest that a potential reason for the complex patterns observed between body size and range size might be the heterogeneity in mechanisms by which body size affects range size. It is interesting that within the Afrotropical realm, the inconsistent positive association between body weight and elevational midpoint and maximum elevation was also found for elevational range. This is likely to be partly due to the high intercorrelation between the three measures of elevational distribution. When controlling for the potential effects of phylogenetic relatedness at the global scale, the relationship between all four morphological traits and elevational range were found to flip in direction compared to that observed across species, i.e. morphological measures were instead found to increase in size with increasing elevational range (Table A4.4a). The general inconsistent relationships found between morphology and elevational distribution in both this study and others, and for studies concerning geographical range size, limits the certainty of any potential interpretations made.

For the remaining life-history traits investigated in this study with respect to elevational range, no previous published research exists with which to compare. However, the findings do seem to mirror those relating to geographical range (Section 2.1.6). To summarise, species with larger geographical ranges have been shown, in taxonomically and geographically constrained studies, to have life-history traits associated with higher rates of population growth, larger population sizes and higher densities, including: larger clutches, higher annual fecundity, eggs of smaller mass, shorter incubation periods and fledging times, earlier age at first breeding, and lower adult survival (e.g. Gaston & Blackburn 1996a; Duncan *et al.* 1999; Laube *et al.* 2013). Prior to this study, next to nothing was known about whether or not trait patterns with respect to elevational range mirror those documented for geographical ranges. The next step in terms of future research is to investigate and compare the underlying intrinsic and extrinsic drivers of such patterns.

4.5.3 Niche breadth variation with elevational distribution

Up until this study, no published research could be found investigating niche-breadth variation with respect to elevation in birds (Section 2.1.6). However, the consistent finding that niche breadth (diet and habitat) increases with both elevational midpoint and maximum elevation provides some evidence of an avian elevational equivalent of the latitude-niche breadth hypothesis (MacArthur 1972, see also Section 2.1.6). In brief, this theory predicts more climatically stable and less seasonal regions (i.e. low latitudes or, in this case, low elevations) to allow for narrower species tolerances and so specialisation.

Across species globally, the positive trend between niche breadth and maximum elevation found when conducting bivariate regressions was also found with respect to comparing discrete maximum elevational bands (Figs. 4.3g,h). However, when diet breadth variation was investigated using discrete elevational midpoint bands, no significant relationship was apparent (Fig. 4.2g). This could be due to the uneven sample sizes that occur across the elevational bands (Fig. A4.1a), or by the loss of data variation as a consequence of taking the mean diet breadth value per band, which results in only six data points. The unimodal relationship found between habitat breadth and elevational midpoint bands (Fig. 4.2h) differs to the positive relationship identified via regression analysis, and implies that habitat breadth is in fact greatest at mid-elevations and lowest at both low elevations and high elevations. This observation could in part be explained by geometric constraints, as land area declines with increasing elevation (Fig. 1.3). However, if geometric constraints were to fully explain this trend, then low-elevation species would have the largest niche-breadth due to greater land area availability. Therefore, perhaps a combination of both geometric constraints and the latitude-niche breadth hypothesis (applied to elevation) could be driving elevational variation in avian niche breadth. As with both species and families, niche breadth was found to broaden with increasing maximum elevation across PICs (Table A4.4b), implying that, independent of phylogeny, species with high physiological tolerances have a broad niche breadth. However, elevational midpoint was found to be unrelated to variation in habitat breadth, and either positively (Hackett tree) or negatively (Ericson tree) related to diet breadth (Table A4.4c). This in turn suggests that further phylogenetic work concerning elevational variation in niche breadth is required.

In contrast to geographical range, no studies could be found explicitly investigating niche breadth variation with elevational range, for any taxa (Section 2.1.6). However, niche breadth was consistently found to be positively correlated with elevational range, with and without controlling for phylogeny, mirroring the relationships identified in previous avian studies with respect to geographical range (e.g. Hurlbert & White 2007; Carrascal *et al.* 2008; Laube *et al.* 2013). This makes intuitive sense, as species with broad (elevational) ranges are likely to experience a wider range of environmental conditions. It is important to note that avian range size (both geographical and elevational) is in itself considered to be, and has been used as, a measure of specialisation (e.g. with respect to elevational range: Badyaev & Ghalambor 1998; Bonier *et al.* 2007; Tobias & Seddon 2009). One of the main justifications for this is that a species' range can provide a reliable index of environmental tolerance, because variation in environmental conditions increases with latitudinal and elevational distributions (Bonier *et al.* 2007).

The finding, across both species and families, that diet breadth is consistently more strongly correlated with elevational distribution than habitat breadth is an interesting result. Perhaps the underlying drivers of niche breadth variation with respect to geographical range and elevational range differ considerably. However, rather than there being an actual ecological reason for the differences in relationship strength found, it may well be that the different methodologies used to measure diet and habitat breadth have an influence. For instance, the definition used to measure diet breadth in this study possesses fewer categories and is less ambiguous than that used for habitat breadth (Section 3.3.3). In fact, caution is needed in general when attempting to meaningfully compare studies that explore spatial variation in niche breadth, as various definitions are used – some more complex, detailed and/or accurate than others. It is important to note that some studies investigating diet and habitat breadth with geographical range find the opposite pattern, i.e. diet breadth varies less with range size than habitat breadth (e.g. Laube *et al.* 2013). They attribute this to the fact that different food sources can occur side by side in the same site, while habitat types cannot. This observation actually mirrors that found in this study with respect to niche breadth and elevational range, across PICs (Table A4.4a).

It is not immediately clear why the Palearctic is the only biogeographic realm to not display a significant relationship between habitat breadth and all three measures of elevational distribution (Table 4.2). Inspection of the frequency distributions of habitat breadth within each biogeographic realm shows that they are all positively skewed, i.e. there are more specialised species than generalists (as is also the case across species globally; Belmaker *et al.* 2011). Clearly both habitat specialists and generalists are found across the elevational gradient in the Palearctic, with elevational distributions varying widely from approximately sea level up to 5000m. However, there also appears to be a higher proportion of habitat specialists occurring at higher elevations compared to other realms, which is likely to be causing the lack of a relationship to a certain degree.

4.5.4 Conclusions

For birds at the global scale, this study consistently found reproduction (specifically clutch size and annual fecundity) to be positively related and development (specifically incubation period and fledging time) to be negatively related to three different measures of elevational distribution (range, maximum and midpoint) – across species, families and PICs. However, when comparing the outputs between species and PICs for certain traits (predominantly morphological), conflicting trends with respect to elevational distribution emerged. At present, it is difficult to assess whether or not these differences are due to confounding issues of phylogenetic non-independence, because opposing results were also found to occur depending on the particular phylogenetic tree used (i.e. Ericson versus Hackett tree). For example, variation in both wing length and tarsus length with respect to elevational midpoint was significantly positive in direction using the Ericson tree to derive PICs from, but significantly negative when using the Hackett tree. Future studies would therefore potentially benefit by comparing the results from more trees and phylogenies (e.g. Sibley & Ahlquist 1990), utilising model averaging techniques, and analysing PICs at the family level. Nevertheless, species are the units of conservation, and the fact that the results were also found to hold at the family level provides reassurance that the species-level patterns are robust.

Focusing on trait relationships with measures of elevational distribution in a bivariate framework enables sample sizes to be maximised, and promotes clarity in the identified trends. However, it does not enable one to disentangle the relative influences and interacting effects of elevational distribution on traits from those of broad geographical factors, namely geographical range and latitude, which are known to influence avian life history and ecology (Sections 2.1.4–2.1.7). Part of Chapter 5 of this thesis addresses this methodological gap by investigating trait variation in a multivariate spatial analysis.

The repeatability of the elevational distribution and trait correlations for species within individual biogeographic realms provides considerable assurance that the relationships observed at the global scale reflect true, underlying patterns. However, the consistency in the results across biogeographic realms may have been inflated through the overlap in species composition, coupled with the use of the same trait data for those species common to more than one realm. Part of Chapter 6 of this thesis addresses the potential issue of overlapping species (i.e. wide-ranging generalists), by investigating such relationships independently for both realm endemics and realm non-endemics.

It is important to question how representative the findings from this study are with respect to other taxonomic groups. For example, are the strong and consistent relationships found for birds, a highly mobile taxa, a general phenomenon characteristic of less-mobile animal groups, or are the findings peculiar to birds? To attempt to answer this question, it would be both necessary and worthwhile to expand this analysis to other groups of organisms for which good data on traits and distributions exist, e.g. mammals. However, taxa-wide, elevational distribution data is scarcer and more dispersed than geographical range data. Nevertheless, the multi-disciplinary field of bioinformatics is developing rapidly, which has the potential to greatly aid incorporating existing elevational data into centralised, digitised and open-access trait databases.

Statistical relationships between elevational distribution and traits provide little information about underlying drivers, such as climate, productivity and biotic interactions (e.g. predation and competition). There is a strong call for large-scale ecological studies to move away from identifying patterns and towards describing processes (Beck *et al.* 2012). This study is the first to investigate global patterns in trait variation with respect to elevational distribution for an entire class. However, this research must be expanded upon in the near future, by focusing on explaining the elevational patterns that I have found – for example, as has been done by Olson *et al.* (2009) with respect to global geographical variation in avian body size.

The finding in this study that fast life histories are dominant at high elevations and across broad elevational ranges, may help explain the results of global-scale studies that, using a grid-cell approach, have found avian species richness hotspots to be predominantly located in tropical mountainous regions (e.g. Orme *et al.* 2005; Davies *et al*. 2007). This is because of the theory that fast life-history traits are the 'engine' for high speciation rates in the tropics (see Cardillo 2002). However, such a theory requires investigation of the following three questions (among others):

1) Is there a latitudinal gradient in speciation/diversification rates that mirrors the latitudinal diversity gradient?
2) Are speciation/diversification rates greatest in mountainous regions, and do rates vary with elevation?

3) Are fast life-history traits linked to high species richness/levels of speciation?

It is beyond the scope of this discussion to go into great detail concerning the above three questions, however, the literature is extensive and often conflicting, and a brief overview is subsequently provided.

Firstly, the ‘diversification rate hypothesis’ for the origin of the latitudinal diversity gradient, proposes that tropical regions diversify faster due to higher rates of speciation (for a detailed review, see Mittelbach *et al.* 2007). Overall, there is mixed evidence for speciation and diversification rates being greater at lower (i.e. tropical) latitudes. Focusing on birds, analyses based on the Sibley & Ahlquist (1990) ‘tapestry’ phylogeny provide evidence for the hypothesis (e.g. Cardillo 1999; Cardillo *et al.* 2005b; Ricklefs 2006), whereas Weir & Schluter (2007) found the opposite pattern. A recent study by Jetz *et al.* (2012), using the first set of complete phylogenies of extant birds, found no latitudinal gradient in the diversification rates of birds (see also Jansson *et al.* 2013). Jetz *et al.* (2012) imply that their results instead promote the ‘time and area hypothesis’ for the origin of the latitudinal diversity gradient (for a detailed review, see Mittelbach *et al.* 2007).

Secondly, regarding speciation with respect to mountainous regions and elevational distribution, a number of studies (predominantly on amphibians) have investigated the role of mountains and elevational/climatic zonation in driving latitudinal gradients in diversity (e.g. Kozak & Wiens 2007; Hua & Wiens 2010; Cadena *et al.* 2012). As summarised by Cadena *et al.* (2012), a possible explanation for biodiversity hotspots being located in montane regions, especially in the tropics, is that the narrow thermal tolerances of tropical species and greater climatic stratification of tropical mountains create more opportunities for climate associated speciation (allopatric or parapatric) in the tropics relative to the temperate zone. This theory is founded on Janzen’s (1967) hypothesis of ‘*why mountain passes are higher in the tropics*’. However, taxon-specific studies to date have obtained different results regarding the role of climate in speciation in tropical versus temperate areas, and the relative importance of niche conservatism and niche divergence (discussed in Hua & Wiens 2010), although see Cadena *et al.* (2012) for a recent study across New World vertebrates. Comparatively few studies could be found investigating potential differences in the timing and rates of diversification along elevational gradients, and they are geographically and taxonomically biased towards the Neotropics and amphibians, respectively (e.g. Smith *et al.* 2007; Wiens *et al.* 2007). However, Weir (2006) did find evidence for higher diversification rates in higher elevation groups of Neotropical birds. Even fewer studies have then tried to relate their findings to elevational patterns of species richness (although see Smith *et al.* 2007). As discussed in Section 1.3, patterns of elevational diversity are varied (for birds, see McCain 2009a) and not directly analogous to the pervasive latitudinal diversity gradient. This in turn complicates and potentially precludes attempts to find any general, large-scale mechanisms between elevational patterns of speciation and elevational gradients of species richness.

Thirdly, and finally, a number of studies have investigated correlates of species richness among taxa. For example, Owens *et al.* (1999) found no support for the hypotheses that high species richness is correlated with small body size and fast life history in birds. Instead they found high avian species diversity to be positively associated with traits including both diet and habitat breadth. Conversely, for mammals, Isaac *et al.* (2005) found strong support for the life-history model of diversification, suggesting that this result can be explained by taxa with fast life histories being more adaptable in the face of harsh and changing environments, due to high rates of evolution and population growth. Related to the findings of Owens *et al.* (1999), at the global scale, avian assemblage species richness has been shown to increase with both diet and habitat specialisation (Belmaker *et al.* 2012). Increased specialisation has been hypothesised to facilitate local coexistence and thus high species richness, and has been put forward as a key driver of the decline in diversity with latitude (MacArthur 1972; references within Belmaker *et al.* 2012). In fact, Belmaker *et al.* (2012) found niche specialisation to be highest at low latitudes, with specialisation also noticeably prevalent in key mountainous regions. Latitudinal variation among species in life-history traits (Section 2.1.6) is often suggested to contribute to high tropical species richness (See Cardillo 2002). However, Cardillo (2002) importantly state that establishing an association between life-history traits and latitude (or in this study, elevation) does not prove, but is a necessary prerequisite for, a link between these traits and spatial diversity gradients.

The inconsistent findings and interpretations from such studies to date, along with current knowledge gaps, will motivate further work in this field for some time to come. However, in order to better understand the spatial distribution of species diversity (particularly within mountainous regions), future work is warranted that explicitly combines theory and research on the biogeography of speciation, extinction and diversification rates (from both a latitudinal and elevational perspective) with that of trait biogeography.

To conclude, quantifying global-scale spatial patterns in life-history and ecological traits, and underlying mechanisms, is an important goal for ecologists. Not only for developing increased understanding of species' life-history and ecological strategies, but also in terms of the current concern about the present and future impacts of anthropogenic activities on global biodiversity. Specifically, the need to understand the creation and maintenance of such patterns is of urgency if we are to effectively and efficiently manage the effects of global anthropogenic environmental change on biodiversity.

4.6 Appendix: Supplementary figures and tables

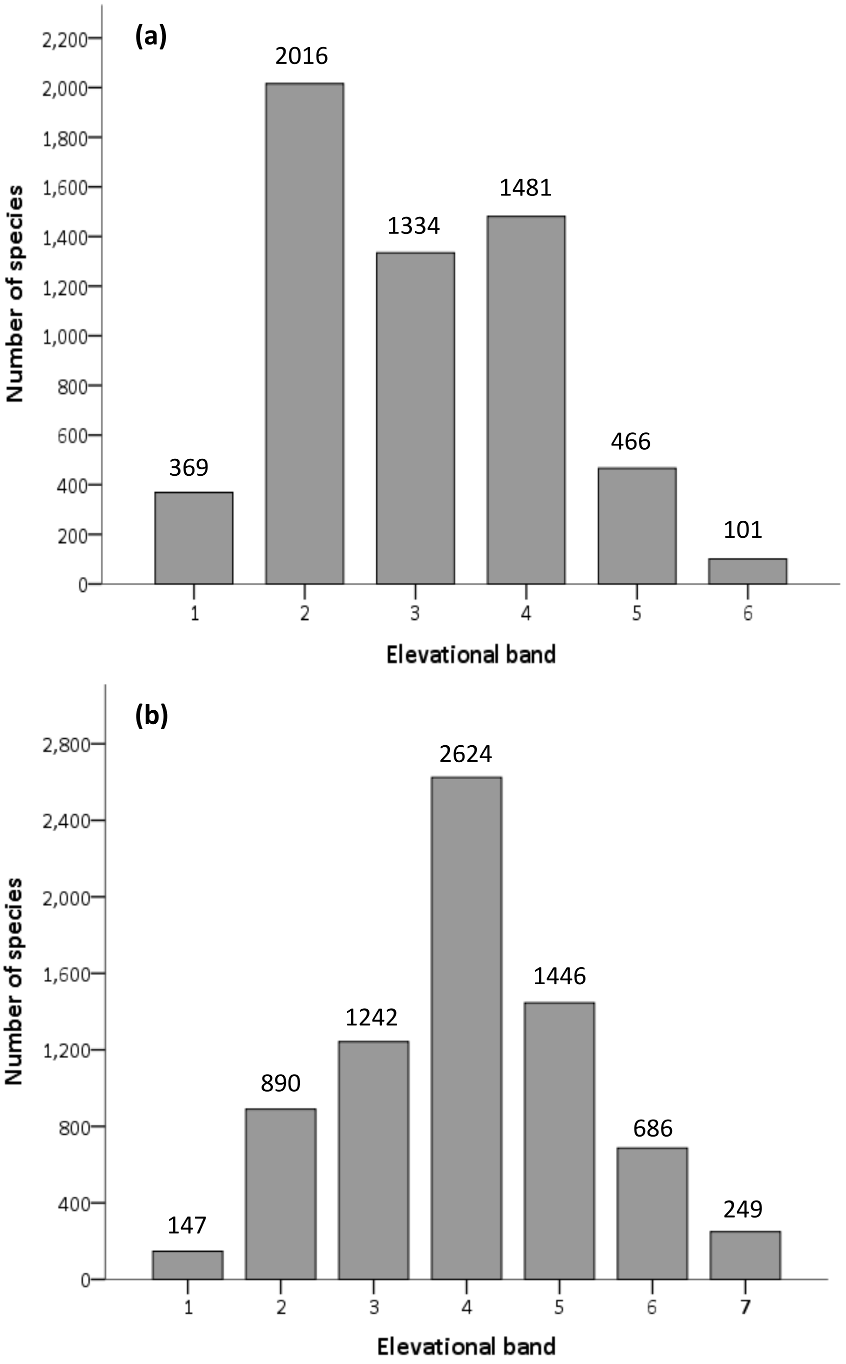


Figure A4.1 Number of bird species in the global dataset with (a) elevational midpoint data (total = 5767 species), and (b) maximum elevation data (total = 7284 species) occurring within discrete elevational bands (UNEP-WCMC 2002). Elevational bands: (a) elevational midpoint method – 1) = <300m, 2) = ≥300 & <1000m, 3) = ≥1000 & <1500m, 4) = ≥1500 & <2500m, 5) = ≥2500 & <3500m, 6) = ≥3500m; (b) maximum elevation method – 1) = <300m, 2) = ≥300 & <1000m, 3) = ≥1000 & <1500m, 4) = ≥1500 & <2500m, 5) = ≥2500 & <3500m, 6) = ≥3500 & <4500m, 7) ≥4500m.

Table A4.1 Pearson correlation coefficients (*r*) between avian traits and elevational range for species-level relationships within biogeographic realms.

	Af		**Au**		**IM**		**Na**		**Nt**		**Oc**		**Pa**	
	n	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Morphological														
Body weight	908	0.11***	788	– 0.25***	771	– 0.25***	383	– 0.21***	2344	0.03	98	– 0.18	729	– 0.12**
Wing length	789	0.01	663	0.12**	516	0.02	227	– 0.23***	783	– 0.10**	75	– 0.01	502	– 0.18***
Tarsus length	767	– 0.13***	647	0.00	488	0.02	201	– 0.06	670	– 0.05	69	0.03	471	– 0.22***
Culmen length	734	– 0.31***	634	– 0.28***	463	– 0.28***	196	– 0.09	784	– 0.29***	62	– 0.18	441	– 0.28***
Reproduction														
Clutch size	789	0.21***	596	0.10**	655	0.07	375	0.37***	1526	0.28***	89	0.40***	679	0.10***
Annual fecundity	198	0.60***	308	0.57***	159	0.55***	253	0.67***	276	0.57***	61	0.55***	292	0.60***
Egg weight	355	– 0.15**	354	– 0.19***	374	– 0.32***	320	– 0.40***	637	– 0.09*	57	– 0.22	463	– 0.44***
Development														
Incubation period	392	– 0.36***	303	– 0.33***	246	– 0.30***	309	– 0.39***	526	– 0.44***	58	– 0.30*	353	– 0.44***
Fledging time	366	– 0.43***	274	– 0.30***	169	– 0.27***	273	– 0.31***	440	– 0.32***	53	– 0.30*	268	– 0.37***
Age first breeding	94	– 0.31**	104	– 0.47***	70	– 0.46***	169	– 0.70***	129	– 0.63***	36	– 0.67***	160	– 0.52***
Survival														
Adult survival	43	– 0.70***	39	– 0.58***	30	– 0.45*	94	– 0.62***	57	– 0.53***	23	– 0.58**	72	– 0.51***
Niche breadth														
Diet breadth	754	0.50***	203	0.54***	282	0.47***	122	0.48***	677	0.46***	51	0.42***	278	0.39***
Habitat breadth	803	0.33***	206	0.38***	317	0.25***	129	0.50***	821	0.37***	55	0.55***	302	0.04

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative elevational range used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). Biogeographic realms: Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001).

Table A4.2 Pearson correlation coefficients (*r*) between avian traits and maximum elevation for species-level relationships within biogeographic realms.

	Af		**Au**		**IM**		**Na**		**Nt**		**Oc**		**Pa**	
	n	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Morphological														
Body weight	1258	0.09**	933	– 0.28***	1084	– 0.23***	443	– 0.21***	2822	– 0.01	106	– 0.25**	987	– 0.05
Wing length	1114	0.01	765	0.09*	718	0.00	265	– 0.22***	907	– 0.11***	80	– 0.07	692	– 0.15***
Tarsus length	1087	– 0.11***	747	0.01	674	– 0.03	238	– 0.10	774	– 0.03	73	0.09	653	– 0.26***
Culmen length	1045	– 0.28***	736	– 0.26***	655	– 0.24***	233	– 0.08	895	– 0.27***	66	– 0.13	624	– 0.33***
Reproduction														
Clutch size	1080	0.16***	698	0.00	918	0.03	434	0.27***	1833	0.20***	96	0.34***	929	0.05
Annual fecundity	263	0.57***	339	0.56***	214	0.47***	285	0.65***	326	0.53***	65	0.46***	397	0.56***
Egg weight	504	– 0.16***	406	– 0.16**	511	– 0.31***	371	– 0.40***	775	– 0.14***	63	– 0.27*	631	– 0.41***
Development														
Incubation period	536	– 0.34***	336	– 0.32***	317	– 0.30***	355	– 0.38***	617	– 0.43***	62	– 0.32*	488	– 0.41***
Fledging time	505	– 0.42***	302	– 0.32***	223	– 0.31***	317	– 0.29***	525	– 0.27***	56	– 0.31*	383	– 0.39***
Age first breeding	118	– 0.32***	116	– 0.47***	83	– 0.45***	196	– 0.72***	146	– 0.62***	38	– 0.63***	205	– 0.57***
Survival														
Adult survival	57	– 0.62***	42	– 0.58***	34	– 0.47**	106	– 0.58***	66	– 0.54***	25	– 0.48*	89	– 0.47***
Niche breadth														
Diet breadth	1052	0.46***	220	0.48***	377	0.46***	142	0.43***	727	0.40***	53	0.39***	351	0.36***
Habitat breadth	1112	0.23***	228	0.32***	422	0.16***	149	0.44***	889	0.20***	57	0.48***	384	– 0.04

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative maximum elevation used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). Biogeographic realms: Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001).

Table A4.3 Pearson correlation coefficients (*r*) between avian traits and elevational midpoint for species-level relationships within biogeographic realms.

	Af		**Au**		**IM**		**Na**		**Nt**		**Oc**		**Pa**	
	n	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Morphological														
Body weight	908	0.11***	788	– 0.29***	771	– 0.26***	383	– 0.24***	2344	– 0.10***	98	– 0.28**	729	– 0.06
Wing length	789	– 0.08*	663	0.07	516	– 0.06	227	– 0.22***	783	– 0.14***	75	– 0.09	502	– 0.24***
Tarsus length	767	– 0.09*	647	0.06	488	0.02	201	– 0.07	670	– 0.02	69	0.11	471	– 0.22***
Culmen length	734	– 0.32***	634	– 0.23***	463	– 0.29***	196	– 0.11	784	– 0.33***	62	– 0.13	441	– 0.33***
Reproduction														
Clutch size	789	0.20***	596	– 0.02	655	0.07	375	0.33***	1526	0.20***	89	0.29**	679	0.09
Annual fecundity	198	0.60***	308	0.58***	159	0.56***	253	0.66***	276	0.52***	61	0.41***	292	0.61***
Egg weight	355	– 0.20***	354	– 0.14**	374	– 0.31***	320	– 0.40***	637	– 0.08*	57	– 0.27*	463	– 0.46***
Development														
Incubation period	392	– 0.34***	303	– 0.30***	246	– 0.34***	309	– 0.37***	526	– 0.40***	58	– 0.29*	353	– 0.47***
Fledging time	366	– 0.41***	274	– 0.29***	169	– 0.30***	273	– 0.29***	440	– 0.26***	53	– 0.28*	268	– 0.38***
Age first breeding	94	– 0.34***	104	– 0.47***	70	– 0.48***	169	– 0.72***	129	– 0.62***	36	– 0.59***	160	– 0.58***
Survival														
Adult survival	43	– 0.70***	39	– 0.59***	30	– 0.48**	94	– 0.58***	57	– 0.55***	23	– 0.43*	72	– 0.53***
Niche breadth														
Diet breadth	754	0.42***	203	0.49***	282	0.43***	122	0.42***	677	0.32***	51	0.36**	278	0.32***
Habitat breadth	803	0.16***	206	0.27***	317	0.15**	129	0.39***	821	0.09**	55	0.44***	302	– 0.08

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative elevational midpoint used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). Biogeographic realms: Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001).

Table A4.4 Pearson correlation coefficients (*r*) between avian traits and elevational distribution (a: elevational range, b: maximum elevation, c: elevational midpoint) at the global scale, across species and phylogenetically independent contrasts (PICs). PICs derived from two independent phylogenetic trees, using the Ericson *et al.* (2006) backbone or the Hackett *et al.* (2008) backbone.

(a) Elevational range	**Species**		**Ericson**		**Hackett**	
	n	*r*	*n*	*r*	*n*	*r*
Morphological						
Body weight	5017	−0.04**	5010	0.06***	5009	0.04**
Wing length	3182	−0.10***	3139	0.14***	3144	0.12***
Tarsus length	2925	−0.03	2892	0.15***	2892	0.04*
Culmen length	2929	−0.12***	2899	0.07***	2896	0.28***
Reproduction						
Clutch size	4049	0.23***	4034	0.11***	4019	0.15***
Annual fecundity	1068	0.38***	1065	0.26***	1067	0.15***
Egg weight	1855	−0.20***	1849	0.02	1836	−0.03
Development						
Incubation period	1642	−0.27***	1626	−0.17***	1638	−0.10***
Fledging time	1370	−0.26***	1366	−0.10***	1368	−0.08**
Age at first breeding	491	−0.42***	483	−0.03	477	0.15**
Survival						
Adult survival	220	−0.53***	216	−0.14*	216	−0.26***
Niche breadth						
Diet breadth	2098	0.16***	2057	0.22***	2082	0.21***
Habitat breadth	2497	0.32***	2473	0.36***	2468	0.41***

(b) Maximum elevation	**Species**		**Ericson**		**Hackett**	
	n	*r*	*n*	*r*	*n*	*r*
Morphological						
Body weight	6376	−0.07***	6364	0.01	6325	0.00
Wing length	4054	−0.11***	4039	0.15***	4046	0.14***
Tarsus length	3739	−0.03	3729	0.10***	3732	0.08***
Culmen length	3747	−0.15***	3743	0.03	3741	0.02
Reproduction						
Clutch size	5154	0.20***	5124	0.10***	5105	0.11***
Annual fecundity	1325	0.31***	1320	0.15***	1321	0.10***
Egg weight	2398	−0.17***	2379	0.00	2369	−0.01
Development						
Incubation period	2056	−0.24***	2032	−0.13***	2031	−0.16***
Fledging time	1745	−0.23***	1726	−0.08***	1724	−0.07**
Age at first breeding	595	−0.39***	586	0.25***	582	0.13**
Survival						
Adult survival	263	−0.49***	258	0.03	258	−0.13*
Niche breadth						
Diet breadth	2611	0.08***	2587	0.05**	2587	0.15***
Habitat breadth	3076	0.16***	3067	0.16***	3068	0.14***

Table A4.4 Continued.

(c) Elevational midpoint	Species		Ericson		Hackett	
	n	*r*	*n*	*r*	*n*	*r*
Morphological						
Body weight	5017	– 0.13***	4998	0.00	4999	– 0.04**
Wing length	3182	– 0.17***	3178	0.11***	3174	– 0.08***
Tarsus length	2925	– 0.04*	2921	0.12***	2921	– 0.04*
Culmen length	2929	– 0.20***	2926	0.00	2925	0.01
Reproduction						
Clutch size	4049	0.15***	4031	0.02	4007	0.04**
Annual fecundity	1068	0.32***	1063	0.08**	1058	0.05
Egg weight	1855	– 0.20***	1843	0.04	1831	0.04
Development						
Incubation period	1642	– 0.25***	1624	– 0.08***	1618	– 0.17***
Fledging time	1370	– 0.26***	1354	– 0.07**	1351	– 0.08**
Age at first breeding	491	– 0.43***	483	0.24***	476	0.03
Survival						
Adult survival	220	– 0.52***	216	0.00	215	– 0.10
Niche breadth						
Diet breadth	2098	0.02	2068	– 0.08***	2083	0.05*
Habitat breadth	2497	0.04	2482	0.04	2474	– 0.03

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). Trait values for both the species and PIC analyses are in their non-residual form.

Table A4.5 Number (*n*) and mean body weight of species with an elevational midpoint <1000m or ≥2500m across biogeographic realms (Olson *et al.* 2001).

	<1000m			≥2500m			t-test		
Realm	*n*	$\bar{x}$	$\bar{x}$ ($\log_{10}$)	*n*	$\bar{x}$	$\bar{x}$ ($\log_{10}$)	*t*	d.f.	*p*
Afrotropical	259	120.9	1.68	**42**	**395.9**	**1.90**	2.21	299	**0.03**
Australasia	458	**515.4**	**1.90**	**31**	68.1	1.62	2.21	487	**0.03**
Indo-Malay	297	**231.4**	**1.87**	**40**	117.5	1.47	3.74	335	**<0.001**
Nearctic	95	**413.5**	**1.91**	**20**	402.8	1.76	0.79	113	*NS*
Neotropical	1008	**177.5**	**1.57**	**281**	82.6	1.37	4.57	1287	**<0.001**
Oceania	42	**322.1**	**1.90**	**2**	28.7	1.44	0.87	42	*NS*
Palearctic	**118**	385.3	1.80	132	**447.2**	**1.83**	0.33	248	*NS*

$\bar{x}$ = mean raw body weight, $\bar{x}$ ($\log_{10}$) = mean $\log_{10}$ transformed body weight. Results of independent samples t-tests (using $\log_{10}$ transformed body weight) are reported (*t* = t-value, d.f. = degrees of freedom, *p* = significance level). Highest values (<1000m versus ≥2500m) and significant results are highlighted in bold.

CHAPTER FIVE

Global biogeography of elevational distribution, and multivariate spatial patterns of avian traits

5.1 Abstract

Mountains are proven hotspots of terrestrial species richness, but the reasons for this are poorly understood. One way to improve current understanding is to develop our limited knowledge concerning variation in life-history and ecological traits with respect to elevation. This was partly addressed in Chapter 4, utilising a bivariate global-scale approach. However, no large-scale studies to date have investigated how elevation influences variation in traits while controlling for known geographical covariates. Here, the biogeography of elevational distribution was first investigated, followed by a multivariate spatial assessment of the variation in a suite of morphological, life-history and ecological (specifically niche-breadth) traits – within an entire taxonomic class (Aves), using a global species-level dataset. Overall, elevational distribution (range, maximum and midpoint) was found to increase with both geographical range and raw mean latitude, and to a lesser extent with absolute mean latitude. Elevational range was also shown to be positively related to elevational midpoint. Both of these findings are discussed with respect to temperature/climatic variability, specialisation and geometric constraints. Finally, even when controlling for geographical range, latitude and body weight, elevational distribution was found to be a significant predictor of both life-history and niche-breadth. The findings from this study provide a vital platform for improving understanding of the underlying drivers of species' range distributions, trait variation, and in turn, known spatial gradients of species richness and the distribution of associated hotspots.

5.2 Introduction

As highlighted in Section 1.3, mountainous regions are proven hotspots of terrestrial species richness. Yet the reasons for this, along with the underlying drivers of elevational diversity gradients are poorly understood. One potential way in which to improve our current understanding is to develop our taxonomically and geographically limited knowledge concerning variation in life-history and ecological traits with respect to elevation (reviewed in Section 2.1). This was partly addressed in Chapter 4, utilising a bivariate global-scale approach. Avian elevational distribution (range, maximum and midpoint) was found to be positively associated with reproduction and niche breadth, whilst being negatively associated with morphology, growth and survival.

As concluded in Section 2.1.7, trait biogeography research has been biased towards both latitude and geographical range, with morphology, life history (hereafter collectively referred to as life history) and niche breadth all shown to vary markedly with respect to these planimetric covariates. There is therefore an inherent need for research investigating trait variation with respect to elevational distribution to simultaneously control for these additional spatial covariates, and at a large spatial scale. As stated by Ruggiero & Hawkins (2006), there is a significant loss of information when a multidimensional process is reduced to one dimension, which in turn can considerably affect the detection of patterns as well as have important implications with respect to their biological interpretation. However, only one previous study could be found. Via multiple regression analysis, Blackburn & Ruggiero (2001) examined the effects of elevation and latitude on the body size of Andean passerines. Incidentally, they found a significant effect of elevation on body mass when controlling for latitude, but no effect of latitude when controlling for elevation. No research to date could be found additionally controlling for geographical range or known trait covariates, at any scale, or across any taxa. Such an analysis would allow for conclusions to be drawn regarding the congruence of trait variation trends with respect to elevational distribution, geographical range and latitude. Although a few global-scale studies have investigated spatial variation in certain traits, they average species-typical trait values within equal-area grid cells, and do not explicitly control for known species' latitudinal or elevational limits (e.g. Jetz *et al.* 2008a; Olson *et al.* 2009).

Before investigating life-history and ecological trait variation with respect to elevational distribution in a multivariate spatial environment, it makes intuitive sense to first establish how species' elevational limits and ranges vary geographically. As with traits, spatial variation in range size is biased towards investigating Rapoport's rule (Rapoport 1982; Stevens 1989), i.e. a latitudinal increase in geographical range size (Section 2.2.1). Comparatively few studies have investigated elevational distribution with respect to latitude, elevation or geographical range (with none found examining all of these trends collectively), and are typically taxonomically and geographically restricted (reviewed in Sections 2.2.2–2.2.3). However, McCain (2009b) used 170 montane gradients (distributed worldwide) to investigate absolute latitudinal variation in elevational range for a variety of vertebrate taxa, finding strong evidence for species possessing smaller elevational range sizes in the tropics. McCain & Knight (2012) used a similar dataset and found weak support for the elevational Rapoport's rule (Stevens 1992), whereby elevational range increases with increasing elevation. No such global-scale studies could be found investigating the relationship between elevational range and geographical range, and no studies could be found examining variation in elevational distribution with respect to raw latitude. In other words, a global perspective of the spatial trends in elevational distribution is missing.

In this study, I addressed these important knowledge gaps, using birds as a model system. Utilising a global avian species-level dataset and a comparative approach, the biogeography of elevational distribution (range, maximum and midpoint) was investigated, followed by a multivariate spatial assessment of the avian life-history (morphological, reproductive, developmental, survival) and ecological (niche-breadth) traits studied in Chapter 4. Specifically, this chapter is split into two connected parts and aimed to answer the following questions:

1) How does elevational distribution vary with respect to geographical range, mean latitudinal position (absolute and raw) of geographical range, and elevation – across species at the global scale?
    a) Are relationships identified at the global species level maintained across families, for species within biogeographic realms, or across phylogenetically independent contrasts?
2) Controlling for body weight, geographical range and latitude, how do life-history and ecological traits vary with respect to elevational distribution – across species at the global scale?
    a) Are relationships identified at the global species level maintained across families or across phylogenetically independent contrasts?
    b) How do identified relationships with elevational distribution differ from those found using bivariate regression analysis (Chapter 4)?
    c) Do relationships identified for elevational range and elevational midpoint support those found for geographical range and absolute mean latitude, respectively?
    d) Do relationships identified for geographical range and latitude support the results of previous studies?

In relation to the above questions, this study tested two broad null hypotheses, namely: (1) no relationship exists between elevational distribution and either geographical range, mean latitudinal position (absolute and raw) of geographical range, or elevation, and (2) elevational distribution is not retained as a significant predictor of avian traits when controlling for body weight, geographical range and latitude. This research should be seen as a continuation and logical extension of that carried out in Chapter 4.

5.3 Materials and methods

The overall methodology and details on the materials used are described and justified in full in Chapter 3.

5.3.1 Study variables

To examine global spatial patterns of avian elevational distribution (range, maximum and midpoint), key species-typical geographical breeding range variables were selected. Namely, geographical range, and mean latitudinal location of geographical range (raw and absolute). To investigate multivariate distributional relationships of life history and ecology in birds at the global scale, the elevational and geographical distribution variables listed above were used, alongside the following species-typical traits, reflecting: (a) morphology (body weight, wing length, tarsus length, culmen length), (b) reproduction (clutch size, annual fecundity, egg weight), (c) development (incubation period, fledging time, age at first breeding), (d) survival (adult survival), and (e) niche breadth (diet breadth, habitat breadth). See Section 3.3 for a concise overview of each study variable. To better comply with the assumptions of normality, all study variables were $\log_{10}$ transformed prior to analysis, except adult survival which was arcsine transformed, and raw mean latitude, diet breadth and habitat breadth which were untransformed (Section 3.4).

5.3.2 Statistical analyses

Bivariate linear regressions: Reduced Major Axis (RMA) bivariate linear regressions were performed between each of the three measures of elevational distribution, and: (a) geographical range, (b) absolute mean latitude, and (c) raw mean latitude – at the global scale, firstly across species and then across families. To test for any regional similarities or differences in the global patterns found, bivariate regressions were also conducted for breeding bird species found within each of the biogeographic realms delimited by Olson *et al*. (2001): Nearctic, Palearctic, Neotropical, Afrotropical, Indo-Malay, Australasia and Oceania (excluding Antarctica due to small sample sizes). Finally, in order to account for variation in the degree of common phylogenetic association, the bivariate relationships were additionally assessed using phylogenetically independent contrasts (PICs) – see Section 3.5.3.

To investigate the elevational extension of Rapoport's rule (Stevens 1992; see discussion in Section 2.2.2) with respect to birds, RMA bivariate linear regressions were conducted between elevational range and elevational midpoint, across species, families and PICs at the global level, and for species breeding within each biogeographic realm.

Elevational and latitudinal bands: Mean species-level geographical breeding range variables (geographical range, absolute mean latitude and raw mean latitude) with respect to discrete elevational bands (UNEP-WCMC 2002) were derived, at the global level, using the protocol outlined in Section 4.3.2. One-way ANOVAs were performed to test for significant differences across elevational bands for each variable, along with associated post-hoc tests. Additionally, to further investigate the elevational extension of Rapoport's rule at the global scale, mean species-level elevational range was determined for and compared between discrete elevational bands (UNEP-WCMC 2002) via the midpoint method (outlined in Section 4.3.2).

A global analysis was also conducted to investigate latitudinal gradients of mean elevational distribution (range, maximum and midpoint) per 5˚ latitudinal bands. Specifically, species were placed in one of 22 latitudinal bands based on the raw mean latitudinal location of their geographical range. For each of the three measures of elevational distribution, a plot of the mean value of all species occurring in the same latitudinal band was produced, and a one-way ANOVA performed to identify significant differences across the latitudinal bands. For a breakdown of sample sizes within each latitudinal band, see Table A5.1.

Multiple regressions: Stepwise multiple regression models (α-to-enter/remove = 0.05) were performed across species and families at the global scale, with each avian life-history and niche-breadth trait (hereafter trait) as the dependent variable in turn. The same independent variables were entered into each model, namely: body weight, geographical range, absolute mean latitude and one measure of elevational distribution - elevational range, maximum elevation or elevational midpoint. Each measure of elevational distribution was entered as a predictor in separate models, due to them being autocorrelated – therefore, a total of three models were produced for each trait. Similarly, both measures of mean latitude of geographical range could not be entered into the same model as they are autocorrelated. The decision was made to enter absolute mean latitude as a predictor in all models rather than raw mean latitude – due to the comparative ease in interpreting outputs of the former.

Multiple regression models were additionally produced at the global scale across PICs (Section 3.5.3). Models were performed to ensure the maximum sample size possible for each group of traits. Consequently, body weight (morphology), clutch size (reproduction), incubation period (development), adult survival (survival) and habitat breadth (niche breadth) were entered as the independent variables.

The elevational Rapoport's rule was originally intended to be applied to species occurring within the same latitude (Stevens 1992). Therefore, at the global scale across species, two multiple regressions were performed to control for this. Specifically, elevational range was the dependent variable for both, and the predictors were: (a) elevational midpoint and raw mean latitude, or (b) elevational midpoint and absolute mean latitude.

5.4 Results

5.4.1 Relationships between elevational distribution, geographical range and latitude

Table 5.1 summarises the bivariate relationships identified between elevational distribution (range, maximum and midpoint) and (a) geographical range, (b) absolute mean latitude, and (c) raw mean latitude – at the species level (globally and within biogeographic realms), and across families at the global scale. Equivalent results across PICs at the global scale are presented in Table A5.2.

A consistent positive relationship was identified between geographical range and elevational range at the global scale across species, families and PICs, and for species within individual biogeographic realms. Geographical range was not as strongly positively correlated with maximum elevation and even less so with elevational midpoint, at all levels of analysis. The only non-significant relationships between geographical range and elevational distribution were found for species within the Neotropical realm with respect to maximum elevation, and for PICs (Ericson tree) with respect to elevational midpoint. A significant negative relationship between geographical range and elevational midpoint was identified for species within both the Neotropical and Palearctic realms.

Species possess a significantly larger elevational range with increasing absolute mean latitude (i.e. with increasing distance from the equator) at the global species level, within the Neotropical realm, and across PICs globally (Hackett tree). Conversely, a significant negative relationship was identified between elevational range and absolute mean latitude across PICs, using the Ericson tree. A significant positive relationship between absolute mean latitude and maximum elevation was found at the global species level, and within the Neotropical and Palearctic realms. Across PICs globally, maximum elevation was found to be either positively (Ericson tree) or negatively (Hackett tree) related to absolute mean latitude. No significant relationship was found between absolute mean latitude and elevational midpoint at the global species level, however, a significant positive relationship was found for species within the Palearctic realm and across PICs using the Ericson tree, and a negative relationship identified within the Afrotropical realm and across PICs using the Hackett tree. All other correlations between elevational distribution and absolute mean latitude, including those at the family level, were not-significant.

At the global scale, across species, families and PICs, all three measures of elevational distribution were found to increase with increasing raw mean latitude (i.e. from the Southern

Table 5.1 Pearson correlation coefficients (*r*) between avian geographical breeding range variables and elevational distribution for species-level (global and within biogeographic realms) and global family-level relationships. Abs. mean latitude = absolute mean latitude.

	Elevational range		**Maximum elevation**		**Elevational midpoint**	
	n	*r*	*n*	*r*	*n*	*r*
Global (species level)						
Geographical range	5655	0.43***	7158	0.20***	5655	0.07***
Abs. mean latitude	4609	0.12***	5887	0.09***	4609	0.02
Raw mean latitude	4609	0.25***	5887	0.23***	4609	0.19***
Afrotropical						
Geographical range	974	0.55***	1338	0.34***	974	0.17***
Abs. mean latitude	827	0.05	1150	– 0.02	827	– 0.12***
Raw mean latitude	827	0.18***	1150	0.19***	827	0.21***
Australasia						
Geographical range	957	0.45***	1145	0.32***	957	0.19***
Abs. mean latitude	803	0.06	960	0.00	803	– 0.07
Raw mean latitude	803	0.42***	960	0.39***	803	0.36***
Indo-Malay						
Geographical range	139	0.35***	140	0.25**	139	0.17*
Abs. mean latitude	137	– 0.16	138	– 0.13	137	– 0.12
Raw mean latitude	137	0.24**	138	0.27**	137	0.21*
Nearctic						
Geographical range	384	0.52***	444	0.41***	384	0.35***
Abs. mean latitude	375	– 0.07	432	– 0.04	375	– 0.05
Raw mean latitude	375	– 0.01	432	0.00	375	– 0.03
Neotropical						
Geographical range	2543	0.32***	3061	0.01	2543	– 0.13***
Abs. mean latitude	2007	0.12***	2426	0.06**	2007	0.00
Raw mean latitude	2007	0.13***	2426	0.11***	2007	0.09***
Oceanic						
Geographical range	112	0.63***	123	0.55***	112	0.48***
Abs. mean latitude	109	0.12	120	0.16	109	0.16
Raw mean latitude	109	0.38***	120	0.42***	109	0.43***
Palearctic						
Geographical range	781	0.33***	1054	0.07*	781	– 0.07*
Abs. mean latitude	718	0.05	979	0.10**	718	0.10**
Raw mean latitude	718	0.04	979	0.06	718	0.03
Global (family level)						
Geographical range	139	0.35***	139	0.25**	139	0.17*
Abs. mean latitude	137	– 0.16	138	– 0.13	137	– 0.12
Raw mean latitude	137	0.24**	138	0.27**	137	0.21*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. Study variables $\log_{10}$ transformed except raw mean latitude (untransformed). Biogeographic realms as delimited by Olson *et al.* (2001).

Hemisphere to the Northern Hemisphere). This relationship was maintained for species within all biogeographic realms, except the Nearctic and Palearctic.

Elevational bands (midpoint method): Both geographical range (Fig. 5.1a) and raw mean latitude (Fig. 5.1e) displayed a unimodal relationship with respect to increasing elevation. However, Tukey's post-hoc tests found raw mean latitude between elevational bands four and five, and five and six, to not differ significantly. Absolute mean latitude was instead found to display an increase with elevation (Fig. 5.1c), with the greatest mean value increase occurring between elevational band five (≥2500 & <3500m) and six (≥3500m). Within bands, Tukey's post-hoc tests found absolute mean latitude to differ significantly between elevational bands two and six, three and six, and four and six.

Elevational bands (maximum elevation method): Geographical range was found to increase with respect to increasing elevation, although this relationship plateaued at mid-elevations (Fig. 5.1b). Raw mean latitude steadily increased with increasing elevation (Fig. 5.1f). Absolute mean latitude also increased with increasing elevation, except for the lowest elevational band (<300m), where a noticeable peak was found (Fig. 5.1d). However, Tukey's post-hoc tests found absolute mean latitude within this lowest elevational band to only differ significantly to the mean value of elevational band seven.

Latitudinal bands: Elevational range (Fig. 5.2a), maximum elevation (Fig. 5.2b) and elevational midpoint (Fig. 5.2c) were all found to vary significantly with respect to discrete latitudinal bands. The overall trend shows an increase in all three measures of elevational distribution with increasing mean raw latitude, i.e. from the Southern Hemisphere to the Northern Hemisphere.

5.4.2 Elevational Rapoport's rule

Bivariate linear regressions revealed a strongly significant positive relationship between elevational range and elevational midpoint, at the species level (global and within all biogeographic realms) and global family level (Table 5.2). This relationship was also found to remain across PICs at the global scale (Ericson tree: n = 5714, r = 0.75, p = <0.001; Hackett tree: n = 5677, r = 0.80, p = <0.001). When breaking elevational range up into discrete elevational bands, mean elevational range was found to increase with increasing elevation up until species with an elevational midpoint ≥1500 and <2500m, whereby after this height it was found to steadily decline (Fig. 5.3). However, Tukey's post-hoc tests found mean elevational range between elevational bands three and five, three and six, and five and six to

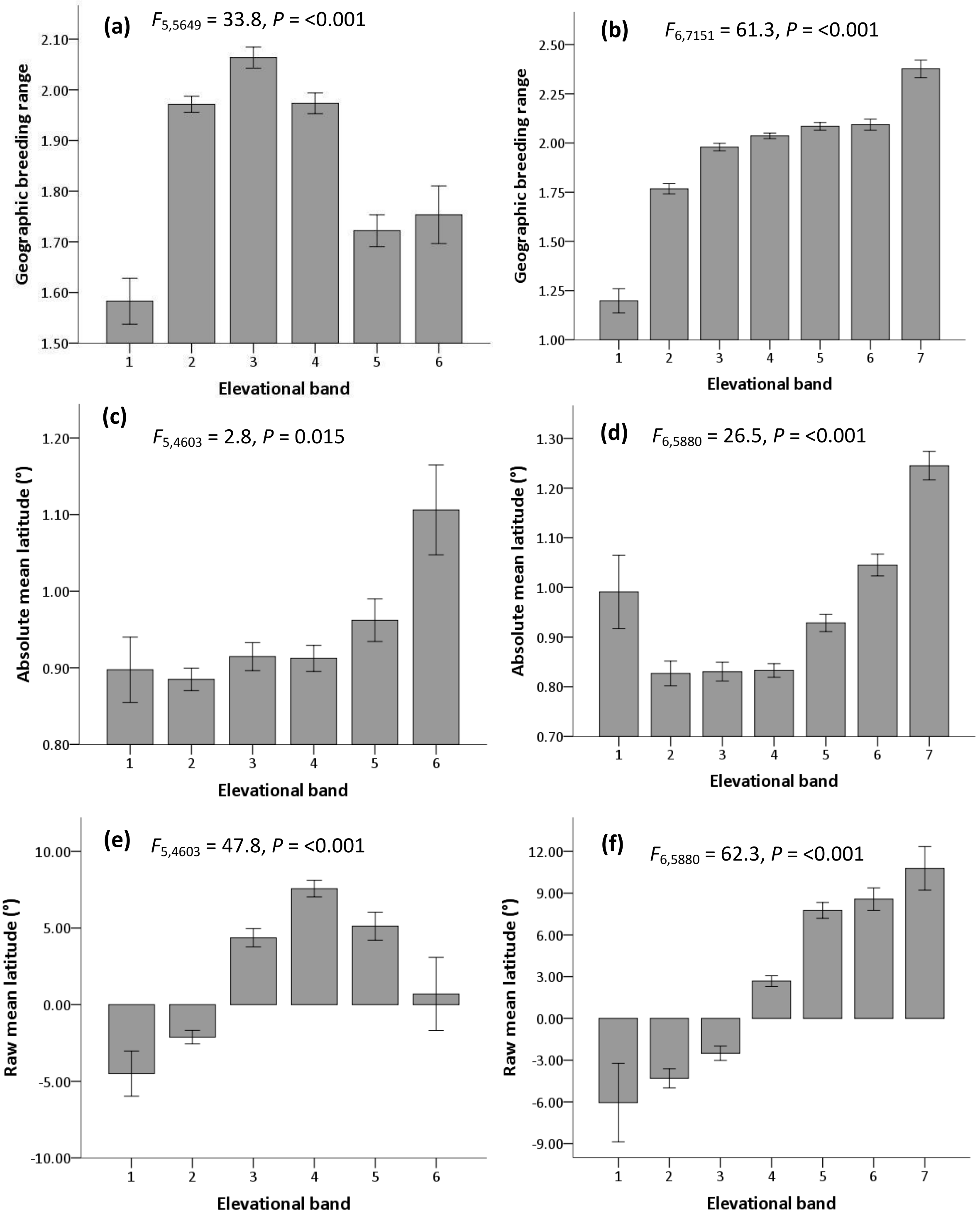


Figure 5.1 Mean (±1SE) species-level avian geographical breeding range values with respect to discrete elevational bands (UNEP-WCMC 2002) at the global scale. All species with elevational midpoint (a,c,e) or maximum elevation (b,d,f) in the same band were pooled. Full ANOVA statistics reported. Study variables $\log_{10}$ transformed except raw mean latitude (untransformed). (a,b) geographical range, (c,d) absolute mean latitude, (e,f) raw mean latitude. Elevational bands (elevational midpoint method): (1) = <300m, (2) = ≥300 & <1000m, (3) = ≥1000 & <1500m, (4) = ≥1500 & <2500m, (5) = ≥2500 & <3500m, (6) = ≥3500m. Elevational bands (maximum elevation method): (1) = <300m, (2) = ≥300 & <1000m, (3) = ≥1000 & <1500m, (4) = ≥1500 & <2500m, (5) = ≥2500 & <3500m, (6) = ≥3500 & <4500m, (7) ≥4500m.

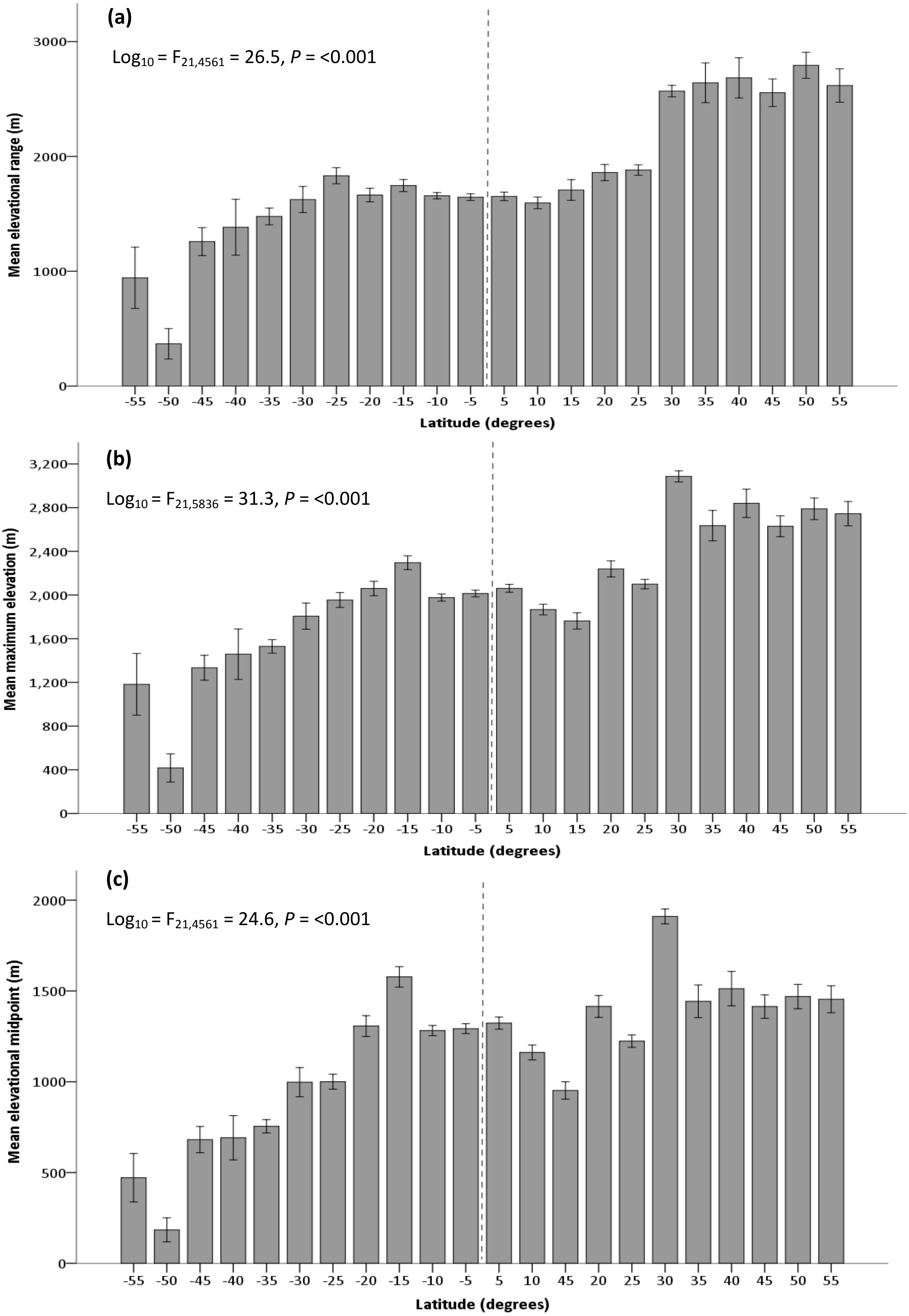


Figure 5.2 Latitudinal gradients of mean (±1SE) species-level avian elevational distribution per 5˚ latitudinal bands, at the global scale: (a) elevational range, (b) maximum elevation, (c) elevational midpoint. Vertical dashed line represents the equator. Full ANOVA statistics reported (derived from $\log_{10}$ transformed elevational distribution variables).

Table 5.2 Pearson correlation coefficients (*r*) between avian elevational range and elevational midpoint for species-level (global and within biogeographic realms) and global family-level relationships.

	n	*r*
Global (species level)	5767	0.72^{***}
Afrotropical	988	0.64^{***}
Australasia	973	0.81^{***}
Indo-Malay	139	0.92^{***}
Nearctic	386	0.87^{***}
Neotropical	2605	0.67^{***}
Oceanic	117	0.93^{***}
Palearctic	784	0.72^{***}
Global (family level)	139	0.92^{***}

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. Study variables $\log_{10}$ transformed. Biogeographic realms as delimited by Olson *et al.* (2001).

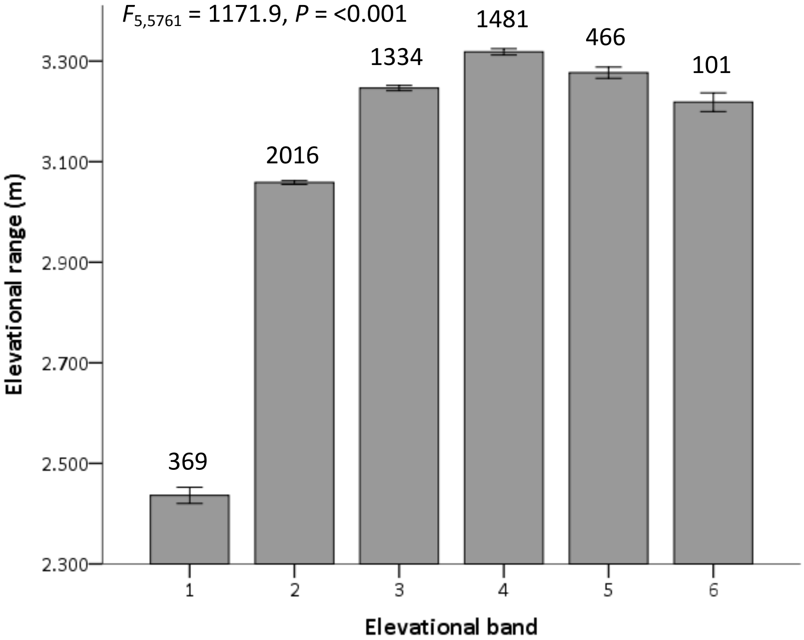


Figure 5.3 Mean (±1SE) species-level avian elevational range with respect to discrete elevational bands (UNEP-WCMC 2002), at the global scale. All species with their elevational midpoint in the same band were pooled. Full ANOVA statistics reported. Elevational range $\log_{10}$ transformed. Elevational bands: (1) = <300m, (2) = ≥300 & <1000m, (3) = ≥1000 & <1500m, (4) = ≥1500 & <2500m, (5) = ≥2500 & <3500m, (6) = ≥3500m. Sample sizes are provided at the top of each column.

not differ significantly. At the global scale across species, elevational midpoint remained a strongly significant ($^{***} = p < 0.001$) predictor of elevational range, when independently controlling for raw mean latitude ($F_{2,4606} = 2818.4^{***}$, $r^2 = 0.55$, β elevational midpoint =

0.71***, β latitude = 0.11***) and absolute mean latitude ($F_{2,4606}$ = 2799.5***, r^2 = 0.55, β elevational midpoint = 0.73***, β latitude = 0.10***).

5.4.3 Multiple regressions of avian traits

Morphological: At the species level (Table 5.3a), when the models are compared the variance explained was greatest for wing length (r^2 = 89–90%) and lowest for body weight (r^2 = 0.02–0.03%). Body weight was by far the strongest predictor of wing length, tarsus length and culmen length, with a positive effect on all three morphological traits. Elevational distribution was found to be a significant positive predictor of tarsus length, and a significant negative predictor of both culmen length and body weight. However, elevation was not retained as a significant predictor of wing length, with only a marginal positive relationship found with respect to maximum elevation. Geographical range had a significant positive effect on wing length and body weight, a significant negative effect on tarsus length, and no effect on culmen length (apart from a marginal positive relationship with respect to elevational range). Latitude (absolute mean latitude) was retained in all models, having a positive effect on wing length, tarsus length and body weight, and a negative effect on culmen length.

At the family level (Table 5.4a), body weight remained the dominant predictor for the remaining three morphological traits. Elevational distribution was retained as a positive predictor of tarsus length and a negative predictor of body weight, but was no longer retained as a negative predictor of culmen length. Geographical range was retained as a positive predictor of wing length and body weight. Latitude was dropped from all models.

Across PICs (Table A5.3), elevational distribution was retained as an overall positive predictor of body weight. Conversely, geographical range was found to have a significant negative relationship with body weight (Hackett tree). Body weight was shown to increase with increasing latitude, but only in the maximum elevation (Ericson tree) and elevational midpoint (both trees) models.

Reproductive: At the species level (Table 5.3b), variance explained was greatest for egg weight (r^2 = 95%) and lowest for clutch size (r^2 = 18–19%). The strongest predictors of clutch size were geographical range and latitude, with an increase in clutch size found with increasing geographical range and higher latitudes. A slight positive relationship between clutch size and body weight was shown, while clutch size was found to increase with all three measures of elevational distribution. Annual fecundity decreased with increasing body weight, but increased with increasing elevational distribution, geographical range and latitude. Conversely, egg weight was strongly positively related to body weight, and negatively related to both elevational distribution and geographical range, with no retention of latitude as a predictor.

Table 5.3 Global species-level distributional relationships of avian traits, revealed by stepwise multiple regression. Dependent variables grouped as: (a) morphological, (b) reproduction, (c) development, (d) survival, and (e) niche breadth. Independent variables entered into each model were body weight, geographical range, absolute mean latitude and one measure of elevational distribution – elevational range, maximum elevation or elevational midpoint (denoted at the top of each model output column).

Dependent	Independent	Elevational range			Maximum elevation			Elevational midpoint		
		β	***p***	***r²***	**β**	***p***	***r²***	**β**	***p***	***r²***
(a) Morphological										
Wing length	Body weight	0.93	***	0.89	0.94	***	0.90	0.93	***	0.89
	Elevation	0.01	*NS*		0.01	*		0.004	*NS*	
	Geog. range	0.06	***		0.06	***		0.06	***	
	Latitude	0.02	***		0.03	***		0.02	***	
		$F_{3,2497} = 6548.7^{***}$			$F_{4,3235} = 7022.3^{***}$			$F_{3,2497} = 6548.7^{***}$		
Tarsus length	Body weight	0.82	***	0.66	0.83	***	0.68	0.83	***	0.67
	Elevation	0.10	***		0.10	***		0.12	***	
	Geog. range	– 0.06	***		– 0.04	***		– 0.03	*	
	Latitude	0.04	**		0.04	***		0.04	***	
		$F_{4,2319} = 1129.0^{***}$			$F_{4,3016} = 1570.9^{***}$			$F_{4,2319} = 1156.9^{***}$		
Culmen length	Body weight	0.69	***	0.48	0.71	***	0.51	0.68	***	0.48
	Elevation	– 0.06	***		– 0.04	**		– 0.06	***	
	Geog. range	0.04	*		0.01	*NS*		0.02	*NS*	
	Latitude	– 0.06	***		– 0.06	***		– 0.06	***	
		$F_{4,2338} = 537.3^{***}$			$F_{3,3037} = 1045.4^{***}$			$F_{3,2339} = 717.3^{***}$		
Body weight	Elevation	– 0.08	***	0.02	– 0.08	***	0.01	– 0.13	***	0.03
	Geog. range	0.12	***		0.09	***		0.09	***	
	Latitude	0.05	**		0.05	***		0.05	**	
		$F_{3,4137} = 22.5^{***}$			$F_{3,5310} = 25.5^{***}$			$F_{3,4137} = 38.8^{***}$		
(b) Reproduction										
Clutch size	Body weight	0.06	***	0.19	0.01	*NS*	0.18	0.07	***	0.19
	Elevation	0.11	***		0.12	***		0.11	***	
	Geog. range	0.25	***		0.25	***		0.28	***	
	Latitude	0.26	***		0.28	***		0.27	***	
		$F_{4,3221} = 183.9^{***}$			$F_{3,4154} = 308.5^{***}$			$F_{4,3221} = 184.2^{***}$		
Annual fecundity	Body weight	– 0.22	***	0.22	– 0.29	***	0.23	– 0.22	***	0.22
	Elevation	0.17	***		0.13	***		0.15	***	
	Geog. range	0.26	***		0.27	***		0.30	***	
	Latitude	0.14	***		0.14	***		0.14	***	
		$F_{4,951} = 68.7^{***}$			$F_{4,1198} = 91.2^{***}$			$F_{4,951} = 67.6^{***}$		
Egg weight	Body weight	0.97	***	0.95	0.97	***	0.95	0.97	***	0.95
	Elevation	– 0.02	***		– 0.02	***		– 0.03	***	
	Geog. range	– 0.03	***		– 0.03	***		– 0.03	***	
	Latitude	0.01	*NS*		0.01	*NS*		0.01	*NS*	
		$F_{3,1695} = 10358.6^{***}$			$F_{3,2204} = 13617.0^{***}$			$F_{3,1695} = 10415.5^{***}$		

Table 5.3 continued.

Dependent	Independent	Elevational range			Maximum elevation			Elevational midpoint		
		β	*p*	r^2	β	*p*	r^2	β	*p*	r^2
(c) Development										
Incubation period	Body weight	0.77	***	0.63	0.78	***	0.63	0.77	***	0.63
	Elevation	– 0.08	***		– 0.07	***		– 0.07	***	
	Geog. range	– 0.06	**		– 0.07	***		– 0.08	***	
	Latitude	– 0.003	*NS*		– 0.02	*NS*		– 0.01	*NS*	
		$F_{3,1462} = 824.2^{***}$			$F_{3,1850} = 1054.7^{***}$			$F_{3,1462} = 821.1^{***}$		
Fledging time	Body weight	0.73	***	0.56	0.75	***	0.57	0.74	***	0.56
	Elevation	– 0.05	*		– 0.03	*NS*		– 0.03	*NS*	
	Geog. range	– 0.06	**		– 0.09	***		– 0.09	***	
	Latitude	– 0.06	**		– 0.06	***		– 0.06	***	
		$F_{4,1227} = 389.5^{***}$			$F_{3,1585} = 704.8^{***}$			$F_{3,1228} = 515.4^{***}$		
Age at first breeding	Body weight	0.57	***	0.46	0.61	***	0.48	0.57	***	0.47
	Elevation	– 0.18	**		– 0.15	***		– 0.18	***	
	Geog. range	– 0.12	***		– 0.14	***		– 0.16	***	
	Latitude	– 0.02	*NS*		– 0.05	*NS*		– 0.02	*NS*	
		$F_{3,445} = 127.4^{***}$			$F_{3,3491} = 166.9^{***}$			$F_{3,445} = 129.4^{***}$		
(d) Survival										
Adult survival	Body weight	0.28	***	0.31	0.34	***	0.32	0.27	***	0.31
	Elevation	– 0.27	***		– 0.20	**		– 0.25	***	
	Geog. range	– 0.21	**		– 0.25	***		– 0.26	***	
	Latitude	– 0.02	*NS*		– 0.10	*NS*		– 0.03	*NS*	
		$F_{3,199} = 29.8^{***}$			$F_{3,241} = 37.0^{***}$			$F_{3,199} = 30.0^{***}$		
(e) Niche breadth										
Diet breadth	Body weight	0.40	***	0.24	0.41	***	0.24	0.39	***	0.24
	Elevation	0.07	**		0.05	**		0.03	*NS*	
	Geog. range	0.22	***		0.22	***		0.25	***	
	Latitude	0.05	*		0.06	***		0.05	*	
		$F_{4,1776} = 143.7^{***}$			$F_{4,2237} = 178.2^{***}$			$F_{3,1777} = 187.8^{***}$		
Habitat breadth	Body weight	0.03	*NS*	0.27	0.02	*NS*	0.24	0.03	*NS*	0.27
	Elevation	0.06	**		0.03	*NS*		– 0.02	*NS*	
	Geog. range	0.49	***		0.48	***		0.51	***	
	Latitude	0.08	***		0.10	***		0.08	***	
		$F_{3,1891} = 234.9^{***}$			$F_{2,2381} = 375.2^{***}$			$F_{2,1892} = 348.1^{***}$		

Significance level for a variable to enter/leave each model was $P<0.05$. β: multiple regression coefficient (standardised). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. r^2: proportion of variance in the dependent variable explained by retained predictor variables. *NS*: independent variable not significant. Degrees of freedom and F-statistic value for each model also reported. All variables $\log_{10}$ transformed, except adult survival (arcsine transformed) and diet/habitat breadth (untransformed).

Table 5.4 Global family-level distributional relationships of avian traits, revealed by stepwise multiple regressions. Dependent variables grouped as: (a) morphological, (b) reproduction, (c) development, (d) survival and (e) niche breadth. Independent variables entered into each model were body weight, geographical range, absolute mean latitude and one measure of elevational distribution – elevational range, maximum elevation or elevational midpoint (denoted at the top of each model output column).

Dependent	Independent	Elevational range			Maximum elevation			Elevational midpoint		
		β	*p*	r^2	β	*p*	r^2	β	*p*	r^2
(a) Morphological										
Wing length	Body weight	0.87	***	0.84	0.87	***	0.84	0.87	***	0.84
	Elevation	0.02	*NS*		0.02	*NS*		0.01	*NS*	
	Geog. range	0.12	**		0.12	**		0.12	**	
	Latitude	– 0.07	*NS*		– 0.07	*NS*		– 0.07	*NS*	
		$F_{2,121} = 322.1^{***}$			$F_{2,122} = 331.2^{***}$			$F_{2,121} = 322.1^{***}$		
Tarsus length	Body weight	0.87	***	0.76	0.88	***	0.76	0.89	***	0.76
	Elevation	0.13	**		0.13	**		0.13	**	
	Geog. range	– 0.04	*NS*		– 0.05	*NS*		– 0.04	*NS*	
	Latitude	0.04	*NS*		0.05	*NS*		0.04	*NS*	
		$F_{2,118} = 190.4^{***}$			$F_{2,119} = 190.8^{***}$			$F_{2,118} = 189.0^{***}$		
Culmen length	Body weight	0.76	***	0.58	0.76	***	0.58	0.76	***	0.58
	Elevation	– 0.02	*NS*		– 0.03	*NS*		– 0.08	*NS*	
	Geog. range	0.08	*NS*		0.07	*NS*		0.08	*NS*	
	Latitude	– 0.08	*NS*		– 0.08	*NS*		– 0.08	*NS*	
		$F_{1,122} = 164.8^{***}$			$F_{1,123} = 169.9^{***}$			$F_{1,122} = 164.8^{***}$		
Body weight	Elevation	– 0.19	*	0.16	– 0.24	**	0.17	– 0.26	***	0.19
	Geog. range	0.42	***		0.40	***		0.39	***	
	Latitude	0.05	*NS*		0.02	*NS*		0.05	*NS*	
		$F_{2,134} = 12.36^{***}$			$F_{2,135} = 13.53^{***}$			$F_{2,134} = 15.36^{***}$		
(b) Reproduction										
Clutch size	Body weight	0.09	*NS*	0.17	0.06	*NS*	0.16	0.10	*NS*	0.15
	Elevation	0.24	**		0.21	*		0.18	*	
	Geog. range	0.26	**		0.30	***		0.31	***	
	Latitude	0.11	*NS*		0.14	*NS*		0.11	*NS*	
		$F_{2,133} = 13.2^{***}$			$F_{2,134} = 12.9^{***}$			$F_{2,133} = 11.5^{***}$		
Annual fecundity	Body weight	– 0.17	*NS*	0.10	– 0.27	**	0.17	– 0.14	*NS*	0.08
	Elevation	0.32	***		0.20	*		0.28	**	
	Geog. range	0.10	*NS*		0.25	*		0.16	*NS*	
	Latitude	0.10	*NS*		0.11	*NS*		0.08	*NS*	
		$F_{1,115} = 12.9^{***}$			$F_{3,114} = 7.90^{***}$			$F_{1,115} = 9.86^{**}$		
Egg weight	Body weight	0.99	***	0.95	0.99	***	0.95	0.99	***	0.95
	Elevation	– 0.02	*NS*		– 0.02	*NS*		– 0.02	*NS*	
	Geog. range	– 0.07	**		– 0.07	**		– 0.07	**	
	Latitude	0.02	*NS*		0.02	*NS*		0.02	*NS*	
		$F_{2,128} = 1115.9^{***}$			$F_{2,129} = 1152.1^{***}$			$F_{2,128} = 1115.9^{***}$		

Table 5.4 Continued.

Dependent	**Independent**	**Elevational range**			**Maximum elevation**			**Elevational midpoint**		
		β	***p***	r^2	**β**	***p***	r^2	**β**	***p***	r^2
(c) Development										
Incubation period	Body weight	0.77	***	0.63	0.83	***	0.63	0.83	***	0.62
	Elevation	– 0.17	**		– 0.11	*NS*		– 0.11	*NS*	
	Geog. range	– 0.12	*NS*		– 0.17	***		– 0.17	**	
	Latitude	0.06	*NS*		0.06	*NS*		0.06	*NS*	
		$F_{2,122} = 102.5^{***}$			$F_{2,123} = 103.2^{***}$			$F_{2,122} = 101.4^{***}$		
Fledging time	Body weight	0.75	***	0.57	0.78	***	0.57	0.75	***	0.57
	Elevation	– 0.02	*NS*		– 0.03	*NS*		– 0.04	*NS*	
	Geog. range	0.10	*NS*		0.10	*NS*		0.10	*NS*	
	Latitude	– 0.04	*NS*		– 0.04	*NS*		– 0.04	*NS*	
		$F_{1,118} = 153.8^{***}$			$F_{1,119} = 157.9^{***}$			$F_{1,118} = 153.8^{***}$		
Age at first breeding	Body weight	0.64	***	0.50	0.62	***	0.52	0.61	***	0.51
	Elevation	– 0.24	**		– 0.26	***		– 0.26	***	
	Geog. range	– 0.11	*NS*		– 0.11	*NS*		– 0.13	*NS*	
	Latitude	– 0.07	*NS*		– 0.06	*NS*		– 0.06	*NS*	
		$F_{2,92} = 46.01^{***}$			$F_{2,92} = 49.05^{***}$			$F_{2,91} = 47.81^{***}$		
(d) Survival										
Adult survival	Body weight	0.51	***	0.35	0.51	***	0.39	0.47	***	0.37
	Elevation	– 0.23	*		– 0.27	**		– 0.28	**	
	Geog. range	– 0.01	*NS*		– 0.04	*NS*		– 0.04	*NS*	
	Latitude	0.12	*NS*		0.07	*NS*		0.11	*NS*	
		$F_{2,62} = 16.72^{***}$			$F_{2,63} = 20.09^{***}$			$F_{2,62} = 18.34^{***}$		
(e) Niche breadth										
Diet breadth	Body weight	0.67	***	0.48	0.67	***	0.45	0.67	***	0.45
	Elevation	0.19	**		0.13	*NS*		0.12	*NS*	
	Geog. range	– 0.01	*NS*		0.08	*NS*		0.08	*NS*	
	Latitude	0.02	*NS*		– 0.02	*NS*		– 0.02	*NS*	
		$F_{2,108} = 50.66^{***}$			$F_{1,109} = 88.67^{***}$			$F_{1,109} = 88.67^{***}$		
Habitat breadth	Body weight	0.11	*NS*	0.37	0.11	*NS*	0.37	0.11	*NS*	0.37
	Elevation	0.06	*NS*		0.04	*NS*		0.00	*NS*	
	Geog. range	0.61	***		0.61	***		0.61	***	
	Latitude	0.08	*NS*		0.08	*NS*		0.08	*NS*	
		$F_{1,115} = 68.44^{***}$			$F_{1,115} = 68.44^{***}$			$F_{1,115} = 68.44^{***}$		

Significance level for a variable to enter/leave each model was $P<0.05$. β: multiple regression coefficient (standardised). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. r^2: proportion of variance in the dependent variable explained by retained predictor variables. *NS*: independent variable not significant. Degrees of freedom and F-statistic value for each model also reported. All variables $\log_{10}$ transformed, except adult survival (arcsine transformed) and diet/habitat breadth (untransformed).

At the family level (Table 5.4b), body weight remained the dominant predictor for egg weight, but was only retained in the annual fecundity model containing maximum elevation, and was not retained in any clutch size model. Elevational distribution was retained as a positive predictor of both clutch size and annual fecundity, but was no longer retained for egg weight. Geographical range was retained as a positive predictor of clutch size and annual fecundity (maximum elevation model only), and as a negative predictor of egg weight. Latitude was dropped from all models.

Across PICs (Table A5.3), elevational distribution was not retained as a significant positive predictor of clutch size. In fact, using the Hackett tree, both maximum elevation and elevational midpoint were found to have a slight negative relationship with clutch size. Increasing geographical range size and latitude were consistently shown to be related to increasing clutch size, whereas smaller-bodied species were found to lay smaller clutches.

Developmental: At the species level (Table 5.3c), variance explained was greatest for incubation period (r^2 = 63%) and lowest for age at first breeding (r^2 = 46–48%). Body weight was by far the strongest predictor of all three developmental traits, and always in a positive direction. Elevational distribution was found to be a significant negative predictor of incubation period and age at first breeding. However, elevation was not retained as a significant predictor of fledging time, with only a marginal negative relationship found with respect to elevational range. Geographical range was retained in all models, and had a negative effect on all three developmental traits. Latitude was only retained in the fledging time models, where it was found to be a negative predictor.

At the family level (Table 5.4c), body weight remained the dominant predictor for all three developmental traits. Elevational distribution was retained as a negative predictor of age at first breeding, while only elevational range was retained as a negative predictor of incubation period. Geographical range was retained as a negative predictor of incubation period (maximum elevation and elevational midpoint models). Latitude was dropped from all models.

Across PICs (Table A5.3), elevational distribution was not retained as a significant negative predictor of incubation period, with body weight consistently found to be the dominant (positive) predictor. Larger-ranged bird species were found to have shorter incubation periods than small-ranged species. Overall, latitude had no significant effect on incubation period. Variance in incubation period explained by the PIC models were considerably less (17–19%) than the species-level models – β-values were also much lower.

Survival: At the species level (Table 5.3d), total variance explained for adult survival ranged from 31 to 32 percent. Body weight was found to be a strong positive predictor of adult survival, whereas both elevational distribution and geographical range were identified as strong negative predictors of adult survival. Latitude had no significant effect on adult survival. At the family level (Table 5.4d), body weight was the dominant (positive) predictor of adult survival, and elevational distribution retained as a negative predictor. Geographical range was dropped from all models, and latitude remained non-significant.

Across PICs (Table A5.3), elevational distribution was not retained as a significant negative predictor of adult survival, with geographical range consistently found to be the dominant (negative) predictor. Body weight was found to be a slightly significant positive predictor of adult survival within the maximum elevation and elevational midpoint models – using PICs derived from the Ericson tree only. Latitude was also found to be a slightly significant positive predictor of adult survival within the elevational range (both trees) and elevational midpoint model (Hackett tree).

Niche breadth: At the species level (Table 5.3e), variance explained was similar for diet and habitat breadth models (diet = 24%, habitat = 24–27%). Body weight was the strongest predictor of diet breadth, with larger bird species having wider diet breadth than smaller species. However, body weight was not a significant predictor of habitat breadth. Elevational range and maximum elevation were found to be positive predictors of diet breadth, whereas only elevational range had a positive effect on habitat breadth. Geographical range was the strongest predictor of habitat breadth, with larger ranged bird species having wider habitat breadth than small-ranged species. A positive relationship with geographical range was also found for diet breadth. Latitude was a significant positive predictor of both diet and habitat breadth.

At the family level (Table 5.4e), body weight remained the dominant predictor of diet breadth. Elevational range was retained as a positive predictor of diet breadth only, whereas geographical range was retained as a positive predictor of habitat breadth only. Latitude was dropped from all models.

Across PICs (Table A5.3), both elevational distribution and geographical range were found to be strong positive predictors of habitat breadth. Larger bodied species were also found to have a wider habitat breadth in the maximum elevation (both trees) and elevational midpoint (Hackett tree) models. Overall, latitude was found to have no effect on habitat breadth, although a negative relationship was identified using the Ericson tree for the elevational range and elevational midpoint models.

5.5 Discussion

Although this chapter is split into two distinct parts, they are clearly interlinked and logically follow on from one another. Before investigating trait variation with respect to elevational distribution in a multivariate spatial environment, it makes intuitive sense to first establish how elevational distribution varies geographically. To the best of my knowledge no other study has attempted such an investigation, for any taxa or at any spatial scale.

5.5.1 Biogeography of avian elevational distribution

Identifying and interpreting the interspecific relationships between elevational distribution and both geographical range and latitude at large spatial scales is an overlooked, yet fundamental, area of research. Knowledge about such interrelationships is not only of standalone interest and importance, but can help improve our understanding of spatial gradients of traits and species richness. The overarching results from this study, at the global scale, find avian elevational distribution to significantly vary with geographical range and its latitudinal distribution – consequently, the first null hypothesis can be conclusively rejected. I can find no other study, for any taxa, that explores such interrelationships at the global scale or for so many species (reviewed in Section 2.2).

Elevational distribution and geographical range: The consistent positive relationship identified between elevational range and geographical range, both globally across species, families and PICs, and for species within all biogeographic realms (Table 5.1; Table A5.2), indicates that species (and families) possessing a large elevational range also typically have a large geographical range. Only five existing studies could be found investigating this relationship (Section 2.2.3), of which three focus on birds (Stevens 1992; Blackburn & Ruggiero 2001; La Sorte & Jetz 2010). These three studies similarly found elevational range and geographical range/lateral extent to be positively related. However, studies of non-avian vertebrates have found no such relationship (McCain 2006).

Species that span wider geographical areas are likely to encounter greater topographical heterogeneity. In addition, empirical evidence has found that species displaying traits characteristic of generalists, typically have the largest geographical ranges (e.g. Hulbert & White 2007; Carrascal *et al.* 2008; Laube *et al.* 2013). In Chapter 4, bivariate analyses found both diet breadth and habitat breadth to be strongly positively related with elevational range (Table 4.1). This result is further backed by the multiple regressions conducted in this study, where both measures of niche breadth were found to be significantly positively associated with elevational and geographical range, across species and PICs (Table 5.3e; Table A5.3a). It therefore seems as though species that are 'elevational generalists' are also ‘geographical generalists’, and that this could, at least in part, be driving the positive relationships seen between elevational and geographical range. However, further research is required in order to better establish whether or not the mechanisms underlying range size distributions differ for geographical and elevational ranges.

Bivariate regression analysis found a comparatively weaker, yet still positive, global relationship between maximum elevation and geographical range (Table 5.1; Table A5.2), implying that species with higher elevational limits also inhabit wider geographical extents. This positive trend remained when breaking maximum elevation up into discrete elevational bands (Fig. 5.1b). The only previous study with which to compare this finding with is by Blackburn & Ruggiero (2001). In contradiction to the global scale results of this study, they found maximum elevation to decline with increasing latitudinal range across Andean passerines. Interestingly, for species within the Neotropics (the biogeographic realm with the largest sample size), no significant relationship was found in this study between maximum elevation and geographical range. In other words, Neotropical species with high maximum elevations possess both small and large geographical ranges, and vice versa - further contradicting the taxonomically restricted results of Blackburn & Ruggiero (2001). It is difficult to assess whether or not these relationships for maximum elevation are influenced by its autocorrelation with elevational range, although this is likely to be partly so. It is important to note that sample sizes for maximum elevation are considerably greater than those for both elevational range and midpoint, thereby increasing the generality and potentially the robustness of its global-scale relationship identified with respect to geographical range.

Overall, species with higher elevational midpoints were found to have larger geographical ranges (Table 5.1). However, elevational midpoint was found to display the weakest positive relationship with geographical range at the global level across species, families and PICs, and to possess the least consistent relationships within individual biogeographical realms (Table 5.1; Table A5.2). This implies that geographical range is a poorer predictor of elevational midpoint than for either elevational range or maximum elevation. Even so, the overall positive trend does match that found by Krűger & Radford (2008), although their analyses were restricted to species within the Accipitridae (true hawk) family. Within the Neotropical realm (and to a lesser extent within the Palearctic), elevational midpoint was instead found to decline with increasing geographical range, i.e. low-elevation species in these two realms typically have larger geographical ranges. Although contradicting the global results of this study, this finding is consistent with that found by Blackburn & Ruggiero (2001) for Andean passerines. When breaking elevational midpoint up into discrete elevational bands, species that possess an elevational midpoint at mid-elevations (300-

2500m) were found to have larger geographical ranges than those with elevational midpoints at low (<300m) or high (>2500m) elevations (Fig. 5.1a). This is an interesting trend, and one that needs further investigation in order to establish whether it is a pattern driven by evolutionary and/or ecological factors, or instead a result of sample size differences or dataset representativeness.

Elevational distribution and absolute mean latitude: The vast majority of published research on range size distribution has been associated with Rapoport's rule (Rapoport 1982; Stevens 1989), i.e. testing for a positive relationship between species' geographical range size and increasing latitude. Overall, support for this 'ecogeographical rule' is weak (Section 2.2.1). In fact, the first global-scale study of Rapoport's rule, conducted on birds using a grid-cell approach, instead found the smallest ranges to be located on islands, within mountainous areas, and largely in the Southern Hemisphere, leading them to suggest that range size may be constrained by land availability (Orme *et al.* 2006).

Latitudinal gradients of elevational range size have received far less attention (Section 2.2.2). This study finds that, across species globally, avian elevational range does increase with absolute mean latitude (i.e. with increasing distance from the equator) of a species geographical breeding range (Table 5.1). This supports McCain (2009b), who studied global divergence in elevational range size with respect to latitude for herpetofauna, rodents, bats and birds. This finding also provides support for the hypothesis proposed by Janzen (1967), who proposed that elevational ranges should be smaller on tropical than temperate mountains. He based this hypothesis on the fact that, at a given elevation, annual temperature variation is greater on temperate mountains than on tropical mountains; therefore, temperate species should evolve broad temperature tolerances and acclimation abilities, and consequently broader elevational ranges, than tropical species (Ghalambor *et al.* 2006). However, the results from this study also suggest that this relationship breaks down for species within biogeographic realms, with only species breeding in the Neotropics displaying a significant positive relationship between elevational range and absolute mean latitude (Table 5.1). The ranges of species' absolute mean latitudes within each of the seven biogeographical realms are essentially equivalent. Therefore, the significant positive trend identified within the Neotropics, mirroring that found by Blackburn & Ruggiero (2001) for Andean passerines, could instead be due to a sample size effect, as its sample size is at least more than double that of the other individual realms.

Both bivariate linear regressions (Table 5.1) and elevational band analysis (Fig. 5.1d) found a positive relationship between maximum elevation and absolute mean latitude for species within the global dataset. A significant positive trend was also found within the

Neotropics, supporting Blackburn & Ruggiero (2001). Therefore, maximum elevation was found to essentially mirror the results for elevational range – these two measures of elevational distribution are autocorrelated. The fact that for species within the Palearctic realm, a positive correlation was also found between absolute mean latitude and maximum elevation, but not for elevational range, is once again likely to be a sample size effect, as more species were analysed for the former correlation than the latter.

In contrast to the other two measures of elevational distribution, distance from the equator was found to have no significant influence on elevational midpoint for species at the global scale (Table 5.1). This implies that species with both low and high elevational midpoints are evenly found from the tropics to the temperate regions. However, elevational midpoint was found to significantly increase with absolute mean latitude for Palearctic species and significantly decrease for Afrotropical species. Therefore more focused regional studies on this relationship and its underlying drivers could help to explain these significant trends that differ from the global result. Although the elevational band study does show an increase in elevational midpoint with absolute mean latitude, the relationship is only just significant (Fig. 5.1c). In fact, the post-hoc tests revealed no significant differences between the mean values for elevational bands <3500m, with the highest elevational band (≥3500m), which has a very small sample size of 74 species. It is important to note that the 'heights' of elevational ranges are instead believed and shown to vary more consistently with elevation than with latitude (Sections 2.2.2 and 5.5.1).

Across families, elevational distribution was not found to vary significantly with absolute mean latitude. This is likely due to the fact that within avian families, both elevational distribution and absolute mean latitude vary most at the interspecific level (Table 3.1).

Elevational distribution and raw mean latitude: A much stronger and consistent relationship was found between elevational range and raw mean latitude compared with absolute mean latitude. This implies that latitudinal gradients in elevational distribution differ according to hemisphere. Specifically, a general trend of declining elevational distribution (range, maximum and midpoint) from high northern latitudes to high southern latitudes was identified at the global scale – across species, families and PICs (Figs. 5.1e-f, 5.2, Tables 5.1 A5.2). In other words, species with larger elevational ranges, higher elevational limits and higher elevational midpoints are more likely to be found in the Northern Hemisphere than the Southern Hemisphere. McCain (2009b) found mountain height to be the strongest predictor of elevational range size in vertebrates (including birds). Therefore this observed trend between elevational distribution and raw mean latitude could partly be explained by the fact that elevational range is constrained by the topographical environment. The majority of the world's mountainous areas (outside of Antarctica) are located in the Northern Hemisphere, predominantly in temperate regions, and the greatest area of high-elevation mountains (≥2500m) are also found within the temperate zone of the Northern Hemisphere (Fig. 5.4; UNEP-WCMC 2002; Körner *et al.* 2011). This asymmetry is in turn largely driven by the biased distribution of the world's land surface, with more than two-thirds located in the Northern Hemisphere (UNEP-WCMC 2002).

A similar trend was also found for species breeding within individual biogeographic realms, with elevational distribution declining from high to low latitudes. The only exceptions were non-significant relationships found for the Nearctic and Palearctic realms. These two realms are the most northerly distributed and both occur entirely within the Northern Hemisphere, where the majority of mountain land area is found (Fig. 5.4). In fact, 41% of the global mountain area occurs within the Palearctic realm (Rodríguez-Rodríguez *et al.* 2011). Therefore, it is possible that these non-significant relationships could be attributed to the fact that, compared to the other five realms studied, the 'potential elevational limits' within the Nearctic and Palearctic are higher, therefore reducing geometric constraints, and are more constant with respect to latitude.

Elevational range and elevational midpoint relationships: Through the use of bivariate linear regressions, strong support was found for Stevens' elevational extension of Rapoport's rule (Stevens 1992) at the global level across species, families and PICs, and for species within all studied biogeographic realms (Table 5.2). In other words, elevational range was consistently found to increase with elevational midpoint. This trend is typically attributed to high-elevation species, particularly those living in the tropics, experiencing larger daily variation in temperature than low-elevation species (Janzen 1967). Therefore, in contrast to lowland species, highland species should possess larger physiological tolerances and acclimation abilities, and accordingly larger elevational ranges (Fig. 2.1b; Ghalambor *et al.* 2006; McCain 2009b). Interestingly, the results from this study are in disagreement with the overall findings of McCain & Knight (2012), who conducted a worldwide study of the elevational Rapoport's rule for montane vertebrates, using datasets from 160 elevational gradients. They found that, on average, evidence for the positive trend was found in only 26% of cases. In fact, empirical support for this 'rule' has been highly variable up until this study (Section 2.2.2). To a certain extent, such inconsistency is likely to be attributed to the array of methodologies, scales, and taxa that have previously been used to test for it (see Ruggiero & Lawton 1998; McCain & Knight 2012).

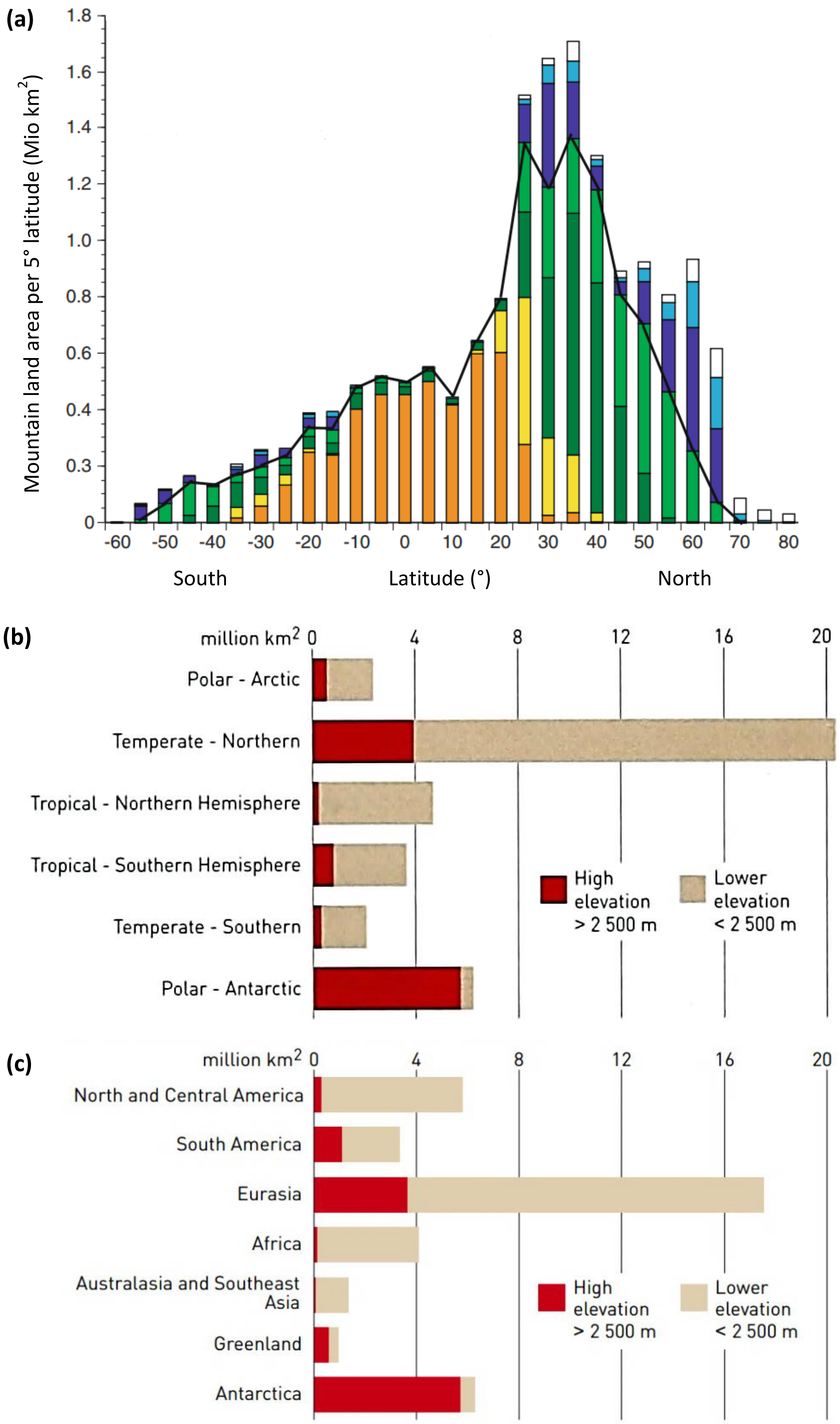


Figure 5.4 Global variation in mountain land area with respect to: (a) latitude, (b) latitude zone, and (c) continent group. (a) From Körner *et al.* (2011) – the different colours within each band represent different thermal belts, and the black line highlights the thermal treeline. (b) and (c) from UNEP-WCMC (2002). The mountain definitions from each source differ slightly, but do not affect the overall trends.

The elevational Rapoport's rule has previously been studied using taxonomically and geographically restricted datasets, and was originally intended to be applied to species occurring within the same latitude (Stevens 1992). However, at the global scale across species, elevational midpoint was still found to be a strongly significant predictor of elevational range, when independently controlling for raw latitude and absolute latitude. It is important to note that despite this study providing strong evidence for the elevational Rapoport's rule, mountains are proven hotspots of endemism (e.g. Orme *et al.* 2005), and that, in mountainous regions, endemics (i.e. restricted range species) have been found to live at higher elevations than non-endemics (Section 1.7.2).

Stevens (1992) originally proposed a positive, monotonic (or generally linear) association between elevational range and increasing elevation. In addition, the underlying theory (which attempts to link decreases in species richness with elevation), would be negated by either a decreasing elevational range relationship, or where the average largest or smallest ranges are not at the upper or lower ends of the gradient respectively (i.e. a unimodal distribution). When breaking elevational midpoint up into discrete elevational bands, mean elevational range was found to increase with increasing elevation up until species with an elevational midpoint ≥1500 and <2500m, whereby after this height it was observed to decline, albeit slightly (Fig. 5.3). Although this could be a sample size effect, as the highest elevational bands do have a comparatively small numbers of species, this finding implies that the linear relationship between elevational range and elevational midpoint is potentially too simplistic. In fact, non-linear (triangular) relationships have been identified previously, where species at intermediate elevations have instead been shown to possess the broadest elevational range amplitudes (e.g. Patterson *et al.* 1998; Fu *et al*. 2004; Ribas & Schoereder 2006). Ribas & Schoereder (2006), justify such a quadratic relationship based on the consideration that the bases and tops of mountains are hard boundaries, i.e. as with latitudinal range distributions, the mid-domain effect may constrain and drive species elevational ranges (Colwell & Hurtt 1994; Rahbek 1997). Further work is required in order to investigate the potential role of geometric constrains and elevational ranges in driving elevational gradients of species richness (Section 1.3).

5.5.2 Multivariate spatial patterns of avian traits

As shown in Chapter 2, current studies concerning trait biogeography are biased, across both taxa and spatial scales, towards trait variation with respect to either latitude or geographical range. In Chapter 4, I addressed this imbalance and knowledge gap, by investigating bivariate relationships between elevational distribution and both avian life-history and ecological traits, at the global scale. Briefly, bivariate analyses found elevational distribution to be positively associated with reproduction and niche breadth, yet negatively associated with morphology, growth and survival. The primary benefit of utilising a bivariate analytical approach is that it maximises sample sizes (and in turn statistical power), and both taxonomic and geographic representativeness. A multivariate approach was adopted for this study in order to establish whether or not significant bivariate relationships are robust when controlling for potentially confounding variables (i.e. body weight) and other known spatial covariates of avian traits (i.e. geographical range and latitude). This study should therefore be seen as a complementary extension to the analyses conducted within Chapter 4.

Overall, at the global scale, species-level elevational distribution was found to be a significant predictor of both life-history and ecological traits, when controlling for body weight, geographical range and latitude (Table 5.3). Consequently, the second null hypothesis can be rejected, with respect to global models built for species. The results obtained from the multiple regressions, across species and families (Tables 5.3, 5.4), were qualitatively similar (except for tarsus length) to those derived from simpler bivariate regressions (Chapter 4). However, a reduction in the number of significant relationships was found. This is partly due to multivariate analyses requiring a value of every predictor for each unit analysed: therefore reducing sample sizes, as the global avian database used in this research is not a full array.

Identified relationships between elevational distribution and avian traits were discussed extensively in Chapter 4. To avoid repetition, only trends that differ from those found using global-scale bivariate analyses (Tables 4.1, A4.4) are discussed here. The following subsections instead focus on answering the second study question as outlined in the chapter introduction.

Morphology: The biogeography of the four morphological traits investigated (wing length, tarsus length, culmen length and body weight) are complex to interpret. Little consistency can be found between the bivariate and multivariate outputs, across the traits, or across species, families and PICs (Tables 5.3, 5.4, A5.3). Such inconsistency, along with relatively low effect sizes, suggests that present-day distribution and range-size parameters have comparatively little influence on morphological variation in birds at the global scale. For example, out of all the traits investigated, body weight has the lowest level of variance explained. This could be linked to the fact that the geography and topography of the Earth today is considerably different to those millennia ago, when the main period of avian body size diversification occurred (Bennett & Owens 2002) For the other three morphological traits, body weight dominates as a positive predictor. Such strong allometric relationships for these traits are highlighted in Table 3.2.

Focusing on the significant relationships found for both elevational and geographical range, regardless of the morphological trait, the directionality of the trends are always opposing. This implies that the underlying drivers of variation in morphology with respect to geographical range and elevational range differ, and warrants further investigation.

Evidence for Bergmann's rule (Bergmann 1847), i.e. a latitudinal increase in body size, was found at the species level, in agreement with Olson *et al.* (2009), who used a grid-cell approach to investigate global body-size distributions in birds. However, in this study the 'rule' was not supported at the family level, and only weakly or not at all when controlling for phylogeny. As discussed in detail by Olson *et al.* (2009), this result implies that some major body plans are phylogenetically constrained, and persist only in certain environmental conditions. If these are associated with particular body sizes, then size distributions may change between different regions because of lineage turnover rather than because of direct selection for size. For example, Spheniscidae (penguins) are all large and predominantly inhabit high-latitudes.

Supporting the bivariate analyses, no evidence for an elevational equivalent of Bergman's rule (i.e. body weight increases with elevational midpoint) was found in either the species- or family-level models – in fact the opposite trend was found. However, across PICs, multiple regressions did find body weight to increase with elevation, in agreement with Blackburn & Ruggiero (2001). Nevertheless, it is important to again highlight the small effect sizes and overall very low percentage of variation explained in these body weight models.

In contrast to the bivariate analysis, limited support was found for Allen's rule (1977), across species and families. Although culmen length was found to decline with increasing elevation and latitude at the species level, this was not maintained across families. Wing length was no longer found to decline with increasing elevation, and was found to increase with latitude across species, with tarsus length shown to increase with both elevation and latitude. The ambiguity of Allen's rule is discussed in Section 2.1.5, and the findings from this study further suggest that it being merited the status of an invariant 'rule' is not valid across birds at the global scale.

Reproduction: Both species- and family-level multiple regressions found a positive association between elevational distribution and reproductive output (i.e. clutch size and annual fecundity), however, a concomitant decline in egg weight was only found across species (Tables 5.3b, 5.4b). Lack of a significant relationship between elevational distribution and egg weight across family models, mirrors that found for PICs using bivariate regressions (Table A4.4), and provides additional evidence that phylogenetic non-independence may be influencing the negative species-level trend. In addition, body weight was found to explain the vast majority of variation in egg weight. Egg weight has been shown to be highly allometric in numerous classic studies (e.g. Huxley 1927; Rahn *et al.* 1975; see also Table 3.2). Egg weight variation is evidently influenced little by geography in comparison to both clutch size and annual fecundity which, in turn, both display weaker allometric relationships (Table 3.2).

The directionality of the relationships found with respect to geographical range and reproduction (across species, families and PICs), were analogous to those shown for elevational range, supporting previous studies (Section 2.1.6), albeit noticeably stronger across species and PICs. Strong evidence was found for the 'classic' (latitudinal) Lack's rule (Lack 1947), i.e. increasing clutch size with greater distance from the equator, supporting previous studies (Section 2.1.6). Related to this, a larger effect size was found for the 'classic' Lack's rule compared to the elevational equivalent (which uses elevational midpoint), across both species and PICs.

Development: Overall, developmental trait values (incubation period, fledging time and age at first breeding) were shown to decline with increasing elevational distribution in bivariate analyses (Section 4.4). In the multivariate analyses, this negative trend largely remained, across both species (Table 5.3c) and families (Table 5.4c). Exceptions to this at the species level were a lack of significance between fledging time and both maximum elevation and elevational midpoint. Exceptions to this at the family level were a lack of significance between, (a) incubation period and both maximum elevation and elevational midpoint, and (b) fledging time and elevational distribution. Despite possessing the smallest sample size out of the three developmental traits, age at first breeding was consistently found to be related to elevational distribution. These exceptions to the general trend are likely due to two factors. Firstly, across all units of study, body weight was by far the strongest predictor of development – a strong positive allometric relationship for these traits has long been known (see Bennett & Owens 2002). However, the effect size of body weight and the allometric relationship was weakest for age at first breeding (Table 3.2), implying that variation in this trait is influenced more by biogeography than the other two traits. Secondly, in the global dataset used, incubation period is the most reliable measure of growth. Fledging time is comparatively much harder to measure consistently, and might partly explain why, in comparison to incubation period, it was not retained in as many of the models.

The directionality of the relationships found with respect to geographical range and development (across species, families and PICs), were analogous to those shown for elevational range, albeit noticeably weaker across species and families, and stronger across PICs. Although the directionality is largely the same between developmental traits and both elevational midpoint and latitude, across all units, latitude was only found to be a significant negative predictor of fledging time at the species level. As highlighted in Section 2.1.6, previous studies have currently found little or no evidence for either incubation or fledging periods differing between temperate and tropical areas (e.g. Geffen & Yom-Tov 2000). However, the results from this study do conflict with the theoretical findings of McNamara *et al.* (2008) who found evidence for greater age at first breeding with increasing latitude.

Survival: Bivariate analyses revealed adult survival to decline with increasing elevational distribution, across all units and spatial scales studied (Section 4.4). Here, this negative trend remained, across both species- and family-level models (Tables 5.3d, 5.4d). Body weight was the strongest predictor, across species and families, and such a strong positive allometric relationship for adult survival has been found in previous studies (e.g. Saether 1989) and in this thesis (Table 3.2). The directionality of the relationships found with respect to geographical range and adult survival (across species, families and PICs), were analogous to those shown for elevational range, albeit noticeably weaker across species and families, and stronger across PICs. No latitudinal equivalent could be found for the negative trend between elevational midpoint and adult survival. This is in agreement with Karr *et al.* (1990), although a lack of a relationship has been debated (Section 2.1.6). It is important to note that the sample size for adult survival in this study is comparatively very small - even more so than for the bivariate analyses. Therefore, it is necessary to be cautious regarding their global taxonomic and geographic representativeness, and to highlight the clear need for more data concerning this understudied (with respect to biogeography) yet highly informative trait. Nevertheless, this is the largest sample size of adult survival data for birds studied to date.

Niche breadth: Bivariate analyses revealed niche breadth (diet and habitat) to broaden with increasing elevational distribution, across both species and families (Section 4.4). Across the same units, in the multiple regressions presented here, this trend broke down (Tables 5.3d, 5.4e). Specifically, although evidence was found for niche breadth to increase with elevational range, the effect size was low. Such a finding suggests that elevational range should not be used as a proxy for specialisation, as it has been in previous research (e.g. Badyaev & Ghalambor 1998; Bonier *et al.* 2007; Tobias & Seddon 2009). In addition, niche breadth was not found to increase with the ‘height’ of a species’ elevational range. This in turn provides no support for an elevational equivalent of the latitude-niche breadth hypothesis (Section 2.1.6), and could be due to the fact that high-elevation zones are known to harbour high numbers of endemics (Section 1.7.2). However, when habitat breadth was analysed across PICs in a multivariate environment, all three measures of elevational distribution were consistently found to be strong positive predictors (Table A5.3). This implies that phylogeny has a significant role in explaining the relationship between niche breadth and elevation.

Interestingly, body weight was only found to be a significant predictor for diet breadth across species and families, and a relatively weak or non-significant predictor of habitat breadth across PICs. As to why diet breadth displays a stronger allometric relationship than habitat breadth is not clear, but could be influenced by the different methodologies used to quantify both measures of niche breadth (Section 3.3.3). Habitat breadth was found to be positively related to geographical range (mirroring the pattern shown for elevational range), as has previously been shown for birds (Section 2.1.6). Unlike Laube *et al.* (2013), a positive species-level relationship was also found between diet breadth and geographical range across species, albeit much weaker than for habitat breadth. As discussed by Laube *et al.* (2013), different food sources can occur side by side in the same site, while habitat types cannot. Therefore, it is perhaps not surprising that a species' geographical range size is a weaker predictor of diet breadth than habitat breadth. Finally, although support was found for the latitude-niche breadth hypothesis (MacArthur 1972) across species, effect sizes were relatively small, and this positive trend was shown to breakdown at both the family level and across PICs. The ambiguity of the latitude-niche breadth hypothesis was highlighted in Section 2.1.6. In fact, the most recent global study by Belmaker *et al.* (2012) found that the relationship between avian specialisation and latitude is not linear, with specialisation decreasing towards middle latitudes, and increasing again at extremely high latitudes.

5.5.3 Conclusions

The results from this study illustrate the complexity of trait biogeography at the global scale, particularly with respect to morphology. Nevertheless, the overall relationship between elevational distribution and core life-history traits (i.e. reproduction, development and survival) mirrors those found in Chapter 4 using a bivariate analytical approach. Specifically, even after controlling for known covariates of avian life-history (body weight, geographical range and latitude), larger elevational ranges and both higher maximum elevation and elevational midpoints were still associated with faster life-histories, and vice-versa. Relationships with all three measures of elevational distribution were most consistent for clutch size, annual fecundity, age at first breeding and adult survival. These are the key variables in theoretical models of life-history evolution in vertebrates (Roff 2002). The high proportions of variance explained by the biogeographical variables in this study are a major contribution to understanding life-history evolution in birds, and elevational distribution is likely to be an important ‘missing’ correlate of existing studies of life-history evolution in other vertebrate groups, including mammals.

In addition, it is interesting to highlight that, apart from the morphological traits, the directionality of significant life-history and niche-breadth trait relationships identified with respect to elevational range and elevational midpoint were found to be the same as those for geographical range and absolute mean latitude, respectively. However, further research is required in order to better establish whether or not the mechanisms underlying range size distributions differ for geographical and elevational ranges. As briefly discussed in Section 3.3.4, the factors that limit species’ elevational ranges are poorly understood (Gifford & Kozak 2012). Although this study finds evidence suggesting that topography limits maximum elevation and elevational range, it is important to note that elevational limits are also believed to be constrained, or at least influenced, by physiology and biotic interactions, e.g. competition, predation, and parasitism (e.g. MacArthur 1972, Connell 1978, Brown *et al.* 1996; Brown & Lomolino 1998; Normand *et al*. 2009).

An informative extension to this study would be to explicitly investigate the role of elevational geometric constraints on the results obtained, by adding ‘maximum potential elevation’ of a species’ range as a covariate. This would enable an examination of both its influence on elevational distribution, and trait variation. Using GIS, ‘potential maximum elevation’ could be extracted relatively easily by overlaying geographical breeding range maps with a digital elevation model (e.g. GTOPO30).

In addition, it would be of interest to investigate and compare avian trait variation with respect to elevational distribution within both the Northern Hemisphere and Southern Hemisphere, as has already been conducted for avian life-history variation with respect to latitude (Cardillo 2002). Such an extension to the existing analysis is of value for two main reasons. Firstly, I found avian elevational distribution to vary noticeably with respect to raw mean latitude of geographical breeding range. Secondly, previous studies examining latitudinal gradients in avian traits have reported significant differences between both hemispheres, although the Southern Hemisphere has been comparatively neglected in studies of trait biogeography (Section 2.1.6).

The purpose of this chapter was to investigate the biogeography of avian traits at the global scale, and compare the predictive power of elevational distribution, geographical range and latitude. However, given that the multiple regressions account for a fraction of the total variability in certain life-history and in both of the niche breadth traits, it is clear that important predictors were lacking. The inclusion of additional variables would likely result in different model outputs - potentially ones where distribution variables are no longer retained. For example, Owens & Bennett (1995) found ‘reproductive effort’ to be significantly negatively correlated with nesting habit. Other potential ecological predictors include: main habitat and diet type, foraging range, developmental mode, and dispersal/migratory behaviour.

As with Chapter 4, the results obtained in this study across PICs should be interpreted with caution. For example, when analysing the biogeography of elevational distribution (Table A5.2), the directionality of the relationships with respect to absolute mean latitude were found to flip depending on the phylogenetic tree used. Further investigation (as discussed in Section 4.5) is also necessary to conclusively establish whether or not the lack of a clear significant relationship, across PICs, between elevational distribution and body weight, clutch size, incubation period and adult survival is valid (Table A5.3). However, the fact that at the family level these associations are all significant (and in the same direction as those shown across species) provides supportive evidence that these relationships are robust and not heavily influenced by phylogeny.

5.6 Appendix: Supplementary tables

Table A5.1 Number of bird species in the global dataset with raw mean latitudinal location of geographical breeding range occurring within discrete 5° latitudinal bands. (a) number of species with elevational range/midpoint data, (b) number of species with maximum elevation data.

		Number of species	
	Latitudinal band (°)	(a) Elevational range/midpoint	(b) Maximum elevation
Northern Hemisphere	50-55	47	59
	45-50	74	111
	40-45	53	76
	35-40	40	54
	30-35	57	81
	25-30	448	563
	20-25	326	419
	15-20	153	189
	10-15	110	141
	5-10	251	327
	0-5	433	568
Southern Hemisphere	0-5	793	1044
	5-10	763	956
	10-15	347	427
	15-20	293	369
	20-25	167	200
	25-30	87	99
	30-35	79	101
	35-40	18	24
	40-45	23	26
	45-50	10	11
	50-55	11	13
	TOTAL:	**4583**	**5858**

Table A5.2 Pearson correlation coefficients (*r*) between global avian geographical breeding range variables and elevational distribution for phylogenetically independent contrasts (PICs). PICs derived from two independent phylogenetic trees, using Ericson *et al.* (2006) or Hackett *et al.* (2008) backbone.

	Elevational range		Maximum elevation		Elevational midpoint	
	n	*r*	*n*	*r*	*n*	*r*
Ericson						
Geographical range	5589	0.47^{***}	7058	0.19^{***}	5562	0.02
Absolute mean latitude	4550	-0.08^{***}	5775	0.03^{*}	4533	0.03^{*}
Raw mean latitude	4564	0.08^{***}	5772	0.20^{***}	4530	0.09^{***}
Hackett						
Geographical range	5587	0.39^{***}	7064	0.18^{***}	5589	0.03^{*}
Absolute mean latitude	4532	0.08^{***}	5773	-0.03^{**}	4555	-0.08^{***}
Raw mean latitude	4526	0.04^{**}	5774	0.20^{***}	4563	0.21^{***}

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. Study variables $\log_{10}$ transformed except raw mean latitude (untransformed).

Table A5.3 Global distributional relationships of avian traits across phylogenetically independent contrasts (PICs), revealed by multiple linear regressions. Independent variables entered into each model were body weight, geographical range, absolute mean latitude (latitude) and elevational distribution (elevation): (a) elevational range, (b) maximum elevation, and (c) elevational midpoint. PICs derived from two independent phylogenetic trees, using Ericson *et al.* (2006) or Hackett *et al.* (2008) backbone.

Dependent	**Independent**	**PICs (Ericson)**			**PICs (Hackett)**		
		β	***p***	***r²***	**β**	***p***	***r²***
(a) Elevational range							
Body weight	Elevation	0.01	*NS*	0.001	0.05	***	0.05
	Geog. range	0.00	*NS*		– 0.03	***	
	Latitude	0.01	*NS*		0.00	*NS*	
		$F_{3,4090} = 1.4$			$F_{3,4111} = 69.2^{***}$		
Clutch size	Body weight	– 0.03	**	0.19	– 0.03	**	0.18
	Elevation	0.01	*NS*		– 0.004	*NS*	
	Geog. range	0.04	***		0.04	***	
	Latitude	0.04	***		0.05	***	
		$F_{4,3169} = 191.1^{***}$			$F_{4,3167} = 178.7^{***}$		
Incubation period	Body weight	0.09	***	0.19	0.08	***	0.18
	Elevation	– 0.004	*NS*		– 0.01	*NS*	
	Geog. range	– 0.01	***		– 0.01	***	
	Latitude	– 0.004	*NS*		– 0.004	*NS*	
		$F_{4,1441} = 81.5^{***}$			$F_{4,1441} = 78.9^{***}$		
Adult survival	Body weight	3.23	*NS*	0.24	2.97	*NS*	0.27
	Elevation	– 2.10	*NS*		– 2.56	*NS*	
	Geog. range	– 4.28	***		– 4.32	***	
	Latitude	2.52	*		2.78	*	
		$F_{4,195} = 15.1^{***}$			$F_{4,196} = 17.7^{***}$		
Habitat breadth	Body weight	0.09	*NS*	0.27	0.35	*NS*	0.26
	Elevation	0.93	***		1.28	***	
	Geog. range	1.19	***		1.13	***	
	Latitude	– 0.21	***		– 0.02	*NS*	
		$F_{4,1845} = 168.3^{***}$			$F_{4,1865} = 169.1^{***}$		
(b) Maximum elevation							
Body weight	Elevation	0.04	***	0.006	0.03	***	0.006
	Geog. range	0.002	*NS*		– 0.01	***	
	Latitude	0.006	*		0.002	*NS*	
		$F_{3,5244} = 10.5^{***}$			$F_{3,5270} = 11.0^{***}$		
Clutch size	Body weight	– 0.02	**	0.19	– 0.04	***	0.17
	Elevation	0.002	*NS*		– 0.01	*	
	Geog. range	0.04	***		0.04	***	
	Latitude	0.04	***		0.04	***	
		$F_{4,4079} = 232.0^{***}$			$F_{4,4087} = 209.4^{***}$		
Incubation period	Body weight	0.09	***	0.18	0.09	***	0.17
	Elevation	– 0.002	*NS*		– 0.002	*NS*	
	Geog. range	– 0.01	***		– 0.01	***	
	Latitude	– 0.008	***		– 0.003	*NS*	
		$F_{4,1825} = 97.3^{***}$			$F_{4,1820} = 94.4^{***}$		

Table A5.3 Continued.

Dependent	**Independent**	**PICs (Ericson)**			**PICs (Hackett)**		
		β	***p***	***r^2***	**β**	***p***	***r^2***
(b) Maximum elevation							
Adult survival	Body weight	4.36	*	0.23	3.35	*NS*	0.24
	Elevation	– 0.59	*NS*		– 2.56	*NS*	
	Geog. range	– 4.60	***		– 4.68	***	
	Latitude	– 1.56	*NS*		– 0.96	*NS*	
			$F_{4,235} = 17.5^{***}$			$F_{4,237} = 19.2^{***}$	
Habitat breadth	Body weight	0.65	**	0.23	0.47	*	0.23
	Elevation	0.91	***		0.99	***	
	Geog. range	1.09	***		1.15	***	
	Latitude	0.00	*NS*		0.03	*NS*	
			$F_{4,2351} = 176.6^{***}$			$F_{4,2345} = 177.8^{***}$	
(c) Elevational midpoint							
Body weight	Elevation	0.04	***	0.01	0.04	***	0.01
	Geog. range	0.001	*NS*		– 0.02	***	
	Latitude	0.01	*		0.01	*	
			$F_{3,4088} = 14.0$			$F_{3,4113} = 15.8^{***}$	
Clutch size	Body weight	– 0.02	**	0.19	– 0.03	**	0.19
	Elevation	– 0.01	*NS*		– 0.02	**	
	Geog. range	0.04	***		0.04	***	
	Latitude	0.04	***		0.05	***	
			$F_{4,3168} = 188.9^{***}$			$F_{4,3168} = 180.1^{***}$	
Incubation period	Body weight	0.09	***	0.19	0.08	***	0.18
	Elevation	0.001	*NS*		0.002	*NS*	
	Geog. range	– 0.01	***		– 0.01	***	
	Latitude	– 0.004	*NS*		– 0.003	*NS*	
			$F_{4,1440} = 83.0^{***}$			$F_{4,1439} = 76.7^{***}$	
Adult survival	Body weight	3.70	*	0.23	2.95	*NS*	0.27
	Elevation	– 1.60	*NS*		– 3.12	*NS*	
	Geog. range	– 4.29	***		– 4.57	***	
	Latitude	1.84	*NS*		2.67	*	
			$F_{4,194} = 14.4^{***}$			$F_{4,196} = 18.0^{***}$	
Habitat breadth	Body weight	0.19	*NS*	0.25	0.61	**	0.23
	Elevation	0.28	*		0.57	***	
	Geog. range	1.34	***		1.19	***	
	Latitude	– 0.24	***		– 0.05	*NS*	
			$F_{4,1843} = 157.0^{***}$			$F_{4,1866} = 137.8^{***}$	

β: multiple regression coefficient (standardised). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. r^2: proportion of variance in the dependent variable explained by retained predictor variables. *NS*: independent variable not significant. Degrees of freedom and F-statistic value for each model also reported. All variables $\log_{10}$ transformed, except adult survival (arcsine transformed) and habitat breadth (untransformed).

CHAPTER SIX

Elevational distribution and trait variation of endemic birds

6.1 Abstract

Endemic species are an enigmatic and irreplaceable subset of species that are of high priority in terms of biodiversity conservation. Mountains are proven hotspots of terrestrial endemic species richness, but the reasons for this are poorly understood. Related to this, there is a distinct lack of studies to date on trait biogeography (especially with respect to elevation) for endemics. In addition, geographical spatial patterns of species richness have been shown to be largely driven by wide-ranging/generalist species, but it is unknown whether or not this is the same for underlying traits. Here, patterns of elevational distribution were investigated for a variety of endemic (and restricted range) global species-level data subsets, followed by an assessment of the relationships such endemic species display between elevational distribution and a suite of morphological, life-history and ecological traits, using both a bivariate and multivariate framework – within an entire taxonomic class (Aves). Such a study effectively removes any potential influence of wide-ranging/generalist species on patterns observed. Although endemic species were found to occur across a wide elevational gradient, such species were also found to possess a higher proportion of high-elevation species and to have narrower elevational ranges than both non-endemics and the full global dataset. Overall, endemic trait variation with respect to elevational distribution (range, maximum and midpoint) was found to mirror the trends found in both Chapters 4 and 5 when studying across species and associated phylogenetically independent contrasts. Namely, endemics with larger elevational ranges and both higher maximum elevations and elevational midpoints were still found to be associated with faster life-histories and broader niche breadth, and vice-versa. The findings from this study provide a vital platform for improving understanding of the underlying drivers of endemic species' range distributions, trait variation, and in turn, known spatial gradients of endemic species richness and the distribution of associated hotspots.

6.2 Introduction

Regardless of the existing ambiguity surrounding the definition of *endemic* (Section 1.7.1), collectively, endemic species are a highly valuable and unique subset of species in terms of biodiversity conservation. Not only are they of inherent conservation value (due to factors including irreplaceability and rarity), but they also play a central role in a number of high-profile global biodiversity conservation priority schemes (Section 1.7.3).

Concerning the biogeography of endemic species, as highlighted in Section 1.7.2 mountainous regions, predominantly in the tropics, are proven hotspots of terrestrial vertebrate endemic richness (e.g. Orme et al. 2005; Jenkins et al. 2013). However, the reasons for this are not clear. Although a number of studies have investigated elevational gradients of endemic species richness, such studies are geographically biased to small-scale research in the Neotropics and are predominantly plant focused; in turn revealing heterogeneous patterns (Section 1.7.2). Related to this, we currently know very little about the elevational range profiles of endemic species, i.e. are there any general characteristics in their elevational distribution and do such patterns differ with respect to non-endemics? The few existing studies find that endemic species possess narrower elevational ranges than non-endemics (e.g. Stotz 1998; Blackburn & Ruggiero 2001; Nogué *et al*. 2013). In addition, Blackburn & Ruggiero (2001) found endemic Andean passerines to possess higher elevational range minima, maxima and midpoints. Nevertheless, these studies are limited in terms of their taxonomic and geographic breadth.

Also, with regard to current understanding of endemic species, there is a surprising lack of studies concerning the biogeography of their traits (morphological, life history and ecological). Existing studies predominantly focus on 'true' island endemics, which in addition to continental mountains are also proven hotspots of endemic species richness (e.g. Orme *et al.* 2005; Jenkins *et al.* 2013). Certain unusual adaptations of endemic island birds are well-known, such as the repeated evolution of flightlessness and dispersal abilities, attributed to reduced predation pressure (Diamond 1981; Roff 1994), coupled with the benefits of energy conservation (McNab 1994). However, with the exception of morphological studies (e.g. Gaston & Blackburn 1995; Clegg & Owens 2002; Olson *et al.* 2009), broad-scale tests of patterns of adaptation in island endemic bird species are rare. Covas (2012) investigated global patterns in reproductive traits of island birds, finding that they generally have lower fecundity, greater reproductive investment and extended developmental periods (i.e. 'slower' life-history strategies) compared to their mainland counterparts, and that some differences between island and mainland birds (e.g. clutch size) are accentuated by latitude. Although the mechanisms underlying life-history evolution on islands remain largely unknown, improved adult survival is believed to be one of the main factors, resulting from reduced seasonality of resources and a stable climate in comparison to continental regions – particularly in temperate latitudes (see discussion in Whittaker & Fernandez-Palacios 2007; Covas 2012). Such stable conditions are also believed to have provided island taxa with a combination of traits that are often linked to the comparatively high extinction rate of oceanic island birds (see Fordham & Brook 2010, and references within).

No similar studies could be found explicitly investigating the traits of montane endemics, at any scale. Regarding trait variation with respect to elevational distribution in endemic species, only one study was found that researched this, for any taxa, and that then compared their results with patterns for corresponding non-endemics (i.e. Blackburn & Ruggiero 2001). For Andean endemic passerines (and for all species of passerine breeding in the Andes), they found a positive relationship between body weight and both maximum elevation and elevational midpoint, but not for elevational range. In contrast, the body weight of non-endemics was shown to not vary with any measure of elevational distribution. Although informative in relation to Bergmann's rule (Bergmann 1847), such an isolated study looking at a single trait precludes any generalities from being established. A large-scale assessment of the role of elevational distribution in determining variation in a variety of life-history and ecological traits for endemics is therefore required.

In this study, I addressed some of the important knowledge gaps highlighted above, using birds as a model system. Utilising a global avian species-level dataset and a comparative approach, the elevational distributions (range, maximum and midpoint) were identified for species falling under a range of endemic definitions. Specifically: (a) biogeographic realm endemics, (b) species with the smallest geographical ranges, and (c) mountain range endemics. This was followed by both bivariate and multivariate assessments of the relationships between avian life-history (morphological, reproductive, developmental, survival) and ecological (niche-breadth) traits associated with these species and elevational distribution, as studied in Chapters 4 and 5 for the full global dataset. This study is split into two connected parts and aimed to answer the following questions:

1) How does species-level elevational distribution vary between realm endemic and realm non-endemic species and between restricted-range species and the full global dataset? With a focus on comparing:
    a) number and proportion of high-elevational species,
    b) number and proportion of restricted elevational range species, and
    c) mean values of the three measures of elevational distribution.
2) How do life-history and ecological traits vary with respect to elevational distribution across endemic/restricted-range species, at the bivariate level and also after controlling for body weight, geographical range and latitude?
    a) Are relationships identified at the species level maintained across phylogenetically independent contrasts?

b) How do identified relationships differ from those found across all species at the global scale (Chapter 4: bivariate, Chapter 5: multivariate)?

In relation to the above questions, this study tested three broad null hypotheses, namely: (1) elevational range profiles do not differ between realm endemic and realm non-endemic species or restricted-range species and the full global dataset, (2) no relationship exists between variation in avian traits and elevational distribution for endemic and restricted-range species at the bivariate level, and (3) elevational distribution is not retained as a significant predictor of avian traits for endemic and restricted-range species when controlling for body weight, geographical range and latitude.

Finally, previous grid-cell based studies have shown that geographical spatial patterns of species richness are determined by the distribution of wide-ranging/generalist species (e.g. Jetz & Rahbek 2002; Lennon *et al.* 2004; see also Section 1.7.2) – but it is unknown as to whether or not this is also the case for underlying traits. This can be explicitly assessed here, as the potential influence of wide-ranging/generalist species on the patterns observed has been effectively removed. Removal of such species also considerably reduces the issue of spatial autocorrelation, as the data subsets to be analysed do not overlap spatially, i.e. they are geographically distinct.

6.3 Materials and methods

The overall general methodology and details on the materials used are described and justified in full in Chapter 3.

6.3.1 Endemic and restricted-range definitions

As no single consensus definition exists as to what constitutes either an endemic or restricted-range species, and pros and cons surround different interpretations of both (see discussion in Section 1.7.1), a complementary suite of both breeding range endemic and restricted breeding range definitions were used to address the aims of this study – derived as follows:

Biogeographic realm breeding range endemics (realm endemics): Defined as any species whose geographical breeding range falls completely within the boundary of a given biogeographic realm (Olson *et al.* 2001). Specifically, realm endemics were determined for the Nearctic, Palearctic, Neotropical, Afrotropical, Indo-Malay, Australasia and Oceania realms. Table 6.1 shows that the Neotropical realm contains by far the largest number of realm endemic species and also the highest proportion. The Oceanic realm contains the lowest number of realm endemic species, whereas the Nearctic and Palearctic have the lowest proportion.

Realm non-endemics: Non-endemic species for each of the above mentioned biogeographic realms were also identified and used as a comparative subset for all analyses. Specifically, realm non-endemics were those species that breed in more than one biogeographic realm.

Table 6.1 Number (*n*) of realm endemics that possess maximum elevation data, and elevational range/midpoint data. 'Total' provides the number of both endemic and non-endemic species for a given biogeographic realm. '% total' gives the proportion of species breeding in a given biogeographic realm that are endemic to it. Biogeographic realms delimited by Olson *et al.* (2001).

	Biogeographic realm breeding range endemics					
	Maximum elevation			**Elevational range/midpoint**		
	Total	***n***	**% total**	**Total**	***n***	**% total**
Afrotropical	1353	1181	87.3	988	862	87.2
Australasia	1162	923	79.4	973	771	79.2
Indo-Malay	1314	678	51.6	954	476	49.9
Nearctic	446	191	42.8	386	159	41.1
Neotropical	3129	2900	92.7	2605	2401	92.2
Oceania	128	75	58.6	117	69	59.0
Palearctic	1060	377	35.6	784	285	36.4

Restricted-range species (lower quartile): Defined as the 25% of species with the smallest geographical breeding ranges, as proposed by Gaston (1994b) and used in global studies of biodiversity hotspots (e.g. Orme *et al*. 2005; Grenyer *et al.* 2006). As this definition is dependent upon the selection of species included in the analysis, two dataset variants were used, specifically:

a) *Lower quartile (broad):* In the full dataset, 9243 species have geographical range data – 25% of 9243 = 2311. The geographical range cut-off occurs within those species with a geographical range of 31 equal-area (1°x1°) grid cells (i.e. approximately 310,000km^2). This definition identified 2277 species with geographical ranges restricted to <31 grid cells, of which 1545 species possess elevational range data.
b) *Lower quartile (narrow):* In the full dataset, 5655 species have both geographical range and elevational range data – 25% of 5655 = 1414. The geographical range cut-off occurs within those species with a geographical range of 27 equal-area (1°x1°) grid

cells (i.e. approximately 270,000km^2). This definition identified 1373 species with geographical ranges restricted to <27 grid cells.

Restricted-range species (BirdLife International): BirdLife International (2013) defines restricted-range species as all landbirds that have had, throughout historical times (i.e. since 1800), a total global breeding range estimated at below 50,000km^2 – the arbitrary threshold value proposed by Terborgh & Winter (1983), and roughly equivalent to the size of Costa Rica. Species with historical ranges estimated to be above this threshold, but which have since been reduced to below 50,000km^2 are not included in their definition, as the Endemic Bird Area (EBA) project aims to locate natural areas of endemism for birds (Stattersfield *et al*. 1998). Using this criterion, BirdLife International recognises around 2,500 (>25% of the world's total) landbirds as restricted-range species (BirdLife International 2013).

Using the full study dataset, 595 species were found to have a geographical range of approximately less than 50,000km^2. This was determined by identifying all species with a geographical range covering ≤5 equal-area (1°x1°) grid cells. Of these, only 355 species possess elevational range data. There is clearly a large discrepancy in the sample sizes obtained by BirdLife International and this study. Nevertheless, for completeness, and because 50,000km^2 is a commonly utilised threshold for defining restricted-range species, all analyses were also conducted using this definition as applied to this study dataset. However, the results are reported as supplementary material only.

This difference in sample size is potentially due to BirdLife International being cautious and consequently overestimating the number of restricted-range species (particularly those around the threshold value). In addition, it could also be attributed to the use in this study of cell-count as a measure of geographical breeding range, rather than the area within the raw extent of occurrence polygons – leading to an overestimation in range size and, in turn, an underestimation in the number of restricted-range species. Via BirdLife International's Data Zone (BirdLife International 2013), endemic species can be filtered for (*n* = 2519 species), and it is clear that some of the species, predominantly those currently listed as Least Concern (LC) under the IUCN Red List (2012.2 update), have extremely large geographical ranges greater than 50,000km^2. For example, *Acanthiza nana* (Yellow thornbill), has a reported distribution of 2,020,000 km^2.

Mountain breeding range endemics (mountain endemics): Defined as those bird species whose geographical breeding range was found to be largely endemic to each of the following three mountainous regions:

a) Andes

b) East African Rift (EAR) mountains (Western and Eastern Great Rift Valley merged)
c) Himalayas

These three mountainous regions were selected over others based on the fact that they are the top three avian species richness hotspots (Orme *et al.* 2005), and so provide the largest sample sizes. For a detailed protocol as to how mountain endemic species were identified, see section 6.3.2.

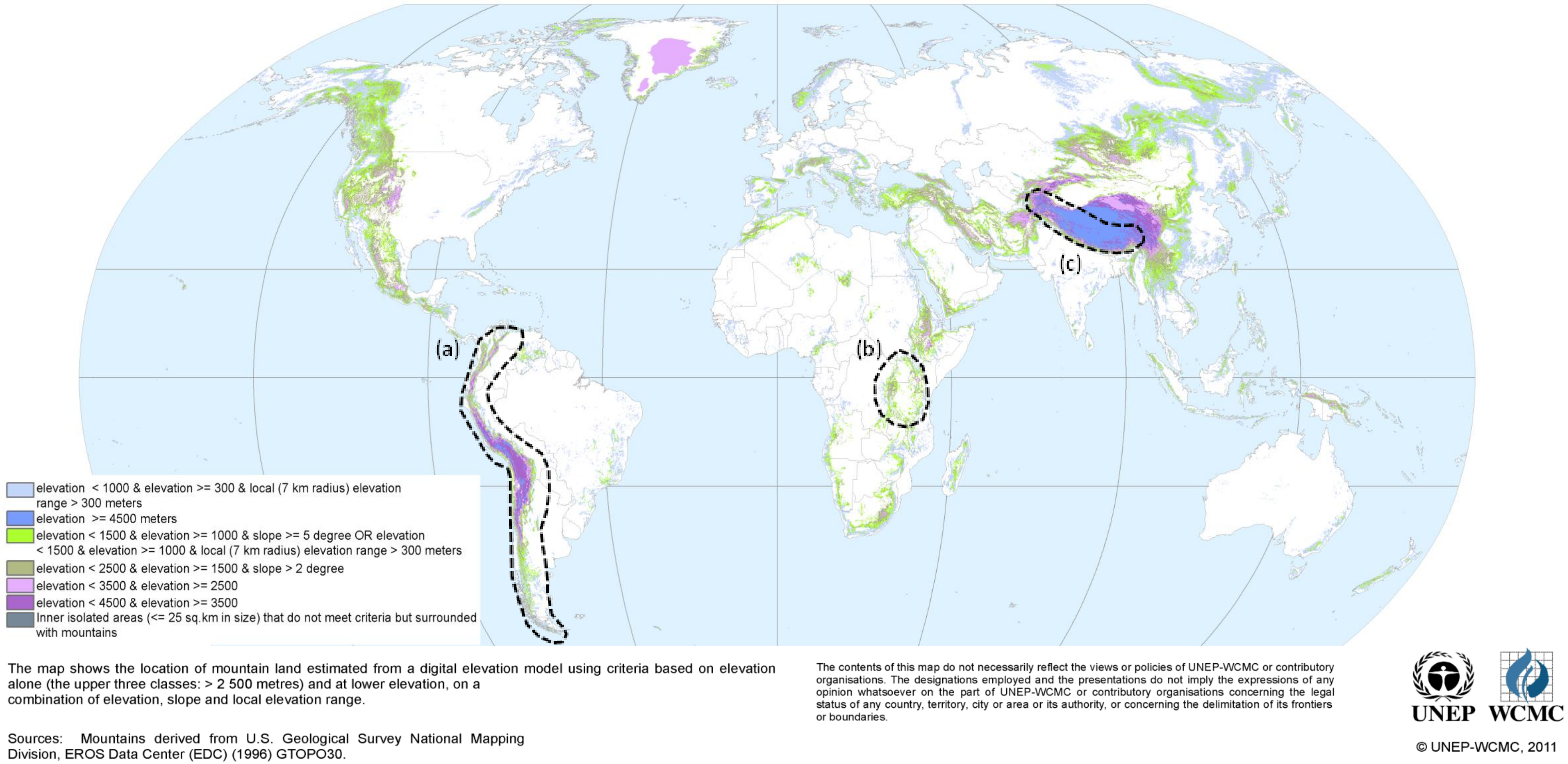
6.3.2 Mountain endemics

Global mountain study definition: To identify mountainous areas for the purposes of this study, the decision was made to use the 2002 UNEP-WCMC version of the 'world mountain map' first developed by Kapos *et al*. (2000). For a discussion of this and other existing global mountain definitions, see Section 1.5. Table 1.1 provides a summary of the seven UNEP-WCMC (2002) mountain classes and the criteria used to define them, and Fig. 6.1 shows the resulting 'world mountain map'.

This global mountain definition was chosen over others (e.g. Meybeck *et al.* 2001; Körner *et al.* 2011) for a number of reasons, including: (1) the combination of criteria used represent the environmental gradients that are key components of the world's mountain environments, and provides a way for consistent comparison of mountain life zones globally; (2) it is more conservative than other methods; (3) the underlying methodology is transparent, standardised and easy to replicate; (4) UNEP-WCMC have made it freely downloadable (see link in Fig. 6.1); (5) it has been widely used in other studies, either in its original or revised format. For example, the UNEP-WCMC (2002) world mountain classification and map were used by Nogués-Bravo *et al*. (2007) to investigate the magnitude of future warming during the 21st century on different mountain systems, by Platts *et al.* (2011) as a starting point for delimiting the Eastern Arc Mountains, by Rodríguez-Rodríguez *et al*. (2011) to assess progress towards international targets for protected area coverage in mountains, and by Rodríguez-Rodríguez & Bomhard (2011) to assess the degree of direct human impact on the world's mountain areas.

Mountain range delineation and extraction of species lists: The following protocol was conducted entirely within ArcMap version 10.0 (ESRI 2011), using a Berhmann equal-area projection.

Data sources: The 'Mountains and Tree Cover in Mountain Regions 2002' dataset was downloaded from the UNEP-WCMC website (http://www.unep-wcmc.org/mountains-and-tree-cover-in-mountain-regions-2002_724.html), and from this dataset, the 'Mountains of



- 🟦 elevation < 1000 & elevation >= 300 & local (7 km radius) elevation range > 300 meters
- 🟦 elevation >= 4500 meters
- 🟩 elevation < 1500 & elevation >= 1000 & slope >= 5 degree OR elevation < 1500 & elevation >= 1000 & local (7 km radius) elevation range > 300 meters
- 🟩 elevation < 2500 & elevation >= 1500 & slope > 2 degree
- 🟪 elevation < 3500 & elevation >= 2500
- 🟪 elevation < 4500 & elevation >= 3500
- ⬛ Inner isolated areas (<= 25 sq.km in size) that do not meet criteria but surrounded with mountains

The map shows the location of mountain land estimated from a digital elevation model using criteria based on elevation alone (the upper three classes: > 2 500 metres) and at lower elevation, on a combination of elevation, slope and local elevation range.

Sources: Mountains derived from U.S. Geological Survey National Mapping Division, EROS Data Center (EDC) (1996) GTOPO30.

The contents of this map do not necessarily reflect the views or policies of UNEP-WCMC or contributory organisations. The designations employed and the presentations do not imply the expressions of any opinion whatsoever on the part of UNEP-WCMC or contributory organisations concerning the legal status of any country, territory, city or area or its authority, or concerning the delimitation of its frontiers or boundaries.

Figure 6.1 Mountains of the world (defined by UNEP-WCMC 2002). Dashed lines represent the rough boundaries of the three study mountainous regions: (a) Andes, (b) East African Rift, and (c) Himalayas. Above map freely downloadable from: http://www.unep-wcmc.org/mountains-and-tree-cover-in-mountain-regions-2002_724.html the World – 2002’ raster was imported and converted to a vector. This was overlaid with polygon breeding range maps (Orme *et al.* 2005) for 9,626 extant, recognised bird species, following the standard taxonomy of Silbley & Monroe (1990, 1993). The species’ breeding range maps were organised into 143 family-level shapefiles and each species’ breeding range were represented by one or more polygons. Details of the methodology and wide range of data sources used for creating the breeding range maps can be found in the Supplementary Material of Orme *et al.* (2005, 2006). Briefly, distributions were compiled from the most accurate sources giving expert opinion range (extent of occurrence) maps for a given broad geographic region or taxonomic group. In order to define the terrestrial land-area boundary, version 2.2.0 of the Global Self-consistent Hierarchical High-resolution shoreline (GSHHS) dataset (Wessel & Smith 1996) was downloaded (http://www.ngdc.noaa.gov/mgg/shorelines/gshhs.html), and from this, the full resolution ocean-land shorelines polygon imported – derived from the World Vector Shoreline (WVS) project (Soluri & Woodson 1990).

Mountain range delineation: No previously defined explicit boundaries could be found for the full extent of the Andes, EAR, or Himalayas – coordinate or descriptive based. Related to this, ecological studies focusing on mountainous areas rarely seem to explicitly define their study area. For example, Ruggiero & Lawton (1998) and Blackburn & Ruggiero (2001) both conducted studies on Andean passerine birds (endemics and non-endemics), yet provide no clear definition or map of the Andes extent that they use. Ruggiero & Lawton (1998) merely state that ‘*the maximum possible latitudinal distribution of the Andean endemics extends from 11°N (the northernmost extent of the Andes) to 55°S*’, with no justification given, and no longitudinal extent or lowland cut-off provided. Such a lack of transparency prevents replication and hinders comparison.

For the purposes of this study, the UNEP-WCMC (2002) world mountain map was used to delineate the boundaries of the three selected mountainous regions. Terrestrial land was considered mountainous if it was included in any one of the seven mountain classes (Table 1.1, Fig. 6.1), including class seven (i.e. isolated inner basins and plateaus). Using this definition imposed a lower cut-off elevation of 300 m.

The Andes mountain region (Figs. 6.1–6.2) was taken to extend from Venezuela in the north, through Colombia, Ecuador, Peru, Bolivia, Chile and Argentina in the south. A crude polygon shapefile was initially created that used the coastline as the western and southern boundary, with the northern and eastern boundary defined by smoothly drawing around the outermost mountainous areas of the Andean region. This shapefile was subsequently refined by clipping it to include only areas above 300 m, and excluding distinct outliers and islands (e.g. the Sierras Pampeanas mountains of northwestern Argentina).

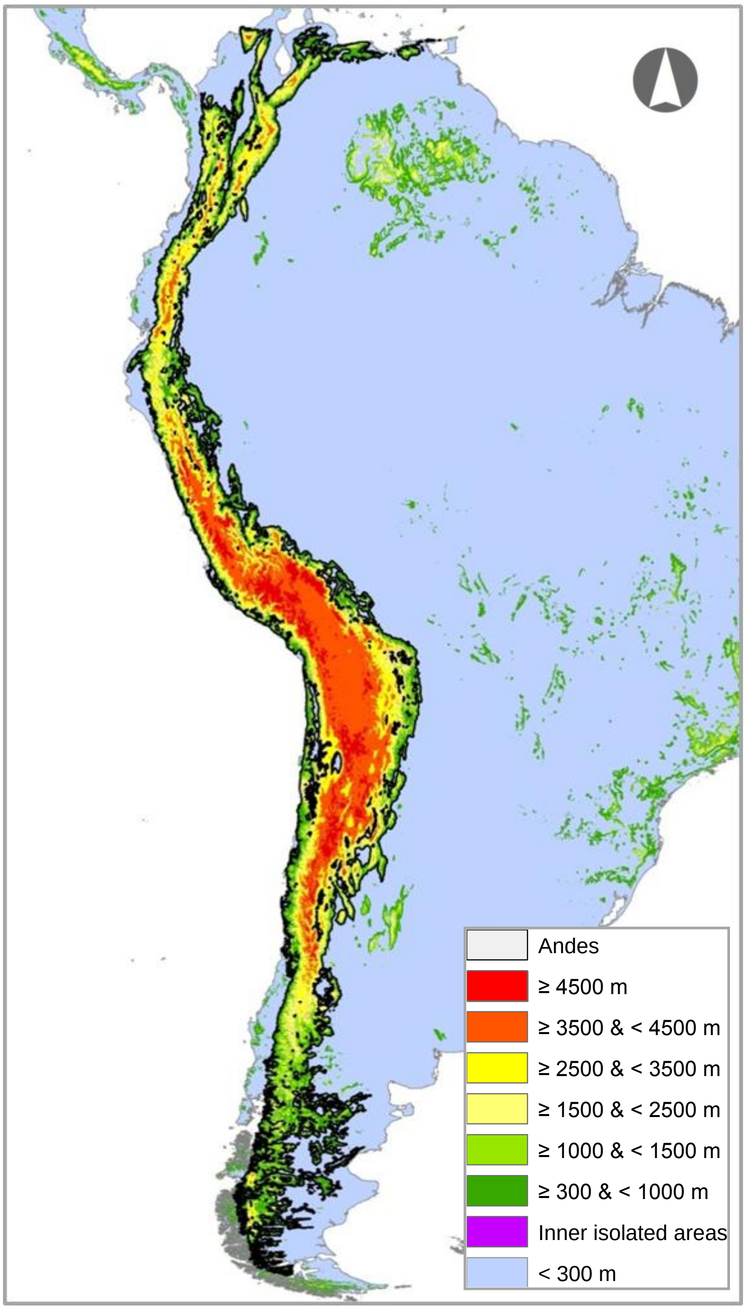


Figure 6.2 Study boundary for the Andean mountainous region, covering an area of 2,580,978 km^2. Mountain classes are those defined by UNEP-WCMC (2002). For a more detailed description of the mountain classes, see Table 1.1.

In equatorial Africa, The East African rift (part of the larger Great Rift System) has two branches. The eastern branch, referred to as the Great Rift Valley or Eastern Great Rift Valley, and the western branch, commonly known as the Albertine Rift or the Western Great Rift Valley. Lake Victoria lies between the two branches. The EAR mountain region (Figs. 6.1, 6.3) proved difficult to delineate, but included the Eastern and Western Great Rift Valley's, the Eastern Arc Mountains, and surrounding continuous mountainous areas. Conservation International's (CI) 'Eastern Afromontane' hotspot shapefile was downloaded (http://www.conservation.org/where/priority_areas/hotspots/africa/Eastern-Afromontane/

Pages/default.aspx) to assist in identifying the Eastern and Western Great Rift Valley's. The southern boundary of the EAR shapefile was taken to be the northernmost point of Lake Malawi. The final shapefile was clipped to include only areas greater than 300 m. The lower cut-off elevation of 300 m removed the central lowland plain in the EAR shapefile, but a few isolated peaks remained. However, the retention of these peaks did not affect the final species list, and so were retained.

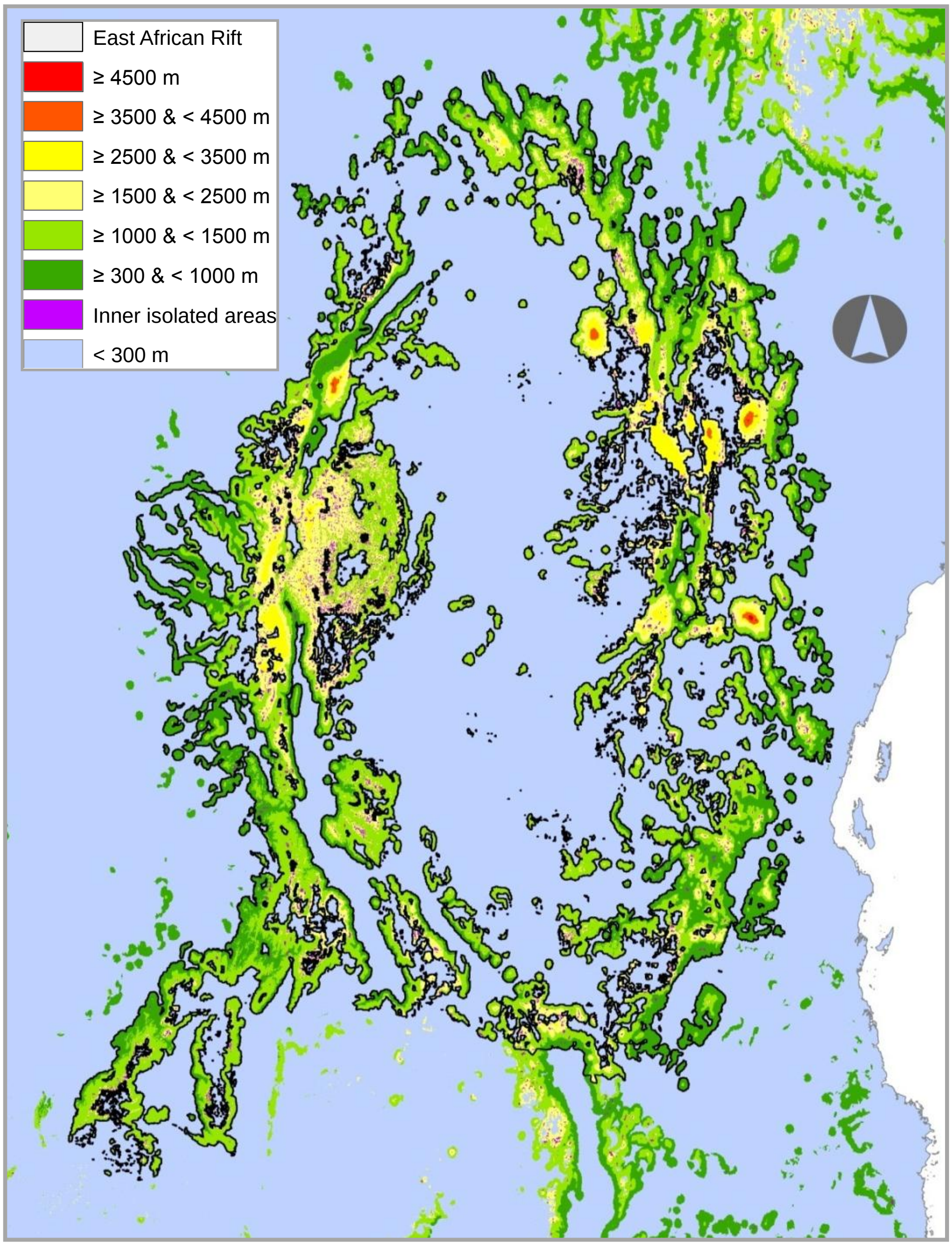


Figure 6.3 Study boundary for the East African Rift mountainous region, covering an area of 575,300km^2. Mountain classes are those defined by UNEP-WCMC (2002). For a more detailed description of the mountain classes, see Table 1.1.

The Himalayas mountain region (Figs. 6.1, 6.4) was largely derived using CI's 'Himalaya' hotspot shapefile, downloaded via (http://www.conservation.org/where/priority_ areas/hotspots/asia-pacific/Himalaya/Pages/default.aspx). This shapefile was subsequently refined by clipping it to include only areas above 300 m. An additional shapefile was created that smoothed the northern boundary, but was found to not affect the final species list obtained and was therefore not used.

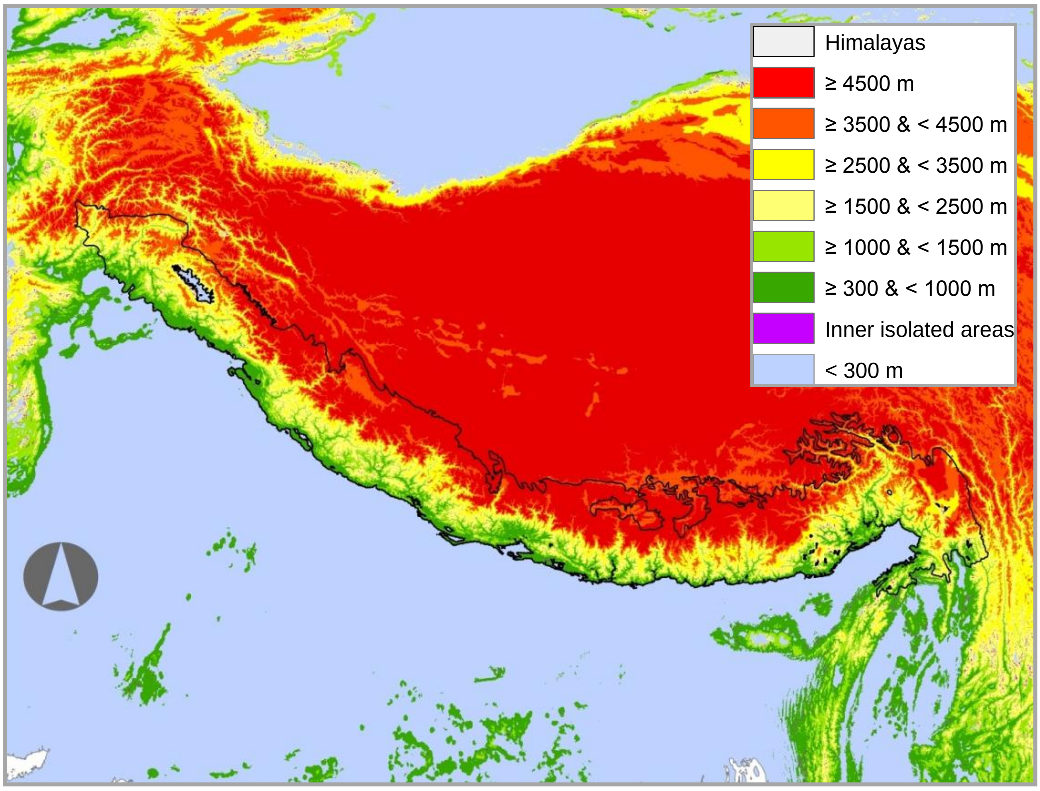


Figure 6.4 Study boundary for the Himalayan mountainous region, covering an area of 635,125 km^2. Mountain classes are those defined by UNEP-WCMC (2002). For a more detailed description of the mountain classes, see Table 1.1.

Compiling mountain endemic species lists: Each family-level shapefile containing species' breeding range polygons was clipped, in turn, to each of the three mountainous region polygons (Figs. 6.2–6.4). If any part of the range map for a given species occurred within the boundary for a given mountainous region, then it was initially included in the mountain endemic species list. When clipping of all breeding range maps was completed for a given mountainous region, the clipped family-level shapefiles were merged and the corresponding DBF attribute file opened up in Excel for further processing.

Species in the global dataset that had been merged after the creation of the breeding range maps, following BirdLife International (2012), were accounted for, slightly reducing the number of species in the mountain endemic species lists. Species were then removed from the lists if they were not endemic to the biogeographic realm encompassing each mountainous region (i.e. Andes = Neotropical, EAR = Afrotropical, Himalayas = Palearctic and/or Indo-Malay). Finally, the remaining species were retained if they possessed:

a) *Mountain endemic (broad):* a maximum elevational limit >300 m, OR
b) *Mountain endemic (narrow):* a maximum elevational limit >300 m AND a minimum elevational limit >300 m.

Table 6.2 summarises the samples sizes of the final mountain endemic species lists. The Andes assemblage contains more than three times the number of endemic species found in the EAR and Himalayan assemblages.

Table 6.2 Number of species (*n*) classified as mountain endemics – Andes, East African Rift (EAR) and the Himalayas. 'Broad' mountain endemics possess a maximum elevational limit >300 m, and 'narrow' mountain endemics possess both maximum and minimum elevational limits >300 m.

	***n* (broad)** *maximum elevation > 300 m*	***n* (narrow)** *maximum & minimum elevation > 300 m*
Andes	1645	746
EAR	541	230
Himalayas	440	236

6.3.3 Statistical analyses

Elevational range profiles: To provide a way with which to effectively visualise and compare patterns of elevational distribution across each of the endemic and restricted-range species subsets outlined in Section 6.3.1, elevational ranges of species were ranked by their elevational midpoints, minima and maxima, then plotted as bar graphs, producing 'elevational range profiles' (Patterson *et al.* 1996). Specifically, these profiles were produced for the full global dataset, total realm assemblages, realm endemics, realm non-endemics, restricted-range species (lower quartile and BirdLife International) and mountain endemics. This graphical treatment has been used before for species occurring along a single elevational gradient (e.g. Patterson *et al.* 1998; Chettri *et al.* 2010; Liew *et al.* 2010). Related to these elevational range profiles, I also compared the number and proportion of realm endemic and realm non-endemic species with high elevational distributions (defined here as any species with a minimum elevation ≥1000m), and the number and proportion with a restricted elevational range (defined here as any species with an elevational range ≤500m). As discussed in Section 1.6, no consensus definition exists for classifying a bird species as montane. Therefore, the decision was made to use a cut-off of 1000m based on the recent global study by La Sorte & Jetz (2010). Similarly, the restricted elevational range definition used here is taken from that used by Sekercioglu *et al.* (2004) in their study based on extinction-prone bird groups and the consequences of bird declines. Finally, independent samples t-tests were performed in order to compare $\log_{10}$ transformed mean elevational range, maximum elevation and elevational midpoint values between realm endemic and realm non-endemic species.

Bivariate relationships between avian traits and elevational distribution: For each of the endemic and restricted range species subsets outlined in Section 6.3.1, bivariate relationships between avian traits and elevational distribution (range, maximum and midpoint) were determined via Reduced Major Axis (RMA) bivariate linear regression analysis, using the same protocol employed in Chapter 4 (Section 4.3.2). The avian traits investigated were: (a) morphology (body weight, wing length, tarsus length, culmen length), (b) reproduction (clutch size, annual fecundity, egg weight), (c) development (incubation period, fledging time, age at first breeding), (d) survival (adult survival), and (e) niche breadth (diet breadth, habitat breadth). See Section 3.3 for a concise overview of each study variable. To better comply with the assumptions of normality, all study variables were $\log_{10}$ transformed prior to analysis, except adult survival which was arcsine transformed, and both diet breadth and habitat breadth, which were untransformed (Section 3.4). In order to account for variation in the degree of common phylogenetic association, the bivariate relationships for all realm endemics were additionally assessed using phylogenetically independent contrasts (PICs) – see Section 3.5.3.

Multivariate relationships between avian traits and elevational distribution: Using the same protocol employed in Chapter 5 (Section 5.3.2), stepwise multiple regression models (α-to-enter/remove = 0.05) were performed to investigate the relative influence of elevational distribution on trait variation when controlling for potentially confounding variables (i.e. body weight) and known geographical spatial covariates of avian traits (i.e. geographical range and absolute mean latitude). Models were produced separately at the species level for: all realm endemics, all realm non-endemics, and each mountain endemic subset (Andes, EAR and Himalayas) – using the broad definition. To ensure the maximum sample size possible for each group of traits, body weight (morphology), clutch size (reproduction), incubation period (development), adult survival (survival) and habitat breadth (niche breadth) were entered as independent variables in turn. The same multiple regression models outlined above were additionally conducted across PICs (Section 3.5.3) for all realm endemics.

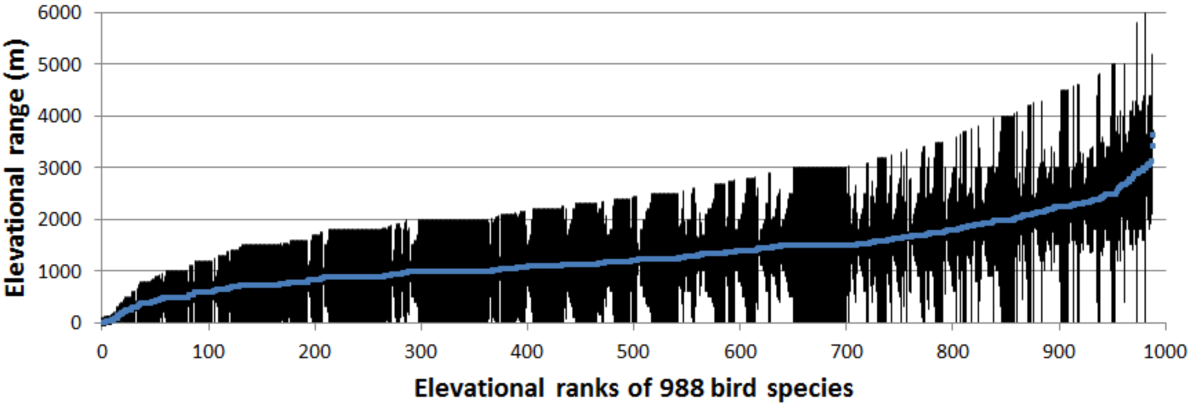
6.4 Results

6.4.1 Elevational range profiles

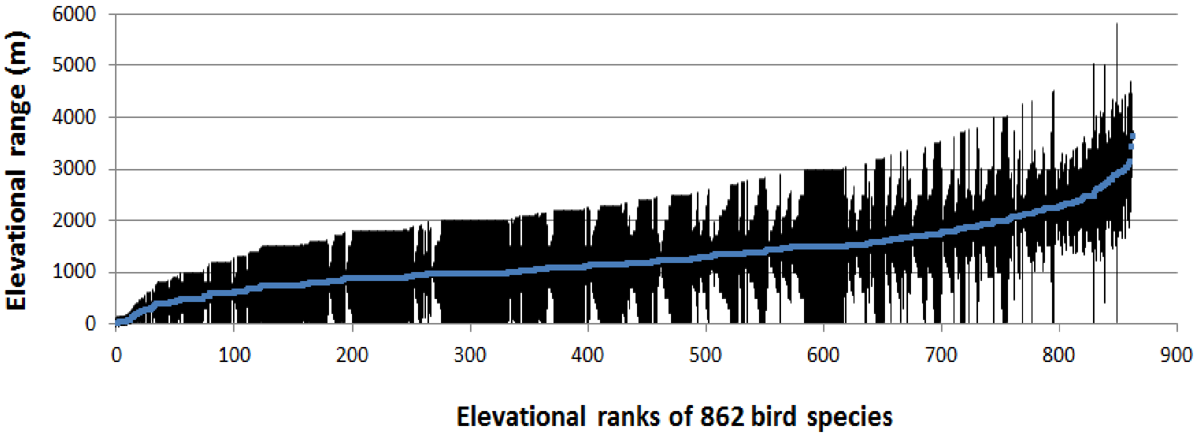
The biogeographic realm elevational range profiles for: (a) all species within a given realm, (b) realm endemics, and (c) realm non-endemics are displayed in Figs. 6.5–6.11. Overall, they show that both realm endemics and realm non-endemics occur across a wide elevational gradient at both low and high elevations. However, realm non-endemics with the highest elevational midpoints typically have large elevational ranges that span from the lowest to the highest elevations, whereas realm endemics with the highest elevational midpoints are instead generally found not to occur at the lowest elevations, i.e. they are restricted to higher elevations. As summarised in Table 6.3, realm endemics comprise of both more and a greater proportion of high-elevation species (i.e. minimum elevation ≥1000m) than realm non-endemics – except for within the Nearctic. In addition, a greater proportion of realm endemics have restricted elevational ranges (i.e. ≤500m) than realm non-endemics (Table 6.4), with the realm endemic elevational range profiles showing that these restricted elevational range species occur across the elevational gradient for any given realm. Mean elevational range, maximum elevation and elevational midpoint were found to be significantly lower for realm endemics than realm non-endemics, except for within the Palearctic realm where mean elevational range was essentially the same for realm endemics and realm non-endemics, and mean maximum elevation and elevational midpoint higher for realm endemics (Table 6.5).

Afrotropical realm

(a) All species



(b) Realm endemics



(c) Realm non-endemics

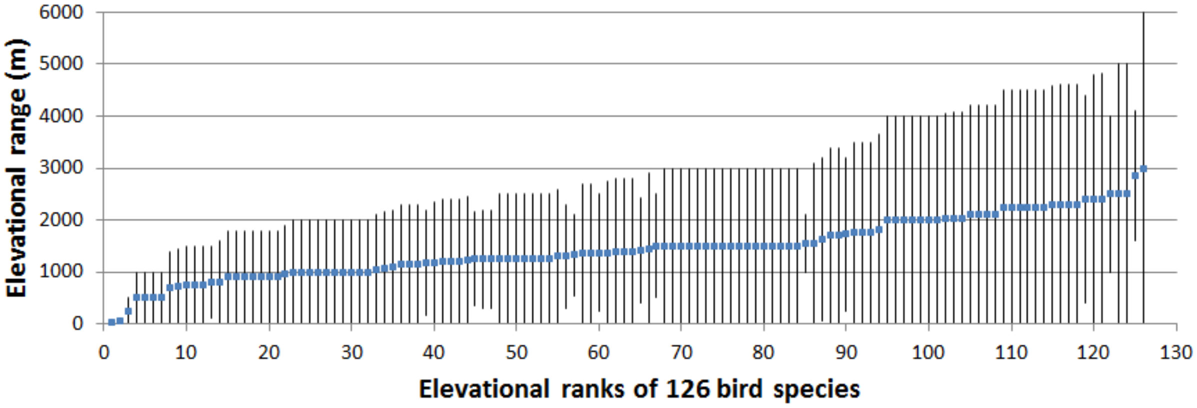
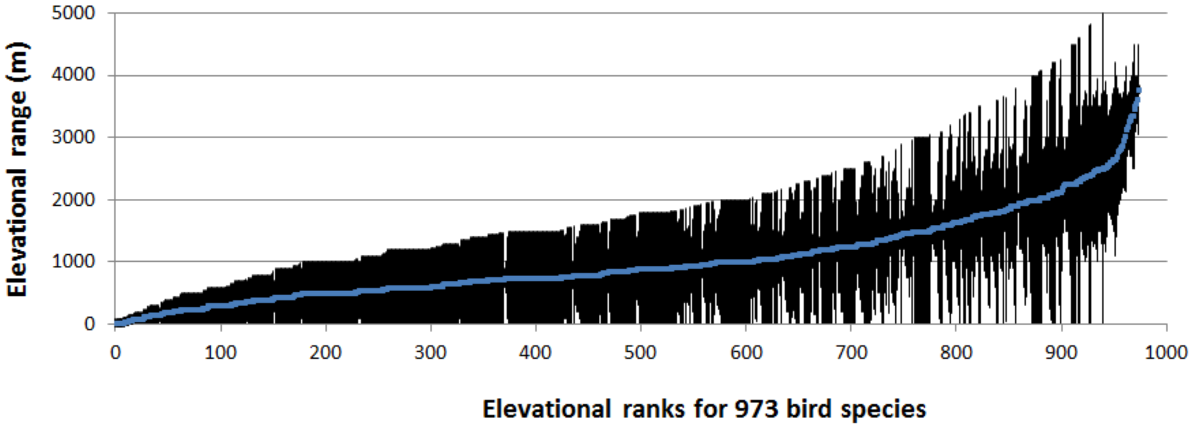


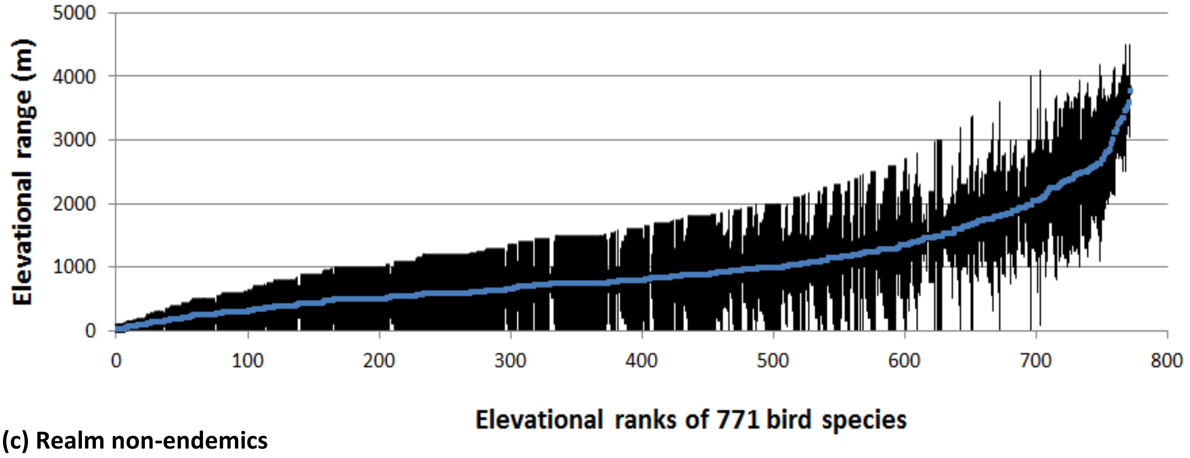
Figure 6.5 Elevational range profile for bird species with breeding ranges occurring within the Afrotropical biogeographic realm (Olson *et al.* 2001) and possessing elevational range data: (a) all species, (b) realm endemics, (c) realm non-endemics. Bars indicate the minimum and maximum elevational limits for each species' range, and species are arranged along the x-axis by ranked elevational midpoints.

Australasia realm

(a) All species



(b) Realm endemics



(c) Realm non-endemics

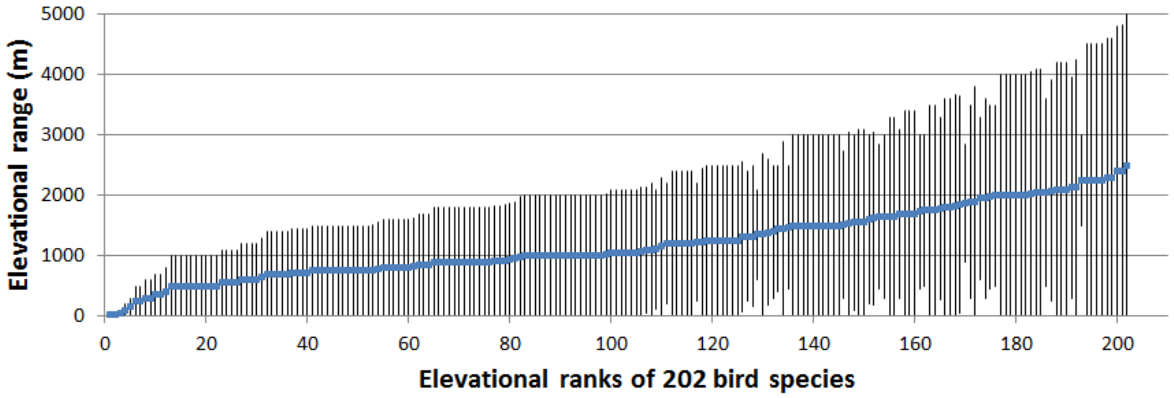
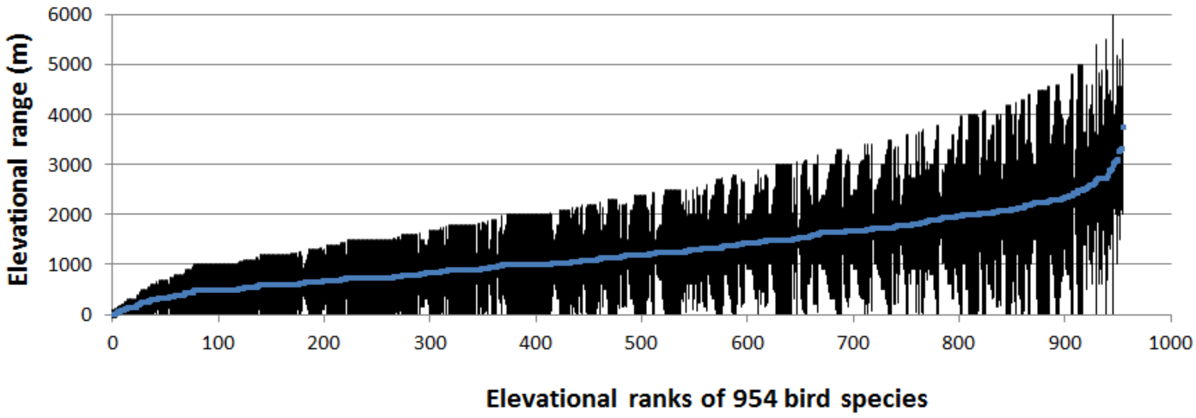


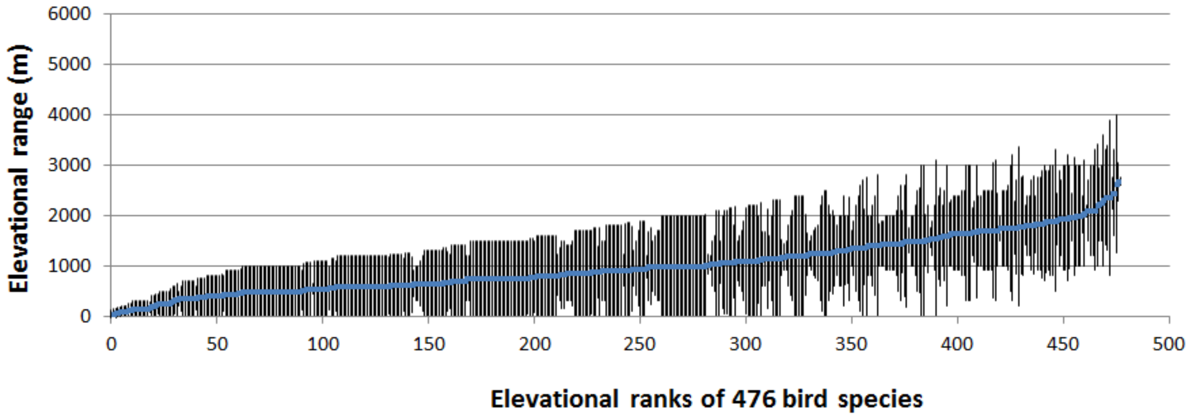
Figure 6.6 Elevational range profile for bird species with breeding ranges occurring within the Australasia biogeographic realm (Olson *et al.* 2001) and possessing elevational range data: (a) all species, (b) realm endemics, (c) realm non-endemics. Bars indicate the minimum and maximum elevational limits for each species' range, and species are arranged along the x-axis by ranked elevational midpoints.

Indo-Malay realm

(a) All species



(b) Realm endemics



(c) Realm non-endemics

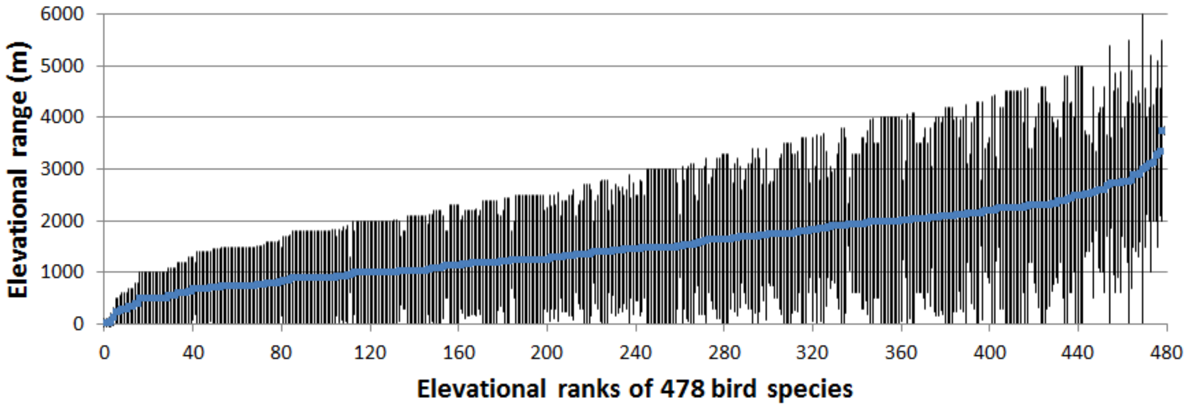
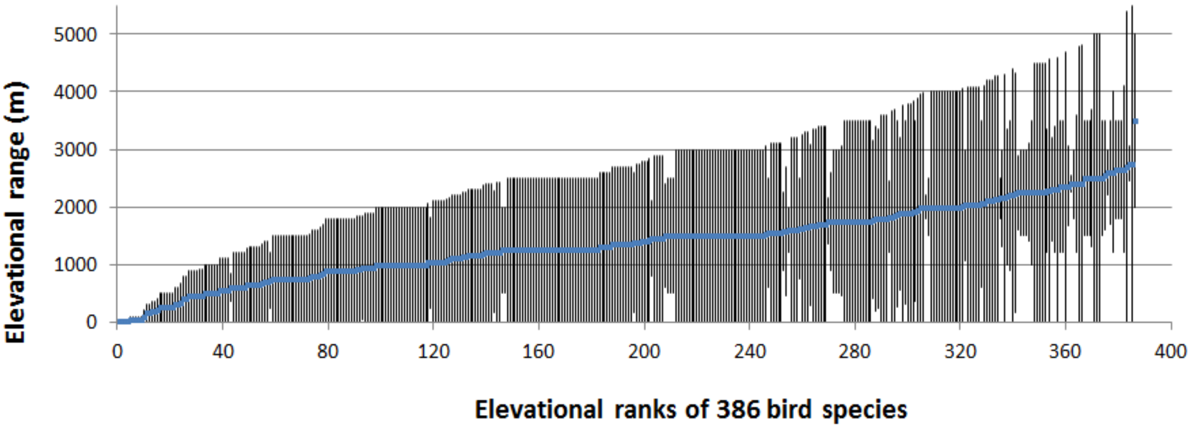


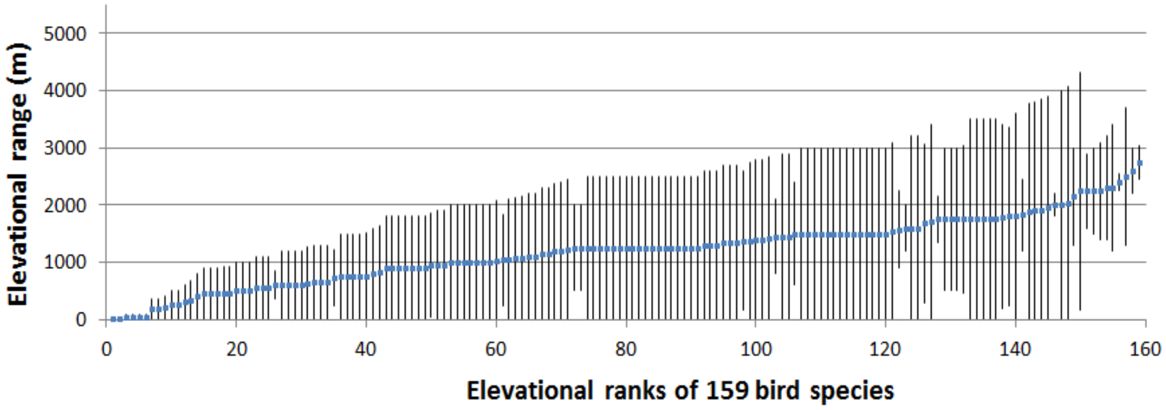
Figure 6.7 Elevational range profile for bird species with breeding ranges occurring within the Indo-Malay biogeographic realm (Olson *et al.* 2001) and possessing elevational range data: (a) all species, (b) realm endemics, (c) realm non-endemics. Bars indicate the minimum and maximum elevational limits for each species' range, and species are arranged along the x-axis by ranked elevational midpoints.

Nearctic realm

(a) All species



(b) Realm endemics



(c) Realm non-endemics

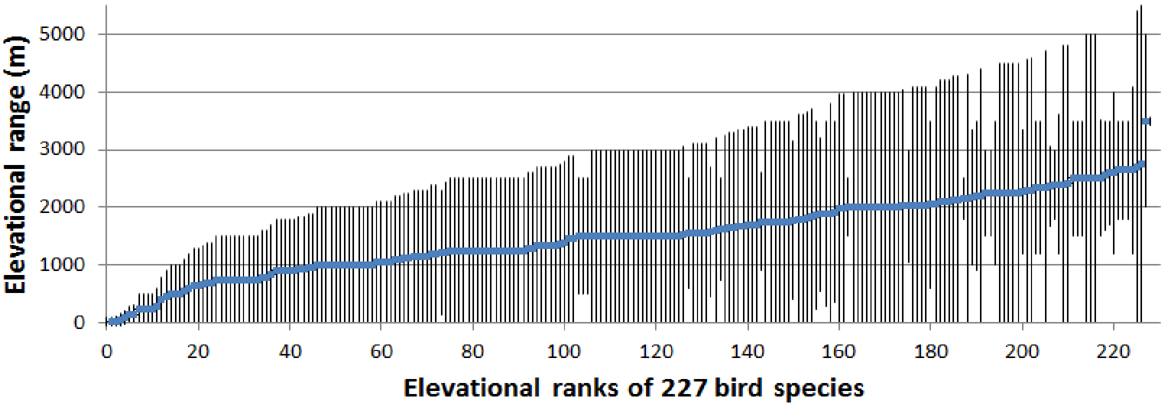
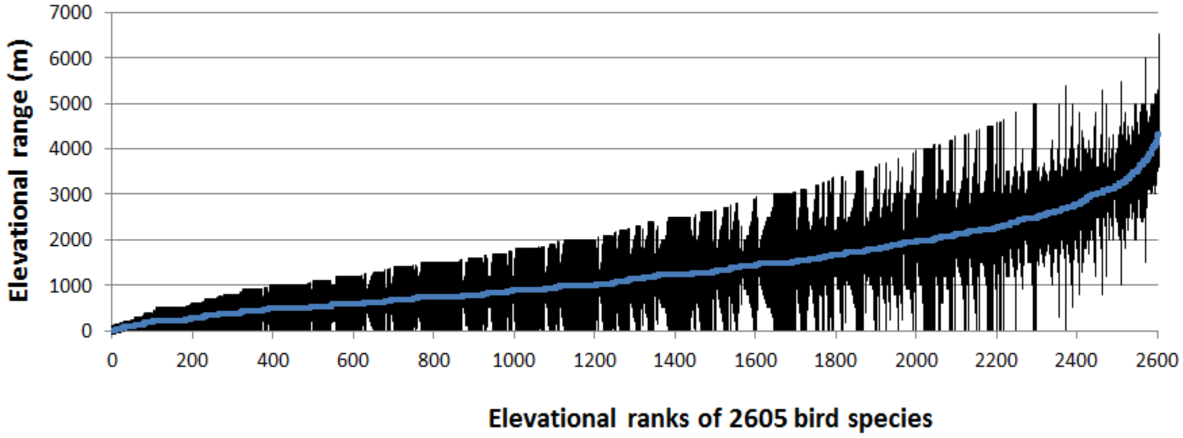


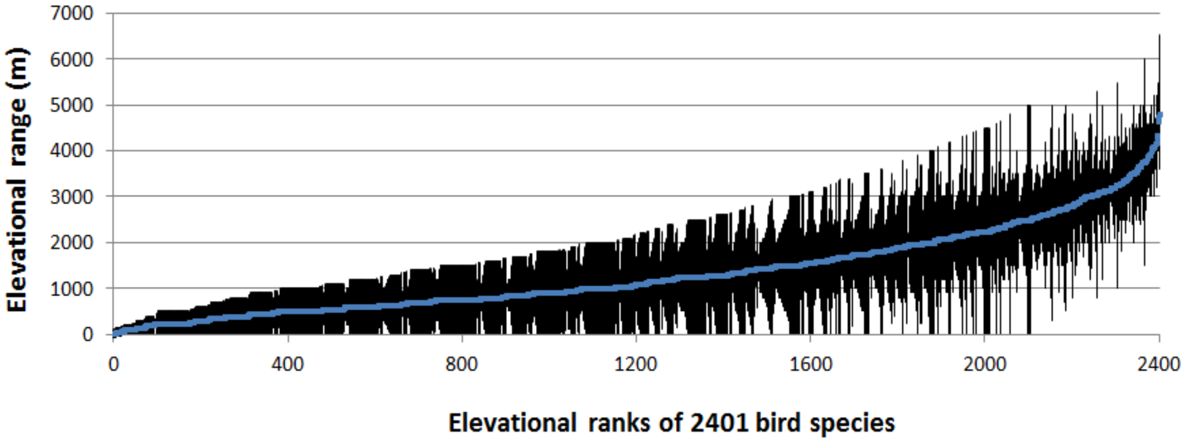
Figure 6.8 Elevational range profile for bird species with breeding ranges occurring within the Nearctic biogeographic realm (Olson *et al.* 2001) and possessing elevational range data: (a) all species, (b) realm endemics, (c) realm non-endemics. Bars indicate the minimum and maximum elevational limits for each species' range, and species are arranged along the x-axis by ranked elevational midpoints.

Neotropical realm

(a) All species



(b) Realm endemics



(c) Realm non-endemics

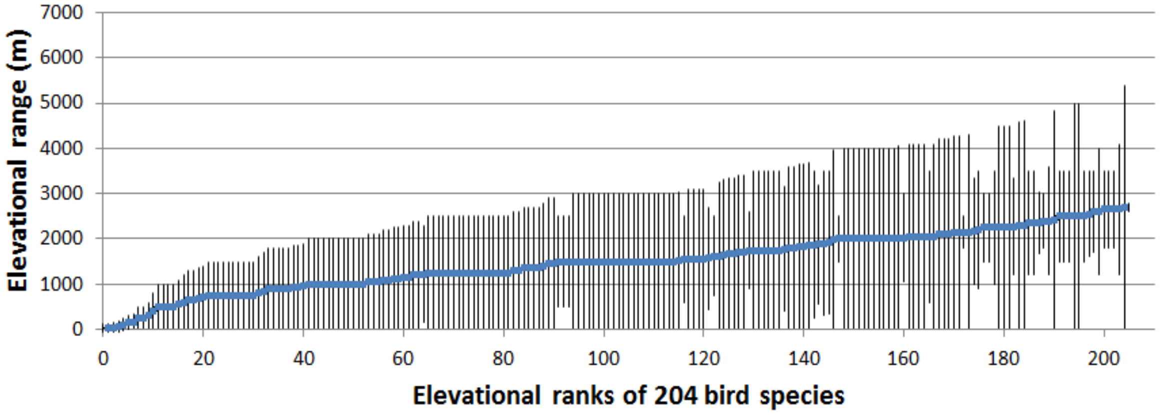
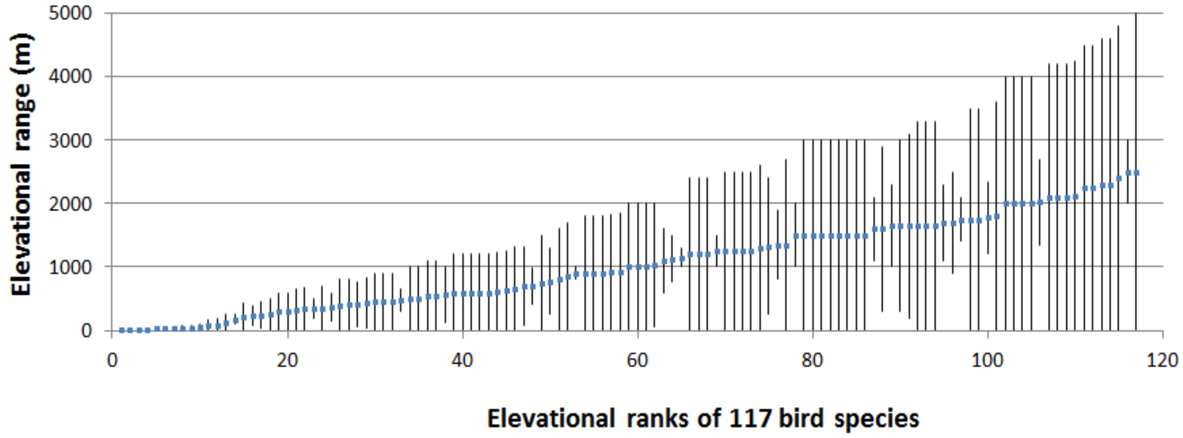


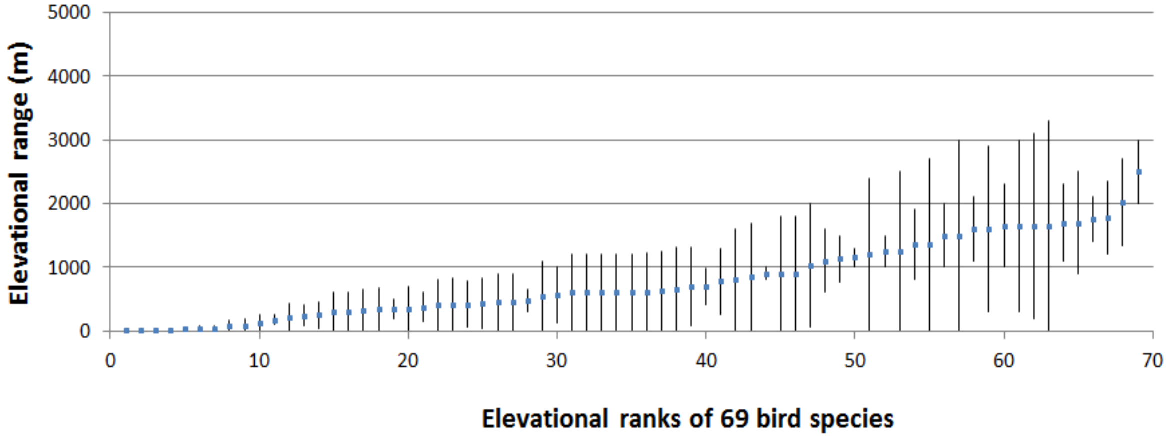
Figure 6.9 Elevational range profile for bird species with breeding ranges occurring within the Neotropical biogeographic realm (Olson *et al.* 2001) and possessing elevational range data: (a) all species, (b) realm endemics, (c) realm non-endemics. Bars indicate the minimum and maximum elevational limits for each species' range, and species are arranged along the x-axis by ranked elevational midpoints.

Oceania realm

(a) All species



(b) Realm endemics



(c) Realm non-endemics

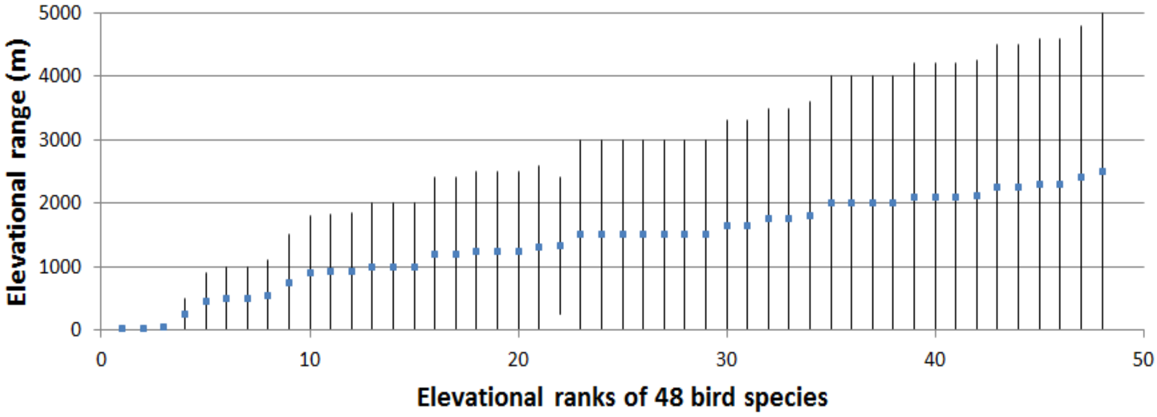
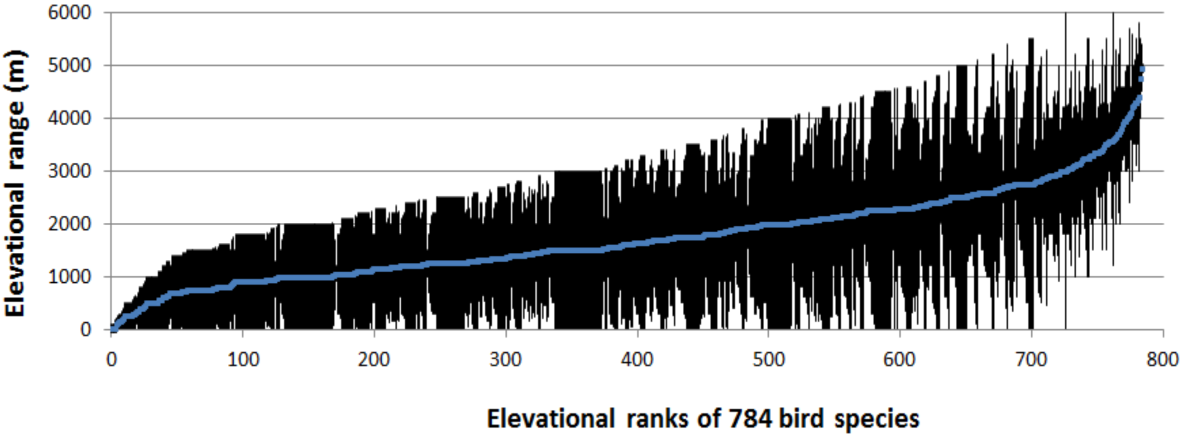


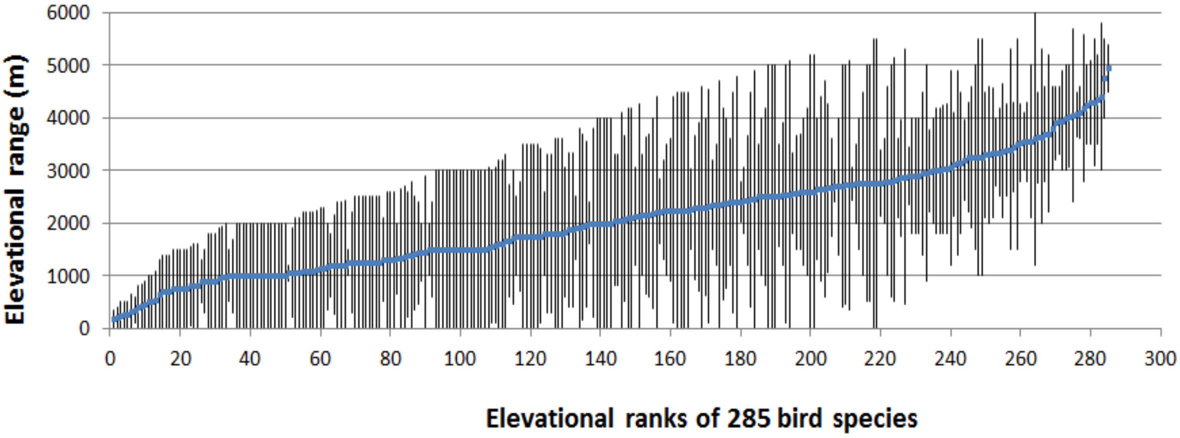
Figure 6.10 Elevational range profile for bird species with breeding ranges occurring within the Oceania biogeographic realm (Olson *et al.* 2001) and possessing elevational range data: (a) all species, (b) realm endemics, (c) realm non-endemics. Bars indicate the minimum and maximum elevational limits for each species' range, and species are arranged along the x-axis by ranked elevational midpoints.

Palearctic realm

(a) All species



(b) Realm endemics



(c) Realm non-endemics

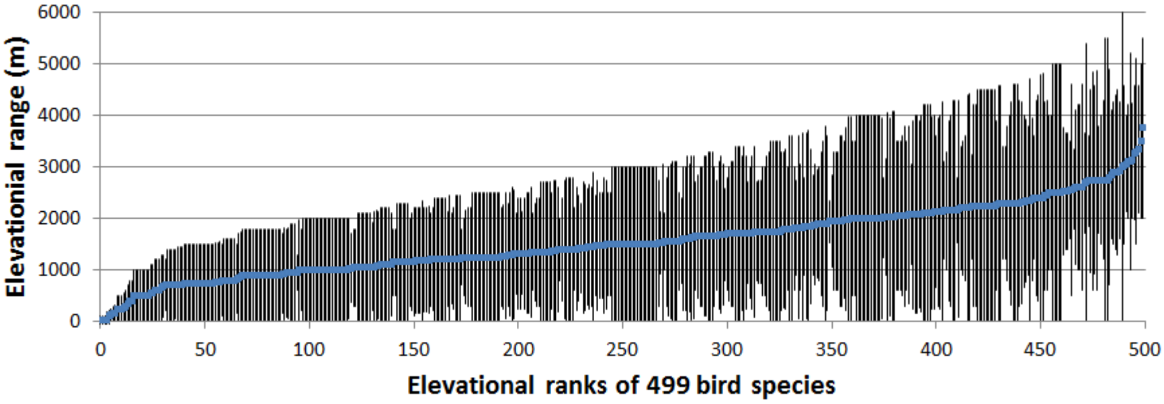


Figure 6.11 Elevational range profile for bird species with breeding ranges occurring within the Palearctic biogeographic realm (Olson *et al.* 2001) and possessing elevational range data: (a) all species, (b) realm endemics, (c) realm non-endemics. Bars indicate the minimum and maximum elevational limits for each species' range, and species are arranged along the x-axis by ranked elevational midpoints.

Table 6.3 Number (*n*) and proportion (%) of realm endemic and realm non-endemic bird species with high-elevational distributions (i.e. minimum elevation ≥1000m). Highest values (endemic vs. non-endemic) highlighted in bold. Biogeographic realms follow Olson *et al.* (2001).

	Endemic		**Non-endemic**	
Biogeographic realm	*n*	%	*n*	%
Afrotropical	**167**	**19.4**	3	2.4
Australasia	**119**	**15.4**	1	0.5
Indo-Malay	**50**	**10.5**	40	8.4
Nearctic	14	8.8	**25**	**9.0**
Neotropical	**579**	**24.1**	24	11.8
Oceania	**10**	**14.5**	0	0.0
Palearctic	**98**	**34.4**	43	8.6

Table 6.4 Number (*n*) and proportion (%) of realm endemic and realm non-endemic bird species with a restricted elevational range (i.e. ≤500m). Highest values (endemic vs. non-endemic) highlighted in bold. Biogeographic realms follow Olson *et al.* (2001).

	Endemic		**Non-endemic**	
Biogeographic realm	*n*	%	*n*	%
Afrotropical	**50**	**5.8**	3	2.4
Australasia	**94**	**12.2**	6	3.0
Indo-Malay	**39**	**8.2**	6	1.3
Nearctic	**14**	**8.8**	10	4.4
Neotropical	**262**	**10.9**	8	3.9
Oceania	**20**	**29.0**	4	8.3
Palearctic	8	**2.8**	**10**	2.0

Table 6.5 Number (*n*) and mean elevational range, maximum elevation, and elevational midpoint for realm endemic and realm non-endemic bird species. Biogeographic realms follow Olson *et al.* (2001).

	Endemic			**Non-endemic**			**t-test**		
	n	$\bar{x}$	$\bar{x}$ ($\log_{10}$)	*n*	$\bar{x}$	$\bar{x}$ ($\log_{10}$)	*t*	d.f.	*p*
(a) Elevational range									
Afrotropical	862	1757	3.19	126	**2791**	3.39	8.36	986	**<0.001**
Australasia	771	1330	3.05	202	**2263**	3.29	10.49	971	**<0.001**
Indo-Malay	476	1396	3.09	478	**2485**	3.35	16.76	952	**<0.001**
Nearctic	159	2040	3.22	227	**2616**	3.35	4.15	384	**<0.001**
Neotropical	2401	1529	3.10	204	**2569**	3.35	11.31	2603	**<0.001**
Oceania	69	1032	2.82	48	**2787**	3.32	5.52	115	**<0.001**
Palearctic	285	**2565**	3.36	499	2561	3.36	0.35	782	*NS*
(b) Maximum elevation									
Afrotropical	862	2167	3.29	126	**2850**	3.40	5.04	986	**<0.001**
Australasia	771	1652	3.13	202	**2321**	3.30	6.91	971	**<0.001**
Indo-Malay	476	1704	3.18	478	**2757**	3.39	13.79	952	**<0.001**
Nearctic	159	2224	3.26	227	**2812**	3.39	3.82	384	**<0.001**
Neotropical	2401	2101	3.21	204	**2777**	3.39	6.70	2603	**<0.001**
Oceania	69	1303	2.92	48	**2792**	3.33	4.29	115	**<0.001**
Palearctic	285	**3354**	3.48	499	2832	3.41	4.42	782	**<0.001**
(c) Elevational midpoint									
Afrotropical	862	1288	3.05	126	**1455**	3.11	2.46	986	**0.01**
Australasia	771	987	2.88	202	**1189**	3.01	4.78	971	**<0.001**
Indo-Malay	476	1005	2.93	478	**1514**	3.12	11.31	952	**<0.001**
Nearctic	159	1204	2.99	227	**1504**	3.11	3.56	384	**<0.001**
Neotropical	2401	1336	3.01	204	**1493**	3.11	4.01	2603	**<0.001**
Oceania	69	787	2.68	48	**1399**	3.03	3.56	115	**<0.001**
Palearctic	285	**2071**	3.25	499	1552	3.14	6.07	782	**<0.001**

$\bar{x}$ = mean elevational distribution, $\bar{x}$ ($\log_{10}$) = mean $\log_{10}$ transformed body weight. Results of independent samples t-tests (using $\log_{10}$ transformed elevational distribution) are reported (*t* = t-value, d.f. = degrees of freedom, *p* = significance level). Highest values (endemic vs. non-endemic) and significant results are highlighted in bold.

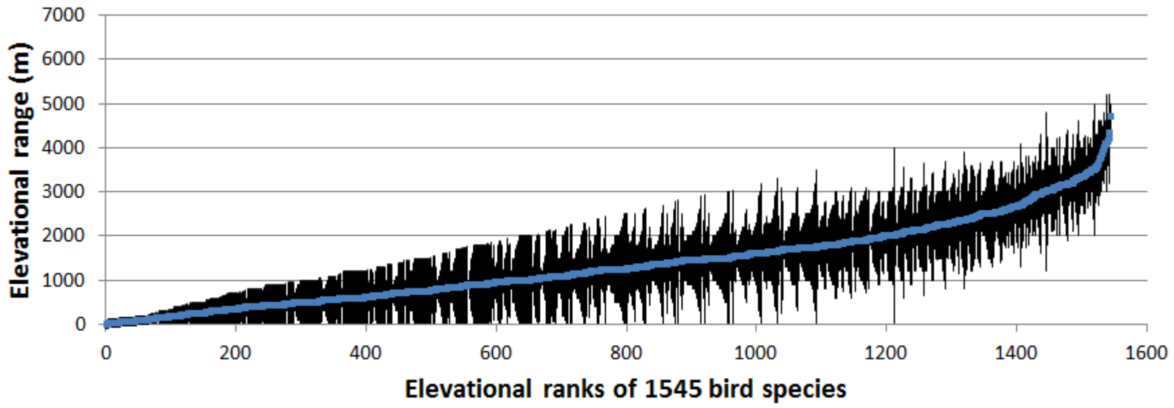
The broad and narrow restricted range (lower quartile) elevational range profiles are qualitatively the same as each other (Fig. 6.12a,b). As with the realm endemic elevational range profiles (Figs. 6.5–6.11), they show that restricted range species occur across a wide elevational gradient at both low and high elevations. However, they only occur above 5000 m for two species, namely the Critically Endangered *Cinclodus palliates* (White-bellied cinclodes) and the Least Concern *Oreotrochilus chimborazo* (Ecuadorian hillstar). They also show that species with an elevational midpoint of approximately 2000 m or above are predominantly high-elevation species. The proportion of high-elevation species was found to be greater for restricted range species (broad: *n* = 523, % total = 33.9%; narrow: *n* = 461, % total = 33.6%) than for the full global dataset (*n* = 1105, % total = 19.2%). Similarly, the proportion of restricted elevational range species was greater for restricted-range species (broad: *n* = 259, % total = 16.8%; narrow: *n* = 238, % total = 17.3%) than for the full global dataset (*n* = 508, % total = 8.8%).

The mountain endemic elevational range profiles are displayed in Figs. 6.13–6.15, for both the broad definition (those species with maximum elevation >300 m) and the narrow definition (those species with a minimum and maximum elevation >300 m). The greatest number and proportion of high-elevation mountain endemic species are located in the Andes (broad: *n* = 102, % total = 6.2%; narrow: *n* = 40, % total = 5.4%), followed by the EAR (broad: *n* = 8, % total = 1.5%; narrow: *n* = 7, % total = 3.0%) and the Himalayas (broad: *n* = 1, % total = 0.2%; narrow: *n* = 0, % total = 0.0%). Similarly, the greatest number and proportion of restricted elevational range mountain endemic species are located in the Andes (*n* = 459, broad % total = 27.9%, narrow % total = 61.5%), followed by the EAR (*n* = 116, broad % total = 21.4%, narrow % total = 50.4%) and the Himalayas (*n* = 114, broad % total = 25.9%; narrow % total = 48.3%).

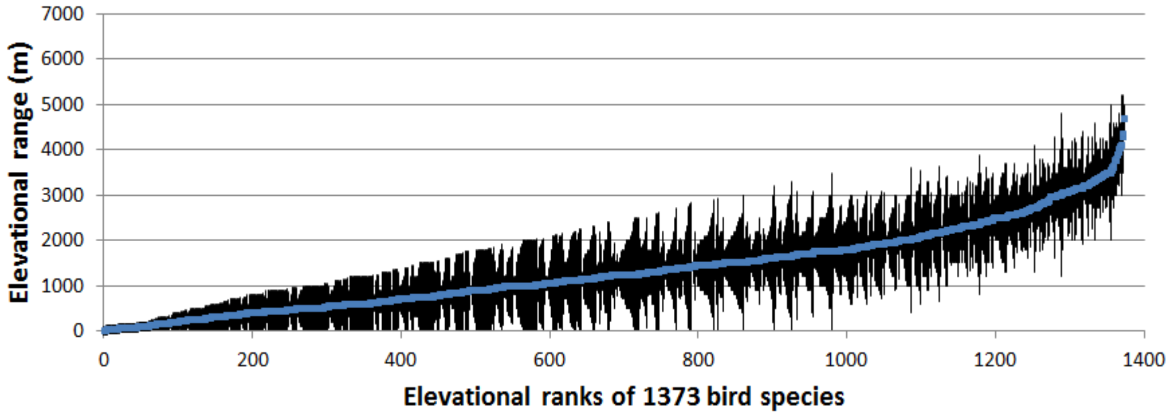
Finally, the elevational range profile for restricted-range species as defined by BirdLife International (i.e. species with geographical breeding ranges ≤50,000 km^2) shows that such species occur across a wide elevational gradient from sea-level up to 4800 m (Fig. A6.1). Both the number and proportion of high-elevation (*n* = 112, % total = 31.5%) and restricted elevational range (*n* = 105, % total = 29.6%) species are found to be very similar.

Restricted range (lower quartile)

(a) Lower quartile (broad)



(b) Lower quartile (narrow)



(C) Full global dataset

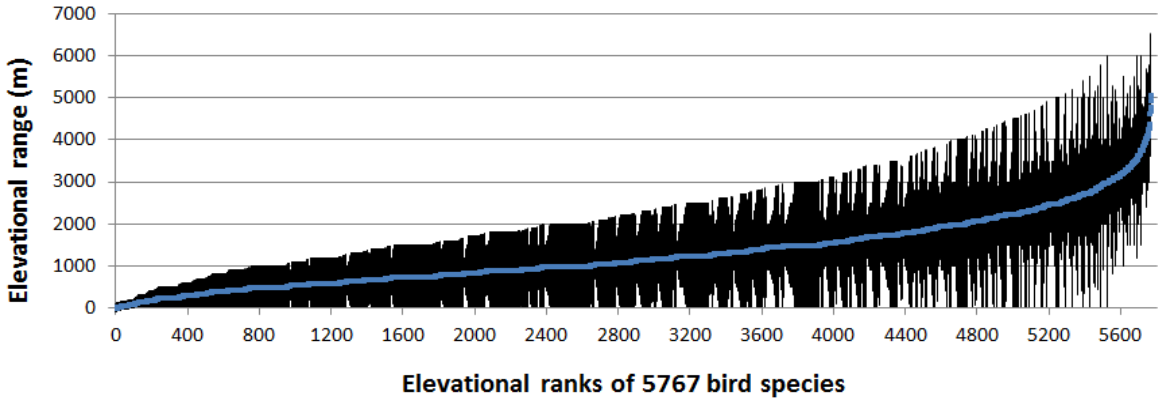
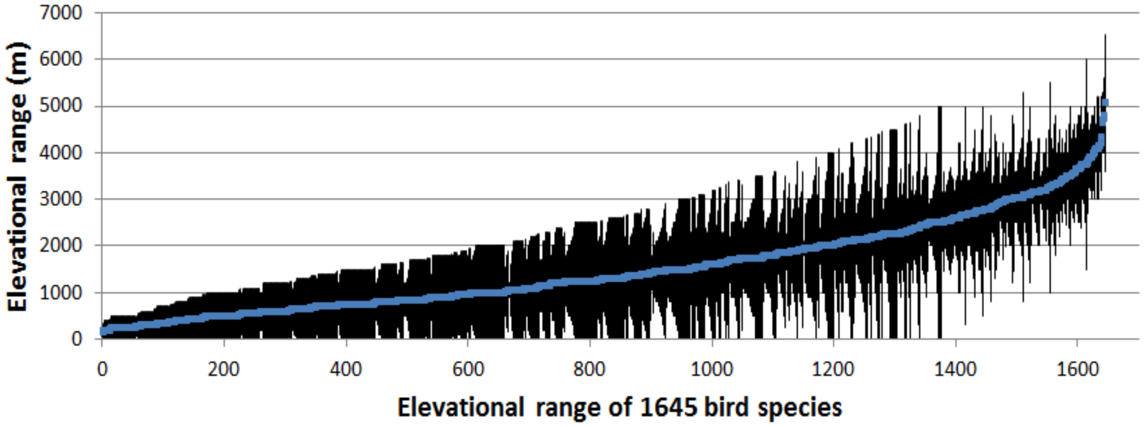


Figure 6.12 Elevational range profile for restricted-range bird species, defined as the 25% of species with the smallest geographical breeding ranges, determined using all species in the dataset with: (a) geographical range data, or (b) geographical range and elevational range data. For comparison, the elevational range profile for the full global dataset (c) is also provided. Bars indicate the minimum and maximum elevational limits for each species' range, and species are arranged along the x-axis by ranked elevational midpoints.

Andes

(a) Mountain endemic (broad)



(b) Mountain endemic (narrow)

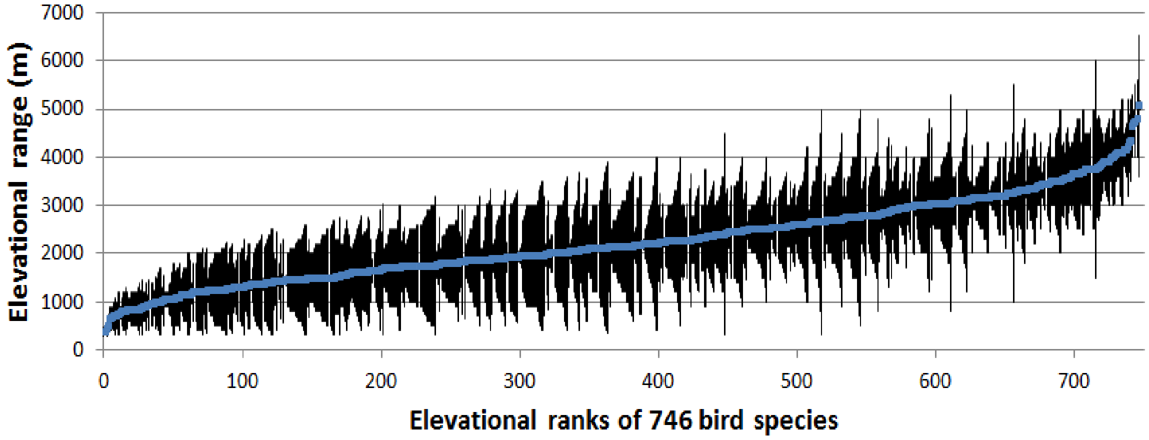
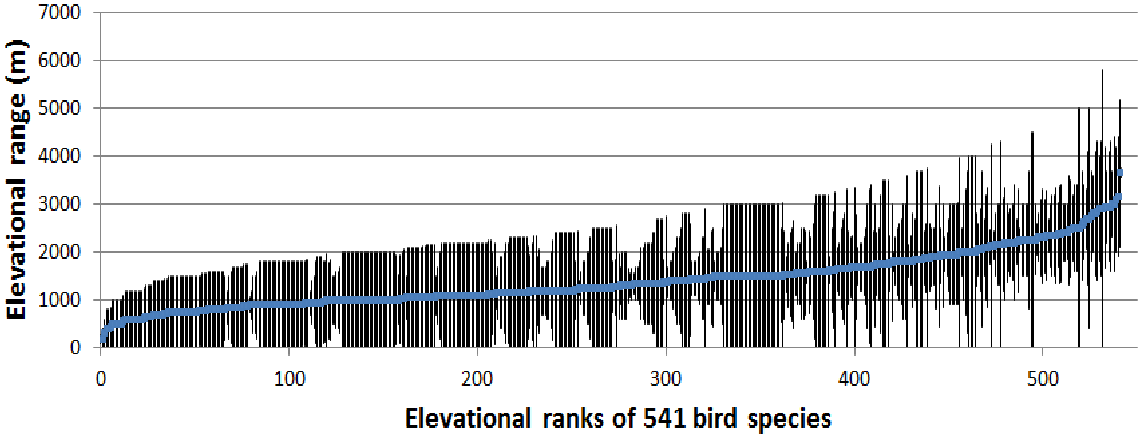


Figure 6.13 Elevational range profile for bird species endemic to the Andes mountain region, for species with: (a) maximum elevation >300 m, or (b) both minimum and maximum elevational limits >300m. Bars indicate the minimum and maximum elevational limits for each species' range, and species are arranged along the x-axis by ranked elevational midpoints.

East African Rift (EAR)

(a) Mountain endemic (broad)



(b) Mountain endemic (narrow)

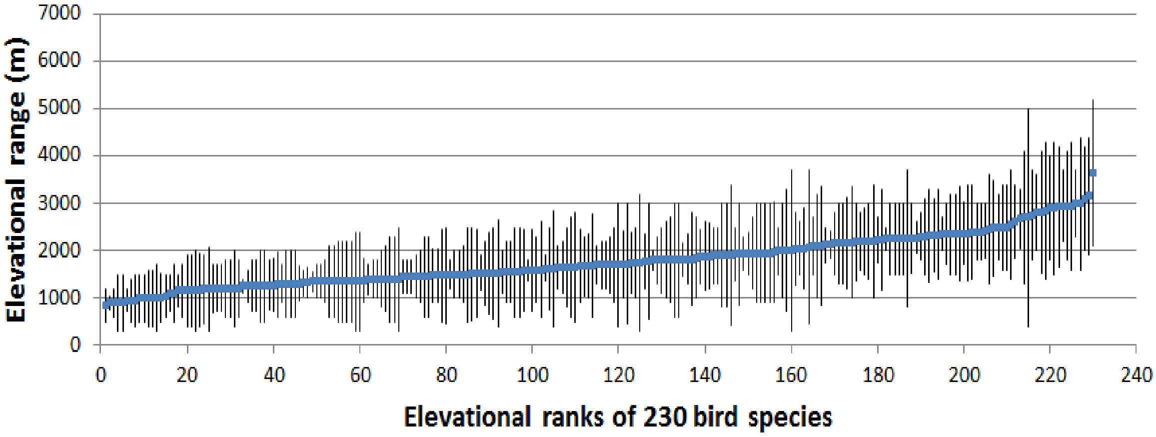
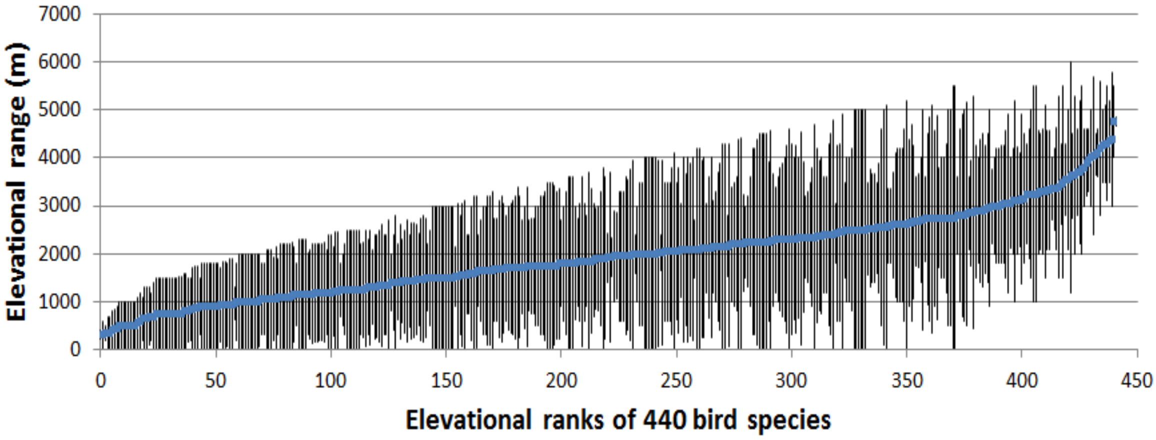


Figure 6.14 Elevational range profile for bird species endemic to the EAR mountain region, for species with: (a) maximum elevation >300 m, (b) both minimum and maximum elevational limits >300m. Bars indicate the minimum and maximum elevational limits for each species' range, and species are arranged along the x-axis by ranked elevational midpoints.

Himalayas

(a) Mountain endemic (broad)



(b) Mountain endemic (narrow)

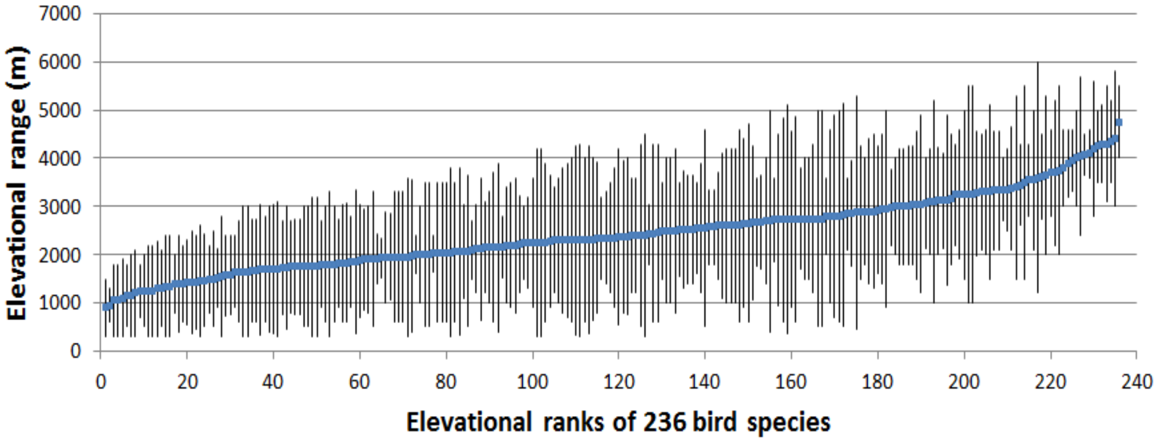


Figure 6.15 Elevational range profile for bird species endemic to the Himalayas mountain region, for species with: (a) maximum elevation >300 m, (b) both minimum and maximum elevational limits >300m. Bars indicate the minimum and maximum elevational limits for each species' range, and species are arranged along the x-axis by ranked elevational midpoints.

6.4.2 Bivariate relationships between avian traits and elevational distribution

Realm endemics: Across biogeographic realms, the elevational distribution of realm endemics was overall found to be negatively associated with morphology, egg weight, development and survival, while positively associated with niche breadth and reproductive output (Table 6.6; for corresponding within-realm correlation coefficients and significance levels, refer to Tables A6.1–A6.3). Several exceptions to these general trends were identified, as follows: (1) a positive relationship between body weight and both elevational range and maximum elevation for Afrotropical endemics; (2) a positive relationship between wing length and elevational range for Australasian endemics (not significant after Bonferroni correction); (3) a negative relationship between clutch size and both maximum elevation and elevational midpoint for Australasian endemics (not significant after Bonferroni correction), and (4) a negative relationship between habitat breadth and both maximum elevation and elevational midpoint for Palearctic endemics. No strongly significant relationships were found between elevational distribution and all study traits for Oceanic realm endemic species, except between habitat breadth and elevational range.

Across PICs for all realm endemics (Table A6.11), morphological trends were found to vary depending on the measure of elevational distribution. Specifically, all four measures of morphology were found to increase with elevational range size, generally decline with higher elevational midpoint, and either increase (Ericson tree) or decrease (Hackett tree) with maximum elevation. A positive relationship was found between reproductive output and both elevational range and maximum elevation – this trend was only maintained with respect to elevational midpoint for clutch size, using the Hackett tree. Overall, no relationship was found between egg weight and elevational distribution (except for a slight positive association with elevational midpoint, using the Ericson tree). Regarding developmental traits, incubation period was consistently found to decline with increasing elevational distribution, however, this positive relationship was weaker for fledging time and not present with respect to age at first breeding. A negative trend was identified between adult survival and elevational distribution. Finally, niche breadth broadened with increasing elevational range and maximum elevation. Diet breadth and habitat breadth were found to narrow and not vary with increasing elevational midpoint, respectively.

Realm non-endemics: As with realm endemics, the elevational distribution of realm non-endemics was found to be negatively associated with growth (i.e. development) and survival, and positively associated with reproduction and niche breadth (Table 6.7; for corresponding within-realm correlation coefficients and significance levels, refer to Tables A6.4–A6.6). Relationships concerning morphology and elevational distribution are less clear and consistent. Body weight was identified to decline with increasing elevational distribution, except for realm non-endemics in the Afrotropics. However, no general relationship could be seen between wing length and elevational distribution, with a strongly significant (negative) trend found to only exist with respect to maximum elevation for Nearctic non-endemics. Similarly, tarsus length was only found to decline (after Bonferroni correction) with increasing maximum elevation for all realm non-endemics collectively and those species within the Palearctic. Overall, culmen length declined with increasing elevational distribution, however, a positive relationship with elevational range for Australasian non-endemics was found (not significant after Bonferroni correction).

Restricted range: For restricted-range species, using the lower quartile method, the trends identified were qualitatively the same for both the broad and narrow definitions (Table 6.8; for corresponding correlation coefficients and significance levels, refer to Tables A6.7–A6.9). Elevational distribution was overall found to be negatively associated with morphology, although both tarsus and culmen length were only strongly related to elevational range. Concerning reproductive traits, the only strongly significant trends were those between annual fecundity and elevational range (positive) and egg weight and maximum elevation (negative). Incubation period and age at first breeding declined with increasing elevational distribution, with no relationship identified for fledging time or adult survival. Niche breadth was only found to be significantly (positively) associated with elevational range.

For restricted-range species identified using BirdLife International's definition (geographical breeding range ≤50,000km^2), body weight was found to be strongly negatively related to elevational distribution and habitat breadth strongly positively related to elevational range (Table A6.10). In addition to this, only three weakly significant relationships were found across all three measures of elevational distribution, namely a negative relationship between: wing length and elevational midpoint, tarsus length and elevational range, and culmen length and elevational range.

Mountain endemics: For species endemic to the mountainous regions of the Andes, EAR and Himalayas (under both the broad and narrow definitions), elevational distribution was generally found to be negatively associated with morphology, development and survival and positively associated with reproduction and niche breadth (Table 6.8; for corresponding correlation coefficients and significance levels, refer to Tables A6.7–A6.9). For Andean endemics, the only exception to the general trends was a positive relationship between body weight and elevational range (not significant after Bonferroni correction). In addition, egg weight was not found to significantly vary with elevational distribution. For EAR endemics, the only exception to the general trends was a positive relationship between body weight and both elevational range and maximum elevation (broad definition only). In addition, no significant trend was found between egg weight and elevational distribution. For Himalayan endemics, exceptions to the general trends were a positive relationship between body weight and elevational midpoint (narrow definition only: not significant after Bonferroni correction), a negative trend between clutch size and elevational range (broad definition only: not significant after Bonferroni correction), and a negative association between habitat breadth and elevational distribution. In addition, after Bonferroni correction, no significant relationship was found between clutch size and elevational distribution for Himalayan endemics.

Table 6.6 Strength and direction of Pearson correlation coefficients between species-level avian traits and elevational distribution for realm endemics.

	Elevational range								Maximum elevation								Elevational midpoint							
	All	Af	Au	IM	Na	Nt	Oc	Pa	All	Af	Au	IM	Na	Nt	Oc	Pa	All	Af	Au	IM	Na	Nt	Oc	Pa
Morphological																								
Body weight	*NS*	++	– –	*NS*	– –	*NS*	*NS*	*NS*	– –	++	– –	*NS*	–	*NS*	*NS*	*NS*	– –	*NS*	– –	*NS*	– –	– –	*NS*	*NS*
Wing length	– –	*NS*	+	*NS*	– –	– –	*NS*	– –	– –	*NS*	*NS*	–	–	– –	*NS*	– –	– –	– –	*NS*	– –	–	– –	*NS*	– –
Tarsus length	– –	– –	–	*NS*	*NS*	*NS*	*NS*	– –	– –	– –	*NS*	*NS*	*NS*	*NS*	*NS*	– –	– –	– –	*NS*	*NS*	*NS*	*NS*	*NS*	– –
Culmen length	– –	– –	– –	– –	*NS*	– –	*NS*	– –	– –	– –	– –	– –	*NS*	– –	*NS*	– –	– –	– –	– –	– –	*NS*	– –	*NS*	– –
Reproduction																								
Clutch size	++	++	*NS*	*NS*	++	++	*NS*	*NS*	++	++	–	*NS*	++	++	*NS*	*NS*	++	++	–	+	++	++	*NS*	*NS*
Annual fecundity	++	++	++	+	++	++	*NS*	++	++	++	++	+	++	++	*NS*	++	++	++	++	+	++	++	*NS*	++
Egg weight	– –	*NS*	–	–	– –	*NS*	*NS*	– –	– –	–	*NS*	–	– –	–	*NS*	– –	– –	–	*NS*	–	– –	*NS*	*NS*	– –
Development																								
Incubation period	– –	– –	– –	–	– –	– –	*NS*	– –	– –	– –	– –	*NS*	– –	– –	*NS*	– –	– –	– –	– –	–	– –	– –	*NS*	– –
Fledging time	– –	– –	– –	*NS*	– –	– –	*NS*	– –	– –	– –	– –	*NS*	– –	– –	*NS*	– –	– –	– –	– –	*NS*	– –	– –	*NS*	– –
Age first breeding	– –	*NS*	– –	*NS*	– –	– –	*NS*	– –	– –	*NS*	– –	*NS*	– –	– –	–	– –	– –	–	– –	*NS*	– –	– –	–	– –
Survival																								
Adult survival	– –	– –	*NS*	*NA*	– –	*NS*	*NS*	– –	– –	– –	*NS*	*NA*	– –	*NS*	*NS*	–	– –	– –	*NS*	*NA*	– –	*NS*	*NS*	– –
Niche breadth																								
Diet breadth	++	++	++	++	*NS*	++	*NS*	*NS*	++	++	++	++	*NS*	++	*NS*	*NS*	++	++	++	++	*NS*	++	*NS*	*NS*
Habitat breadth	++	++	+	*NS*	*NS*	++	++	*NS*	++	++	*NS*	*NS*	*NS*	++	+	– –	*NS*	++	*NS*	*NS*	*NS*	*NS*	*NS*	– –

–/+ negative/positive correlation (*P* <0.05). – –/++ correlation remains significant under Bonferroni correction of α-level (*P*<0.05/7=0.007). *NS*: Correlation not-significant. *NA*: Sample size too small to calculate correlation coefficient. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative elevational distribution used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). All = all realm endemics. Biogeographic realms: Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001).

Table 6.7 Strength and direction of Pearson correlation coefficients between species-level avian traits and elevational distribution for realm non-endemics.

	Elevational range								**Maximum elevation**								**Elevational midpoint**							
	All	Af	Au	IM	Na	Nt	Oc	Pa	All	Af	Au	IM	Na	Nt	Oc	Pa	All	Af	Au	IM	Na	Nt	Oc	Pa
Morphological																								
Body weight	– –	*NS*	– –	– –	– –	– –	– –	–	– –	*NS*	– –	– –	– –	– –	– –	– –	– –	*NS*	– –	– –	– –	– –	– –	– –
Wing length	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	+	– –	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	–	*NS*	*NS*	*NS*
Tarsus length	*NS*	*NS*	–	*NS*	*NS*	*NS*	*NS*	*NS*	– –	*NS*	*NS*	–	*NS*	*NS*	*NS*	– –	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Culmen length	– –	*NS*	+	– –	*NS*	*NS*	*NS*	– –	– –	–	– –	– –	*NS*	*NS*	*NS*	– –	– –	*NS*	– –	– –	–	*NS*	*NS*	– –
Reproduction																								
Clutch size	++	++	+	*NS*	++	++	++	*NS*	+	+	*NS*	*NS*	++	++	++	*NS*	++	+	+	*NS*	++	++	++	*NS*
Annual fecundity	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
Egg weight	– –	– –	– –	– –	– –	–	*NS*	– –	– –	– –	– –	– –	– –	– –	*NS*	– –	– –	– –	– –	– –	– –	–	*NS*	– –
Development																								
Incubation period	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –
Fledging time	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –
Age first breeding	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –
Survival																								
Adult survival	– –	– –	–	–	– –	– –	–	– –	– –	– –	–	– –	– –	– –	– –	– –	– –	– –	–	–	– –	– –	–	– –
Niche breadth																								
Diet breadth	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
Habitat breadth	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	+	++	+	++	++	++	++	++	+

–/+ negative/positive correlation (*P* <0.05). – –/++ correlation remains significant under Bonferroni correction of α-level (*P*<0.05/7=0.007). *NS*: Correlation not-significant. *NA*: Sample size too small to calculate correlation coefficient. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative elevational distribution used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). All = all realm non-endemics. Biogeographic realms: Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001).

Table 6.8 Strength and direction of Pearson correlations between avian traits and elevational distribution for restricted-range (lower quartile: LQ) species and mountain endemics.

	Elevational range								Maximum elevation								Elevational midpoint							
	LQ		Andes		EAR		Hims.		LQ		Andes		EAR		Hims.		LQ		Andes		EAR		Hims.	
	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N
Morphological																								
Body weight	– –	– –	+	+	++	*NS*	– –	*NS*	– –	– –	*NS*	*NS*	++	*NS*	– –	*NS*	– –	– –	– –	*NS*	*NS*	*NS*	– –	+
Wing length	–	*NS*	– –	–	*NS*	– –	– –	– –	– –	– –	– –	– –	*NS*	– –	– –	– –	– –	– –	– –	– –	–	– –	– –	– –
Tarsus length	– –	– –	*NS*	– –	– –	– –	– –	– –	–	*NS*	*NS*	– –	– –	– –	– –	– –	*NS*	*NS*	*NS*	– –	– –	– –	– –	– –
Culmen length	– –	– –	– –	– –	– –	– –	– –	– –	–	–	– –	– –	– –	– –	– –	– –	–	–	– –	– –	– –	– –	– –	– –
Reproduction																								
Clutch size	*NS*	*NS*	++	++	+	*NS*	–	*NS*	*NS*	*NS*	++	++	+	*NS*	*NS*	*NS*	*NS*	*NS*	++	++	+	*NS*	*NS*	*NS*
Annual fecundity	++	++	++	++	++	+	++	+	+	+	++	++	++	+	++	++	+	*NS*	++	++	++	+	++	++
Egg weight	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	– –	– –	– –	–	*NS*	*NS*	*NS*	*NS*	– –	– –	–	–	*NS*	*NS*	*NS*	*NS*	– –	– –
Development																								
Incubation period	– –	– –	– –	– –	– –	– –	– –	–	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	–	– –	– –
Fledging time	*NS*	*NS*	– –	– –	– –	– –	– –	*NS*	*NS*	*NS*	– –	–	– –	– –	– –	*NS*	*NS*	*NS*	– –	–	– –	– –	– –	*NS*
Age first breeding	– –	– –	– –	–	–	*NA*	– –	*NS*	– –	– –	– –	–	–	*NA*	– –	*NS*	– –	– –	– –	–	–	*NA*	– –	*NS*
Survival											– –													
Adult survival	*NS*	*NS*	–	*NA*	– –	–	–	*NA*	*NS*	*NS*	– –	*NA*	– –	–	–	*NA*	*NS*	*NS*	– –	*NA*	– –	*NS*	–	*NA*
Niche breadth																								
Diet breadth	++	++	++	++	++	++	+	+	*NS*	*NS*	++	+	++	++	+	++	*NS*	*NS*	++	+	++	++	+	++
Habitat breadth	++	++	++	++	++	+	*NS*	– –	*NS*	*NS*	*NS*	*NS*	++	*NS*	–	– –	*NS*	*NS*	+	*NS*	*NS*	*NS*	– –	– –

–/+ negative/positive correlation (*P* <0.05). – –/++ correlation remains significant under Bonferroni correction of α-level (*P*<0.05/7=0.007). *NS*: Correlation not-significant. *NA*: Sample size too small to calculate correlation coefficient. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative elevational distribution used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). Andes = Andean endemics, EAR = East African Rift endemics, Hims. = Himalayan endemics. B = Broad lower quartile/mountain endemics. N = Narrow lower quartile/mountain endemics.

6.4.3 Multivariate relationships between avian traits and elevational distribution

Multiple regression model outputs exploring distributional relationships of avian traits for realm endemics, realm non-endemics, and mountain endemics (Andes, EAR and Himalayas) across species are summarised in Table 6.9, with model outputs for realm endemics across PICs summarised in Table A6.12.

Body weight: Variance explained (r^2) ranged from 0.004–15% across all subsets studied. Elevational distribution was retained as a negative predictor for species-level realm endemics (apart from elevational range), realm non-endemics and Himalayan endemics, and retained as a positive predictor for realm endemics (across PICs) and EAR endemics. No relationship was found for Andean endemics. Across species, body weight increased with geographical range for all subsets except Himalayan endemics, where no strongly significant trend was found. Across PICs for realm endemics, geographical range was found to be a negative predictor of body weight (Hackett tree only). Latitude (i.e. absolute mean latitude) was largely found to be a non-significant predictor of body weight, except for realm endemics across both species and PICs (Ericson tree only), where it was retained as a positive predictor.

Clutch size: Variance explained (r^2) ranged from 6–24% across all subsets studied. Elevational distribution was retained as a positive predictor of clutch size for species-level realm endemics and realm non-endemics, and retained as a negative predictor for realm endemics (across PICs). No relationship was found for mountain endemics. Body weight was found to be positively (species-level realm endemics and Andean endemics), negatively (realm non-endemics, Himalayan endemics and PIC-level realm endemics) and unrelated (EAR endemics) to clutch size. Both geographical range and latitude were retained as positive predictors of clutch size, except for both Andean and Himalayan endemics with respect to geographical range.

Incubation period: Variance explained (r^2) ranged from 16–72% across all subsets studied. Elevational distribution was retained as a negative predictor of incubation period for species-level realm endemics and realm non-endemics, and dropped from all other subsets. Body weight was consistently retained as the strongest (positive) predictor of incubation period. Geographical range was found to be negatively (realm endemics across both species and PICs), positively (Himalayan endemics) or unrelated (realm non-endemics, Andean endemics and EAR endemics) to incubation period. No relationship was identified between incubation period and latitude for all subsets.

Adult survival: Variance explained (r^2) ranged from 0–97% across all subsets studied. No predictors were retained for either EAR or Himalayan endemics (due largely to small sample sizes). Elevational distribution was retained as a negative predictor of adult survival for Andean endemics (apart from elevational range) and species-level realm endemics, and dropped from all other subsets. Body weight was a positive predictor of adult survival for species-level realm endemics (apart from in the elevational range model), realm non-endemics and Andean endemics. However, for realm endemics across PICs, body weight was only retained in the elevational range model using the Hackett tree. A negative trend was found between adult survival and geographical range, whereas no relationship was identified between adult survival and latitude for all subsets.

Habitat breadth: Variance explained (r^2) ranged from 17–36% across all subsets studied. Elevational distribution was retained as a positive predictor of habitat breadth for Andean endemics (elevational range only), realm endemics (across PICs) and EAR endemics, and retained as a weak negative predictor for species-level realm endemics (elevational midpoint only). No relationship was found for realm non-endemics or Himalayan endemics. Body weight was found to be positively (realm endemics across PICs), negatively (Himalayan endemics) or unrelated (realm endemics across species, realm non-endemics, Andean endemics and EAR endemics) to habitat breadth. Geographical range was consistently retained as the strongest (positive) predictor of habitat breadth. No relationship was identified between latitude and habitat breadth for all subsets, except for realm endemics (across species) where a positive trend was found.

6.5 Discussion

Ambiguity surrounding the definition of *endemic* and *restricted range* is largely a result of the inherently subjective nature of the two terms (see discussion in Section 1.7.1). It is for this reason that a range of definitions were used in this study, covering a variety of key aspects associated with endemism.

Concerning the mountain endemic subsets (Andes, EAR and Himalayas), delineating these three mountain ranges and obtaining associated lists of endemic species was a challenging process. For landbirds, oceanic islands are natural units for defining and measuring endemism, because their boundaries are clearly defined and linked to the evolutionary processes giving rise to unique species. However, this is less true for almost any other kind of geographical unit, including mountains. Strict endemism would suggest that species were retained only if their breeding ranges were fully encompassed within the delineated mountain range boundaries (Figs. 6.2-6.4). However, based on the protocol used

Table 6.9 Distributional relationships of avian traits for realm endemics, realm non-endemics and mountain endemics (broad definition) – revealed by stepwise multiple regressions. Independent variables entered into each model were body weight, geographical range, absolute mean latitude (latitude) and one measure of elevational distribution – elevational range, maximum elevation or elevational midpoint (denoted at the top of each model output column).

Dependent	**Independent**	**Elevational range**			**Maximum elevation**			**Elevational midpoint**		
		β	***p***	r^2	**β**	***p***	r^2	**β**	***p***	r^2
(a) Realm endemics										
Body weight	Elevation	– 0.03	*NS*	0.01	– 0.04	*	0.01	– 0.10	***	0.02
	Geog. range	0.07	***		0.06	***		0.07	***	
	Latitude	0.07	***		0.07	***		0.07	**	
		$F_{2,3443} = 18.8^{***}$			$F_{3,4422} = 15.0^{***}$			$F_{3,3442} = 23.3^{***}$		
Clutch size	Body weight	0.10	***	0.16	0.04	**	0.15	0.10	***	0.16
	Elevation	0.07	***		0.09	***		0.08	***	
	Geog. range	0.23	***		0.22	***		0.25	***	
	Latitude	0.26	***		0.28	***		0.27	***	
		$F_{4,2566} = 117.6^{***}$			$F_{4,3315} = 145.9^{***}$			$F_{4,2566} = 118.9^{***}$		
Incubation period	Body weight	0.76	***	0.60	0.76	***	0.61	0.76	***	0.60
	Elevation	– 0.05	*		– 0.05	**		– 0.04	*	
	Geog. range	– 0.08	***		– 0.09	***		– 0.09	***	
	Latitude	0.01	*NS*		-0.01	*NS*		0.004	*NS*	
		$F_{3,1107} = 556.9^{***}$			$F_{3,1407} = 719.9^{***}$			$F_{3,1107} = 556.9^{***}$		
Adult survival	Body weight	0.16	*NS*	0.19	0.30	***	0.26	0.18	*	0.23
	Elevation	– 0.43	***		– 0.19	*		– 0.26	***	
	Geog. range	– 0.15	*NS*		– 0.25	***		– 0.25	***	
	Latitude	– 0.33	*NS*		– 0.09	*NS*		– 0.02	*NS*	
		$F_{1,131} = 30.0^{***}$			$F_{3,160} = 18.2^{***}$			$F_{3,129} = 13.2^{***}$		
Habitat breadth	Body weight	0.02	*NS*	0.24	0.01	*NS*	0.21	0.01	*NS*	0.24
	Elevation	0.05	*NS*		0.02	*NS*		– 0.05	*	
	Geog. range	0.49	***		0.45	***		0.49	***	
	Latitude	0.10	***		0.12	***		0.10	***	
		$F_{2,1601} = 252.3^{***}$			$F_{2,2019} = 266.2^{***}$			$F_{3,1600} = 170.0^{***}$		
(b) Realm non-endemics										
Body weight	Elevation	– 0.31	***	0.14	– 0.29	***	0.13	– 0.32	***	0.15
	Geog. range	0.31	***		0.26	***		0.24	***	
	Latitude	– 0.03	*NS*		0.01	*NS*		– 0.02	*NS*	
		$F_{2,692} = 56.2^{***}$			$F_{3,885} = 65.3^{***}$			$F_{2,692} = 60.1^{***}$		
Clutch size	Body weight	– 0.08	*	0.19	– 0.14	***	0.17	– 0.08	*	0.18
	Elevation	0.22	***		0.17	***		0.18	***	
	Geog. range	0.29	***		0.30	***		0.34	***	
	Latitude	0.17	***		0.20	***		0.17	***	
		$F_{4,650} = 37.8^{***}$			$F_{4,833} = 43.1^{***}$			$F_{4,650} = 35.5^{***}$		
Incubation period	Body weight	0.79	***	0.72	0.80	***	0.71	0.79	***	0.71
	Elevation	– 0.15	***		– 0.14	***		– 0.13	***	
	Geog. range	– 0.04	*NS*		– 0.03	*NS*		– 0.06	*NS*	
	Latitude	– 0.04	*NS*		– 0.03	*NS*		– 0.04	*NS*	
		$F_{2,352} = 441.0^{***}$			$F_{2,440} = 548.0^{***}$			$F_{2,352} = 428.8^{***}$		

Table 6.9 Continued.

Dependent	**Independent**	**Elevational range**			**Maximum elevation**			**Elevational midpoint**		
		β	***p***	***r*²**	**β**	***p***	***r*²**	**β**	***p***	***r*²**
(b) Realm non-endemics										
Adult Survival	Body weight	0.48	***	0.47	0.47	***	0.44	0.48	***	0.47
	Elevation	– 0.16	*NS*		– 0.15	*NS*		– 0.17	*NS*	
	Geog. range	– 0.38	***		– 0.38	***		– 0.38	***	
	Latitude	– 0.03	*NS*		– 0.12	*NS*		– 0.03	*NS*	
		$F_{2,67} = 29.7^{***}$			$F_{2,78} = 30.9^{***}$			$F_{2,67} = 29.7^{***}$		
Habitat breadth	Body weight	0.02	*NS*	0.18	0.01	*NS*	0.17	0.02	*NS*	0.18
	Elevation	0.09	*NS*		0.06	*NS*		0.04	*NS*	
	Geog. range	0.42	***		0.41	***		0.42	***	
	Latitude	– 0.08	*NS*		– 0.06	*NS*		– 0.08	*NS*	
		$F_{1,289} = 63.5^{***}$			$F_{1,360} = 71.8^{***}$			$F_{1,289} = 63.5^{***}$		
(c) Andean endemics										
Body weight	Elevation	0.05	*NS*	0.02	0.004	*NS*	0.02	–0.02	*NS*	0.02
	Geog. range	0.15	***		0.15	***		0.15	***	
	Latitude	0.03	*NS*		0.03	*NS*		0.03	*NS*	
		$F_{1,1278} = 29.1^{***}$			$F_{1,1278} = 29.1^{***}$			$F_{1,1278} = 29.1^{***}$		
Clutch size	Body weight	0.28	***	0.13	0.28	***	0.13	0.28	***	0.13
	Elevation	0.03	*NS*		– 0.03	*NS*		– 0.06	*NS*	
	Geog. range	0.03	*NS*		0.03	*NS*		0.03	*NS*	
	Latitude	0.20	***		0.20	***		0.20	***	
		$F_{2,796} = 59.6^{***}$			$F_{2,796} = 59.6^{***}$			$F_{2,796} = 59.6^{***}$		
Incubation period	Body weight	0.68	***	0.46	0.68	***	0.46	0.68	***	0.46
	Elevation	– 0.07	*NS*		– 0.02	*NS*		0.001	*NS*	
	Geog. range	– 0.06	*NS*		– 0.06	*NS*		– 0.06	*NS*	
	Latitude	– 0.07	*NS*		– 0.07	*NS*		– 0.07	*NS*	
		$F_{1,256} = 221.2^{***}$			$F_{1,256} = 221.2^{***}$			$F_{1,256} = 221.2^{***}$		
Adult Survival	Body weight	0.61	***	0.95	0.07	***	0.96	0.68	***	0.97
	Elevation	– 0.07	*NS*		– 0.44	***		0.08	***	
	Geog. range	0.47	***		0.21	*NS*		– 0.45	*NS*	
	Latitude	– 0.17	*NS*		– 0.002	*NS*		– 0.02	*NS*	
		$F_{2,8} = 70.5^{***}$			$F_{2,8} = 94.9^{***}$			$F_{2,8} = 109.8^{***}$		
Habitat breadth	Body weight	0.06	*NS*	0.36	0.07	*NS*	0.34	0.07	*NS*	0.34
	Elevation	0.14	***		0.05	*NS*		0.01	*NS*	
	Geog. range	0.55	***		0.59	***		0.59	***	
	Latitude	0.02	*NS*		0.03	*NS*		0.03	*NS*	
		$F_{2,448} = 126.1^{***}$			$F_{1,449} = 234.4^{***}$			$F_{1,449} = 234.4^{***}$		
(d) EAR endemics										
Body weight	Elevation	0.13	**	0.09	0.13	**	0.10	0.10	*	0.09
	Geog. range	0.22	***		0.29	***		0.31	***	
	Latitude	0.01	*NS*		0.02	*NS*		0.02	*NS*	
		$F_{2,485} = 25.2^{***}$			$F_{2,485} = 25.8^{***}$			$F_{2,485} = 23.5^{***}$		
Clutch size	Body weight	0.06	*NS*	0.24	0.06	*NS*	0.24	0.06	*NS*	0.24
	Elevation	– 0.03	*NS*		0.04	*NS*		0.07	*NS*	
	Geog. range	0.20	***		0.20	***		0.20	***	
	Latitude	0.12	**		0.12	**		0.12	**	
		$F_{2,426} = 13.3^{***}$			$F_{2,426} = 13.3^{***}$			$F_{2,426} = 13.3^{***}$		

Table 6.9 Continued.

Dependent	Independent	Elevational range			Maximum elevation			Elevational midpoint		
		β	*p*	r^2	β	*p*	r^2	β	*p*	r^2
(d) EAR endemics										
Incubation period	Body weight	0.82	***	0.67	0.82	***	0.67	0.82	***	0.67
	Elevation	0.01	*NS*		0.03	*NS*		0.03	*NS*	
	Geog. range	– 0.01	*NS*		– 0.004	*NS*		– 0.004	*NS*	
	Latitude	0.06	*NS*		0.06	*NS*		0.06	*NS*	
		$F_{1,216} = 431.0^{***}$			$F_{1,216} = 431.0^{***}$			$F_{1,216} = 431.0^{***}$		
Adult survival	Body weight	*NA*	*NA*		*NA*	*NA*		*NA*	*NA*	
	Elevation	*NA*	*NA*		*NA*	*NA*		*NA*	*NA*	
	Geog. range	*NA*	*NA*		*NA*	*NA*		*NA*	*NA*	
	Latitude	*NA*	*NA*		*NA*	*NA*		*NA*	*NA*	
		N = 14			N = 14			N = 14		
Habitat breadth	Body weight	-0.04	*NS*	0.29	-0.04	*NS*	0.29	-0.04	*NS*	0.29
	Elevation	0.09	*		0.11	**		0.11	**	
	Geog. range	0.49	***		0.53	***		0.56	***	
	Latitude	0.02	*NS*		0.03	*NS*		0.03	*NS*	
		$F_{2,478} = 95.5^{***}$			$F_{2,478} = 98.6^{***}$			$F_{2,478} = 97.6^{***}$		
(e) Himalayan endemics										
Body weight	Elevation	– 0.23	***	0.05	– 0.15	**	0.02	– 0.13	**	0.02
	Geog. range	0.13	*		0.06	*NS*		0.04	*NS*	
	Latitude	– 0.01	*NS*		– 0.001	*NS*		– 0.02	*NS*	
		$F_{2,384} = 10.3^{***}$			$F_{1,385} = 9.3^{**}$			$F_{1,385} = 6.6^{**}$		
Clutch size	Body weight	– 0.18	***	0.06	– 0.18	***	0.06	– 0.18	***	0.06
	Elevation	0.05	*NS*		0.09	*NS*		0.09	*NS*	
	Geog. range	– 0.03	*NS*		– 0.03	*NS*		– 0.03	*NS*	
	Latitude	0.15	**		0.15	**		0.15	**	
		$F_{2,349} = 10.3^{***}$			$F_{2,349} = 10.3^{***}$			$F_{2,349} = 10.3^{***}$		
Incubation period	Body weight	0.87	***	0.71	0.87	***	0.71	0.87	***	0.71
	Elevation	– 0.01	*NS*		– 0.01	*NS*		– 0.01	*NS*	
	Geog. range	0.13	*		0.13	*		0.13	*	
	Latitude	0.02	*NS*		0.02	*NS*		0.02	*NS*	
		$F_{2,121} = 145.0^{***}$			$F_{2,121} = 145.0^{***}$			$F_{2,121} = 145.0^{***}$		
Adult survival	Body weight	*NA*	*NA*		*NA*	*NA*		*NA*	*NA*	
	Elevation	*NA*	*NA*		*NA*	*NA*		*NA*	*NA*	
	Geog. range	*NA*	*NA*		*NA*	*NA*		*NA*	*NA*	
	Latitude	*NA*	*NA*		*NA*	*NA*		*NA*	*NA*	
		N = 15			N = 15			N = 15		
Habitat breadth	Body weight	– 0.15	*	0.21	– 0.15	*	0.21	– 0.15	*	0.21
	Elevation	– 0.002	*NS*		– 0.08	*NS*		– 0.11	*NS*	
	Geog. range	0.42	***		0.42	***		0.42	***	
	Latitude	– 0.05	*NS*		– 0.05	*NS*		– 0.05	*NS*	
		$F_{2,141} = 18.3^{***}$			$F_{2,141} = 18.3^{***}$			$F_{2,141} = 18.3^{***}$		

Significance level for a variable to enter/leave each model was $P<0.05$. β: multiple regression coefficient (standardised). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. r^2: proportion of variance in the dependent variable explained by the relevant predictor variables. *NS*: independent variable not-significant. *NA*: Sample size too small to perform multiple regression. Degrees of freedom and F-statistic value for each model also reported. All variables $\log_{10}$ transformed, except adult survival (arcsine transformed) and habitat breadth (untransformed).

(Section 6.3.2), a number of mountain endemics possess breeding ranges that also occur outside of these boundaries, and as such are not truly endemic to their corresponding mountain range. For example, a number of Andean ‘endemic’ species also breed in the Caribbean and/or Central America, because these areas are still within the Neotropical realm. The biggest overestimation is likely to have occurred for the Himalayan endemic subset. This is due to the delineated area spanning two biogeographic realms (i.e. Palearctic and Indo-Malay). It is for this reason that, in my ‘broad’ definition of a Himalayan endemic (maximum elevation limit >300m), *Phylloscopus collybita* (Common chiffchaff) is included, which also breeds in the UK, and whose mean latitude is above the northernmost extent of my delineated Himalayas boundary. Nevertheless, the protocol employed in this study for defining mountain endemics was chosen because it is simple to employ with the dataset being used, the resultant sample sizes were not unusably small, and because no previous studies could be found from which to utilise or develop their methodologies. Notably, as refined a boundary as possible was used to minimise the inclusion of extraneous species. The most important aspect of the mountain endemic subsets is that they contain species that reside in montane habitat, and that their breeding ranges at least partially span the mountain range in question. In fact, the ‘narrow’ definition (maximum and minimum elevation limit >300m) helped to ensure that the species considered did not include any lowland endemics. In the future, these lists could certainly be further refined based on expert opinion.

The potential issue of range overestimation was briefly mentioned regarding BirdLife International’s restricted-range definition (Section 6.3.1). However, it is important to reemphasise that the geographical ranges of individual species in this study (and throughout this thesis) were estimated as the sum of the areas of the cells in which they were scored as occurring. This will tend disproportionately to overestimate the range areas of particularly narrowly distributed species, as even if only a small portion of a given species’ range is located within a given cell it was included in the measure of its geographical range. As each cell represents approximately 10,000km^2, this could potentially lead to considerable range overestimation. Studies have critically assessed the utility of determining geographical range size from grid cells and extent of occurrence maps, along with highlighting the conservation implications of overestimating range size (e.g. Jetz *et al.* 2008b). However, for the purposes of this large-scale study it is unlikely to have greatly influenced the results produced – the main consequence being an underestimation in the number of realm endemics. For global-scale studies at present, there is unfortunately no alternative, as area of occupancy maps are only available for a relatively small number of bird species.

It is important to highlight that the largest number of realm endemics and mountain endemics were found in the Neotropics (3129 species) and Andes (broad: 1645 species, narrow: 746 species), respectively. This concurs with the findings of both Orme *et al.* (2005) and Jenkins *et al.* (2013), who used a grid-cell approach to investigate the global spatial distribution of endemic (i.e. restricted-range) species. They both conclusively found the Andes to not only be the top mountainous hotspot for avian endemic richness, but also overall species richness.

6.5.1 Elevational distributions of endemic and restricted-range species

Elevational range profile plots have previously only been used for investigating elevational distribution patterns of species along single elevational gradients (e.g. Patterson *et al.* 1998; Chettri *et al.* 2010; Liew *et al.* 2010). However, the plots produced in this study (Figs. 6.5-6.15, A6.1) provide a useful way for simultaneously visualising the elevational distributions of a large number of species, for either a specific geographical area (i.e. biogeographic realm or mountain range) or global subset (i.e. restricted-range species). Specifically, this study was novel in the fact that it investigated the elevational distributions of extant birds with respect to: (a) realm endemics versus realm non-endemics, (b) restricted-range species versus the full global dataset, and (c) mountain endemics. As discussed below, the results found enable the null hypothesis that elevational range profiles do not differ between realm endemic and realm non-endemic species or restricted-range species and the full global dataset to be conclusively rejected.

As discussed in Section 1.7.2, little is known about the elevational distribution and elevational gradients of endemism, in comparison to total species richness. Here, I show that endemic and restricted-range species can be found to occur across a wide elevational gradient at both low and high elevations. Yet, an interesting finding was that whereas realm non-endemics with the highest elevational midpoints were typically found to have large elevational ranges spanning from the lowest to the highest elevations, realm endemics with the highest elevational midpoints were instead generally found not to occur at the lowest elevations. In other words, there is evidence to suggest that, regardless of the endemic or restricted-range definition used, those species occurring at the highest elevations are largely restricted to such areas, and are not found in the lowlands. This implies that many endemic and restricted-range species found at high elevations are specially adapted to their montane environment, and less well adapted to lowland conditions, where they may also be outcompeted by wide-ranging generalist species. Related to this and focusing on realm endemics, overall, a higher number (and a greater proportion) were found to have high-elevational distributions (i.e. minimum elevation ≥1000m) than realm non-endemics (Table 6.3). The same was also found for the proportion of high-elevation species with respect to both lower quartile and BirdLife International restricted-range species, in comparison to the full global dataset.

The lack of studies defining and studying restricted elevational range for a large number of species was highlighted in Section 1.7.1 (and Table 1.2 within). Such an oversight in the current literature is surprising given both the importance of mountains as hotspots of endemism and restricted range as a strong negative correlate of extinction risk (Section 1.9.3). As with the definition used for determining high-elevation species, this study also used an arbitrary threshold when defining restricted elevational range species (i.e. elevational range ≤500m). Along the entire elevational gradient, a consistently greater proportion of restricted elevational range species in this study were found to be realm endemics than realm non-endemics (Table 6.4) and restricted-range species in comparison to the full global dataset. Related to this, realm endemics were also overall found to have smaller elevational ranges than realm non-endemics (Table 6.5a). These results are likely to link back to the finding in Chapter 5 that narrow-ranging species, in terms of geographical range, also span narrow elevational ranges, and vice versa (see Table 5.1 and associated discussion in Section 5.5.1). Interestingly, the general results mirror those of the few existing studies, focusing on birds (e.g. Stotz 1998; Blackburn & Ruggiero 2001) and plants (e.g. Nogué *et al.* 2013). These previous investigations have attributed the finding that endemic species possess narrower elevational ranges in a variety of ways, including: (1) recent *in situ* speciation, (2) it represents the relict distribution of formerly more widely distributed species, (3) sampling artefact, (4) a lack of higher elevations suitable for species survival, (in the case of summit species), or (5) such species are poor dispersers and specialists. In contrast, the wide elevational ranges of non-endemic species has previously been attributed to these species potentially being good dispersers, and having a wide climatic tolerance and ability to adapt to novel environments (Nogué *et al.* 2013).

The only biogeographic realm where elevational range was not smaller for realm endemics was the Palearctic, where no significant difference was found between the elevational ranges of endemics and non-endemics (Table 6.5a). In fact, the mean elevational ranges of both realm subsets were relatively large (i.e. >2500m). This could potentially be due to the high northerly latitudes that this realm spans, which are highly seasonal (Janzen 1967), in turn promoting larger elevational ranges (Section 2.2.2), along with the fact that the highest mountains are found in this realm (Fig. 5.4). This directly relates to the finding in Chapter 5 that species inhabiting higher raw and absolute latitudes have larger elevational ranges than those in the Southern Hemisphere or the tropics, respectively (see Table 5.1 and associated discussion in Section 5.5.1).

Overall, realm endemics were shown to have lower maximum elevational limits and occur at lower elevations than realm non-endemics (Table 6.5b,c). This is contrary to the finding of Blackburn & Ruggiero (2001) who found endemic Andean passerines to possess higher elevational range maxima and midpoints than non-endemics. This also potentially conflicts with a number of studies that have found endemism (and proportion of endemism) to increase monotonically with elevation (Section 1.7.2), as the results suggest that most realm endemics do not occur at the highest elevations. Instead, there is potential evidence for an overall hump-shaped (i.e. unimodal) pattern of endemism with respect to elevation (Section 1.7.2), based on the fact that the mean elevational midpoint for all realm endemic subsets occur at intermediate elevations (Table 6.5c). In fact, Kessler (2002) proposed that at the highest elevations, only the most widespread and adaptable species can survive (i.e. wide-ranging and generalist non-endemics), based on the harshness of the environment (see also Janzen 1967). However, I do also provide evidence that endemic species with restricted elevational ranges do occur at very high elevations. Another aspect to consider is that both maximum elevation and elevational midpoint are positively correlated and autocorrelated with each other and elevational range. As previously discussed, species with larger elevational ranges also have larger geographical ranges (Table 5.1). Therefore, the observed trends could in fact be related to species with larger elevational ranges, also typically having a higher maximum elevation and elevational midpoint. The Palearctic realm was the only realm to display the opposite trend to the general one, i.e. endemics possess higher elevational range maxima and midpoints than non-endemics. Without more in depth regional studies it is difficult to provide a sensible interpretation of this result. Ultimately, it is important to remember that this study is looking at a much larger number of species than previous studies, and at a much larger geographical scale. In the future, what is required is a study similar to McCain (2009a), who conducted a global analysis of patterns and underlying drivers of species richness and elevation in birds based on data collected from individual elevational gradients, but purely for endemics.

Finally, focusing on the mountain endemics (Figs. 6.13-6.15), the greatest number and proportion of high-elevation species were found to be located in the Andes. However, the corresponding sample sizes and resulting proportions for all mountain endemic subsets are low (i.e. 0-102 species and 0.0-6.2%). In comparison, all three mountain endemic subsets contain a relatively large number and proportion of restricted elevational range species. This highlights that although a large proportion of endemics possess a restricted elevational range, they are not predominantly located at high elevations, rather throughout the elevational gradient. In order to understand the underlying processes behind these patterns, foucused smaller-scale regional studies are recommended.

6.5.2 Trait variation with elevational distribution for endemic and restricted-range species

There has been a distinct lack of research, at any scale and across taxa, on the traits possessed by both endemic and restricted-range species and how they vary with respect to elevational distribution. This is surprising considering the well-established fact that mountains (particularly those in the tropics) are hotspots of not only total species richness but endemic species richness (Sections 1.3 and 1.7.2). It is therefore important to highlight the novelty of this study, which addressed this knowledge gap for birds at the global scale, using both a bivariate and multivariate framework.

Such a lack of similar studies precludes any meaningful comparisons being made between the results presented here and the existing literature. In fact, the only previous study to compare endemic and non-endemic trait variation with respect to elevational distribution was by Blackburn & Ruggiero (2001) for Andean passerines in relation to body weight – both across species and controlling for phylogenetic non-independence. In general, they found body mass to be positively related and unrelated to elevational distribution (maximum elevation and elevational midpoint) for endemic and non-endemic species, respectively. In addition they found no significant trend between body weight and elevational range for both endemics and non-endemics, and that their endemic results matched those that they identified for all Andean passerines. This contradicts with the results from my study, where bivariate analyses found body weight for Andean mountain endemic species to be positively related to elevational range (albeit weakly significant), unrelated to maximum elevation and strongly negatively associated with elevational midpoint using the broad definition (Table 6.8). Corresponding multivariate analysis found body weight to be unrelated to elevational distribution (Table 6.9c). The results of Blackburn & Ruggiero (2001) also largely go against those found here when scaling up to both Neotropical and total biogeographic realm endemics and non-endemics. There are a number of potential reasons as to why my results differ to those of Blackburn & Ruggiero (2001). For example different datasets and endemic definitions are used. In addition, whereas their study identified 412 Andean endemic passerines, my study identified 1645 ‘broad’ Andean endemics and 746 ‘narrow’ Andean endemics, across all bird orders. These differences highlight the difficulties of comparing such studies in an informative manner.

As discussed below, the results found enable the null hypotheses that no relationship exists between variation in avian traits and elevational distribution for endemic and restricted-range species at both the bivariate and multivariate to be conclusively rejected.

Bivariate relationships: All endemic and restricted-range subsets investigated in this study have sample sizes that are, to varying degrees, reduced in comparison to the global dataset analysed in Chapter 4. This in turn led to a reduction in power when undertaking statistical analyses. Nevertheless, across both species and PICs, bivariate relationships between avian traits and elevational distribution for all endemic and restricted-range subsets investigated (Tables 6.6, 6.8, A6.11) remained largely qualitatively unchanged to those found at the global scale and for the full species assemblages within each biogeographic realm (Tables 4.1a, 4.2, A4.4), albeit with fewer significant results. Specifically, elevational distributions (range, maximum and midpoint) of endemic and restricted-range species were, overall, found to be positively associated with reproductive output and niche breadth, whilst being negatively associated with growth and survival. Linked to this, evidence was found for endemic and restricted-range bird species with larger elevational ranges, higher maximum elevations and higher elevational midpoints to possess traits consistent with a fast life history, and vice versa (see associated discussion in Section 4.5). Regarding the four morphological traits (body weight, wing length, tarsus length and culmen length), the flip from a negative to a positive trend with elevational distribution, when analysing species and PICs respectively, at the global scale (Tables 4.1a, A4.4) was also found for realm endemics (Tables 6.6, A6.11).

The fact that such relationships were identified for endemic and restricted-range subsets makes the results of Chapter 4, using the full dataset, more convincing and robust. This is because the results in this study imply that large-scale relationships between avian traits and elevational distribution are not merely shaped by the comparatively small number of wide-ranging generalist species, which has been shown to be the case for spatial patterns of species richness (e.g. Jetz & Rahbek 2002; Lennon *et al.* 2004; Orme *et al.* 2005; Jenkins *et al.* 2013) in grid-cell based studies. These results in turn suggest that similar trends regarding variation in avian traits with respect to elevational distribution have evolved independently a number of times in unrelated taxa and geographically distinct areas.

An important question to ask is '*are relationships between avian traits and elevational distribution expected to differ between endemic/restricted-range subsets and both the full global dataset or non-endemic subsets?*' In relation to mountain endemics in particular, the answer would be expected to be 'yes', if such species possess unusual adaptations to their environment, like oceanic endemics. Although little studied, for mountain endemics these specialities are likely to be physiological, in order to cope with the harsh and varied environment, and related to basal metabolic rate and thermoregulation, e.g. torpor (see McNab 2009). Overall, I show that that the traits possessed by species inhabiting 'sky islands' (i.e. high-elevation species) follow lowland mainland patterns, specifically those of high latitudes (Section 2.1.6).

In their study, Blackburn & Ruggiero (2001) suggested that the different relationships they observed for Andean endemics and non-endemics, with respect to elevational and latitudinal variation in body weight, were due to the significant differences in the extent and location of the elevational and latitudinal ranges for these two groups of species. However, despite finding elevational distribution to be significantly different between realm endemics and realm non-endemics (Table 6.5), my results for both subsets are very similar to each other (Tables 6.6-6.7). The main difference being that fewer significant relationships were found for realm endemics in comparison to realm non-endemics. For certain trends this can be at least partially explained via sample-size effects. The sample sizes for Afrotropical, Australasia, Neotropical realm endemics and all realm endemics were larger than those for corresponding non-endemics, following the fact that, in general, very few species are wide-ranging (Orme *et al.* 2006). In contrast, the sample sizes for Indo-Malay, Nearctic and the Palearctic were larger for non-endemics, with Oceania endemics and non-endemics possessing similar sample sizes to one another (Tables A6.1-A6.6). However, for the non-morphological traits, it is clear that non-endemics display, not necessarily stronger, but more consistently significant trait-elevation relationships than realm endemics, similar to total realm assemblages (Table 4.2).

Concerning similarities and differences between the trends found for realm endemics versus total realm assemblages, Oceanic endemics displayed noticeably fewer significant relationships, followed by Indo-Malay endemics. In fact only one highly significant relationship could be found for Oceanic endemics – a positive association between elevational range and habitat breadth. Certainly, the very small sample sizes for Oceanic endemics accounts for a large number (if not all) of the non-significant trends found. Similarly, where non-significant trends were identified for Indo-Malay endemics, sample sizes were much small than for the full realm assemblage. Although looking from an elevational perspective, there is therefore no evidence that oceanic island species possess slow life histories, as has been found previously by Covas (2012), who compared avian traits between island species and their mainland counterparts. Interestingly, the positive relationship identified between body weight and elevational distribution for the full Afrotropical assemblage was also found for Afrotropical endemics. In addition, the positive association found within the full Australasia assemblage between wing length and both elevational range and maximum elevation was also maintained for realm endemics. The fact that these anomalous results found across all species within the realm are found for endemics, but not for realm-endemics, implies that these trends are driven by endemic species.

Realm non-endemics closely mirror the results found for total realm assemblages for the majority of trait-elevation relationships. However, the trend between body weight and elevational distribution was found to be more consistently negative with the removal of endemic species. In addition, an overall lack of a significant relationship between elevational distribution and both wing length and tarsus length was found. As discussed in Sections 2.1.5 and 4.5.1–4.5.2, evidence for Allen's rule with respect to elevation is limited for these two morphological variables.

Relationships between life-history traits and elevational distribution for restricted-range species (lower quartile) were qualitatively the same in direction as those found at the global species level. The only difference being a reduction in the number of significant relationships found. Of particular note, both clutch size and fledging time were unrelated to elevational distribution – the reasons for which are unclear. However, other measures of reproductive output (i.e. annual fecundity) and growth (i.e. incubation period and age at first breeding) were still found to increase and decrease with elevation, respectively. Another important trend to highlight is that both the strength and significance of trait relationships decline from elevational range to maximum elevation to elevational midpoint. This in turn implies that for those species with the smallest geographical ranges, trait variation with respect to elevation is less than that associated with elevational range.

Concerning mountain endemics, the three study mountain ranges cover different areal extents (the Andes covering approximately five times the area than both the EAR and Himalayas, Figs. 6.2-6.4), are of different ages, and possess vastly different topographies and levels of both connectedness and isolation. Comparing the results of these three mountains is therefore highly informative, as it shows whether or not patterns generalise across spatially separated mountainous regions, that occur in different continents – in turn alleviating issues surrounding spatial autocorrelation that are potentially present when analysing the full dataset. Also, studying trait-elevation relationships in three of the world's major mountain ranges ensures that maximum variation in elevational gradients are used to test for percentage variation explained. With this in mind, the significant relationships found for all three mountain endemic subsets were qualitatively the same as those found at the global species level. The only exception for Andean endemics was a slight positive relationship identified between body weight and elevational range, which actually matches the direction found by Blackburn & Ruggiero (2001), albeit they found the trend to be not-significant. Similarly, for EAR endemics the only exception was a strongly significant positive relationship between body weight and both elevational range and maximum elevation.

Finally, focusing on niche breadth, for endemic and restricted-range subsets at the species level, significant positive relationships with elevational distribution were less prevalent for habitat breadth than diet breadth, as also found for realm non-endemics and in Chapter 4 for the full dataset (see associated discussion in Section 4.5). In addition, relationships between elevational distribution and both measures of niche breadth (particularly habitat breadth) were identified as being stronger and more significant for realm non-endemics than realm endemics. This makes intuitive sense because realm non-endemics possess larger geographical and elevational ranges than endemics, and thus are more likely to be diet/habitat generalists than endemics. An interesting result to highlight is that for both Palearctic and Himalayan endemics, a strong negative relationship was found between habitat breadth and elevational distribution, where for the full Palearctic realm assemblage no significant relationship was found and for Palearctic non-endemics a positive trend identified. As to why this is the only realm to show such a trend is unclear and requires further study.

Multivariate relationships: At the global species level, as with bivariate analyses, elevational distribution was consistently retained as a significant negative predictor of body weight, incubation period and adult survival, and as a positive predictor of habitat breadth (elevational range only) and clutch size – while controlling for body weight, geographical range and absolute mean latitude (Table 5.3). However, collectively, the outputs from the species-level multiple regressions for realm endemics, realm non-endemics and the three mountain endemic subsets are far more complex to disentangle and interpret (Tables 6.9). It is important that these multivariate results are considered with respect to three key factors, namely: (1) extent of environmental variation (geometric constraints), (2) lineage sorting and extent of trait variation, and (3) sample size (i.e. influence of well-studied species). For all five predictors, realm endemics displayed qualitatively similar outputs to those found for all species globally. This perhaps is not surprising considering the relatively similar sample sizes between the two datasets. However, the same was also largely found for realm non-endemics, despite considerably smaller sample sizes – there being only two main differences. Firstly, no evidence for Bergmann’s rule (Bergmann 1847) with latitude was identified. This is due to the species in this subset possessing large geographical ranges with a lot of overlap, therefore meaning variation in their mean latitudinal location is limited. Secondly, habitat breadth was not found to increase with either elevational distribution or latitude. Once again, this is linked to the fact that the majority of the widespread species also possess a broad habitat niche, with comparatively limited variation. For mountain endemics, many of the predictors are not retained as significant – including elevational distribution. Yet, it is important to remember that the samples sizes are relatively small for these mountain endemic subsets, especially with respect to adult survival. Focusing on geometric constraints, for example, latitudinal effects would be expected for the Andes (a mountain range with a latitudinal extent spanning from roughly 55°S to 11°N), but possibly not the EAR (11°S to 5°N) and Himalayas (26°N to 36°N). However, all three mountain endemic subsets showed evidence of Lack’s rule (Lack 1947), with latitude not found to influence variation in the other four traits. The difference in the trend between body size and elevational distribution for the three mountain ranges is especially interesting (i.e. Andes: not significant, EAR: positive, Himalayas: negative). It was originally thought that perhaps the Andes are dominated by passerines (unlike the EAR and Himalayas) and that this would have an influence on the extent of variation in body size. However, this was not found to be case, as all three mountain endemic subsets comprise of roughly the same proportion of passerines (>60%). Detailed phylogenetic-based analyses are needed in order to determine whether or not these differences are independent of phylogenetic relationships. Concerning the trait-elevation relationships found for realm endemics via multiple regression analysis across PICs (Table A6.12), they were found to be qualitatively the same to those found for the full global dataset – see Table A5.3 and associated discussion in Sections 5.5.2–5.5.3. Ultimately, there is a real need to obtain and collect trait data for missing species so as to increase sample sizes and so the representativeness of the data for each subset in question.

6.5.3 Conclusions

This study highlights the complexities and challenges of investigating elevational distributions of endemics and associated trait variation, at such a large spatial scale and for so many species. Nevertheless, as shown and discussed above, some general and informative patterns were found. Yet, there are many potential routes to pursue in terms of further research relating to this study and its findings, of which a few are highlighted below.

Future studies, both at the global and regional scale, are needed that explicitly attempt to model and identify the underlying processes for the patterns found here. Specifically, although macroecology aims to explain biotic patterns (such as trait distributions) predominantly using current environmental conditions, there is an inherent need to also integrate the past into such large-scale analyses. Beck *et al.* (2012) discuss in detail three main ways for integrating historical information into the macroecological research agenda, namely by: (1) incorporating paleo-data on aspects including species distributions, climate, landcover and geology (i.e. plate tectonics and orogeny), (2) considering phylogenetic relatedness of taxa, and (3) integrating analytical approaches from historical biogeography. Utilising such an integrated methodology with both spatial and temporal elements would undoubtedly benefit our current understanding of contemporary patterns of endemic species and their underlying traits.

True oceanic islands, defined by Davies *et al.* (2006) as encompassing ‘*any land area located further than 200 km from the edge of continental shelf*’, are known to differ markedly in the kinds and intensities of evolutionary and threatening processes affecting constituent avifauna, in comparison with continental locations (e.g. Manne *et al*. 1999; Blackburn *et al*.

2004; Duncan & Blackburn 2004). Although there are limited studies comparing the traits of island and continental species (e.g. Covas 2012), I can find none that explicitly compare island and montane species. In terms of future work, it would therefore be novel and informative to extend this study by comparing the avian characteristics of true oceanic island endemics with those of montane/sky island endemics. Additionally, it would be of interest to identify similarities or differences regarding elevational range profiles and trait relationships with respect to elevational distribution for bird species inhabiting island and continental landmasses.

The three mountain ranges studied here were selected based on them being the top three mountainous hotspots for avian species richness, as identified by Orme *et al.* (2005). However, not only would it be beneficial to conduct more detailed studies within these mountainous regions, but also to study other such areas. For example, the next richest hotspot recognised by Orme *et al.* (2005) is the 'Guyana highlands'. This mountainous region in northern South America is topographically unique, comprising isolated flattop mountains (tepuis) that are arguably the most dramatic example of sky islands in the world (Salerno *et al.* 2012). They rise to heights of 1500-2800m above sea-level and are isolated from their surroundings by up to 1000m high vertical cliffs (BirdLife International 2013). The tepuis are well known for their high number of relict endemics, often to a single plateau (Kok *et al.* 2012, see also Nogué *et al.* 2013). For example, within the Pantepui, 60% of the vascular plant species and 87% of the frog species are endemics (see Salerno *et al.* 2012). In addition, the tepuis have been designated an EBA, with a number of associated Important Bird Areas (IBAs) (BirdLife International 2013). The restricted-range species in this EBA are primarily montane birds occurring in the subtropical and temperate zones from around 600m upwards, e.g. *Crypturellus ptaritepui* (Tepui Tinamou), *Nannopsittaca panychlora* (Tepui parrotlet) and *Emberizoides duidae* (Duida Grass-finch). Due to the largely inaccessible nature of this isolated region, the tepuis have not yet been seriously affected by anthropogenic activities, and at present remain relatively undisturbed. Yet, these endemic birds warrant further research as they are currently so poorly studied that we know very little about their life history and ecology, and in turn their true vulnerability to potential future threats.

It is important to note that all of the endemic and restricted-range definitions used in this study are in relation to breeding ranges (as in previous studies, e.g. Stattersfield *et al.* 1998; Orme *et al.* 2005), and have therefore not accounted for the fact that birds are a highly mobile taxa, with many species being short- to long-distance migrants. As discussed further in Section 8.6.2, migratory behaviour is a highly complex variable, and difficult to incorporate into large-scale studies such as this. It is difficult to envisage how the patterns found in this study may differ if total range rather than breeding range were to be used as the main criteria for defining endemic and restricted-range species. For taxa such as plants, definitions are considerably easier to devise and more robust, due to their sessile nature, and this is probably a major reason as to why studies concerning the spatial distribution of endemics have traditionally been plant focused.

To conclude, endemic species are a highly valuable and unique subset of species in terms of biodiversity conservation. Not only do they play a central role in a number of high-profile global biodiversity conservation priority schemes, but are also of inherent conservation value. The future prognosis of endemic species is of immediate interest as extinction of these species represents an irreplaceable loss of species-level diversity (Shoo *et al.* 2005). Consequently, they are an important subset of global biodiversity for continued study, particularly with respect to spatial gradients (especially elevation) of their distribution and underlying traits, at a variety of spatial scales – not only for birds, but other taxa as well.

6.6 Appendix: Supplementary figures and tables

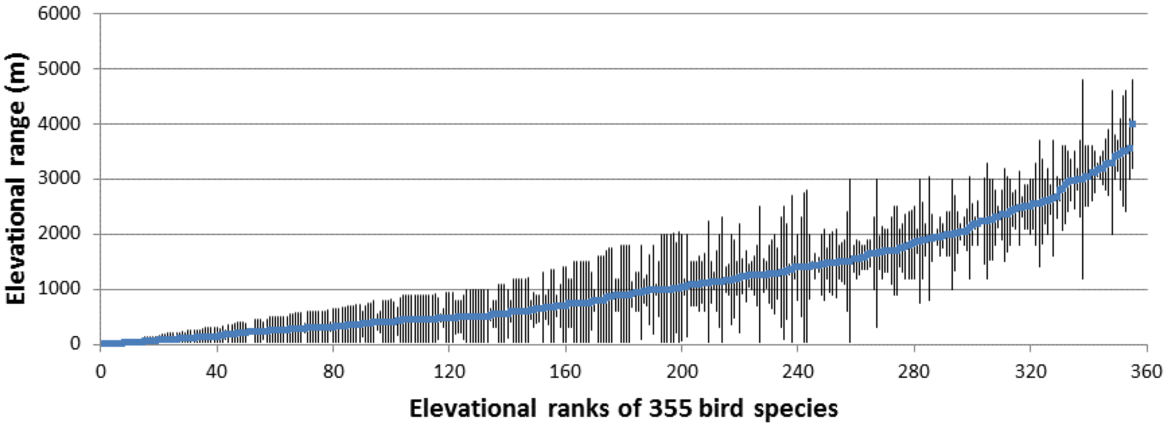


Figure A6.1 Elevational range profile for restricted-range (BirdLife International) species (i.e. bird species with geographical breeding ranges ≤50,000 km^2). Bars indicate the minimum and maximum elevational limits for each species' range, and species are arranged along the x-axis by ranked elevational midpoints.

Table A6.1 Pearson correlation coefficients (*r*) between species-level avian traits and elevational range for realm endemics.

	All		**Af**		**Au**		**IM**		**Na**		**Nt**		**Oc**		**Pa**	
	n	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Morphological																
Body weight	4308	-0.02	782	0.12^{***}	595	-0.22^{***}	327	-0.09	157	-0.27^{***}	2141	0.03	50	0.15	256	-0.12
Wing length	2417	-0.10^{***}	670	-0.03	522	0.10^{*}	237	-0.12	90	-0.30^{**}	665	-0.11^{**}	35	0.03	198	-0.39^{***}
Tarsus length	2223	-0.14^{***}	650	-0.22^{***}	511	-0.09^{*}	215	-0.01	77	-0.16	564	-0.09	30	-0.18	176	-0.46^{***}
Culmen length	2235	-0.32^{***}	618	-0.36^{***}	495	-0.32^{***}	193	-0.41^{***}	76	-0.03	678	-0.31^{***}	23	-0.25	152	-0.32^{***}
Reproduction																
Clutch size	3083	0.21^{***}	713	0.14^{***}	452	0.00	314	0.09	155	0.51^{***}	1416	0.21^{***}	54	0.14	256	0.03
Annual fecundity	754	0.57^{***}	107	0.57^{***}	218	0.51^{***}	15	0.61^{*}	114	0.67^{***}	157	0.51^{***}	23	0.35	120	0.56^{***}
Egg weight	1354	-0.20^{***}	256	-0.09	213	-0.15^{*}	95	-0.25^{*}	136	-0.54^{***}	473	-0.06	17	-0.21	164	-0.39^{***}
Development																
Incubation period	1240	-0.39^{***}	287	-0.33^{***}	199	-0.26^{***}	75	-0.24^{*}	139	-0.43^{***}	378	-0.45^{***}	22	0.04	140	-0.45^{***}
Fledging time	1035	-0.31^{***}	261	-0.42^{***}	190	-0.27^{***}	38	-0.06	123	-0.35^{***}	304	-0.29^{***}	20	0.00	99	-0.36^{***}
Age first breeding	342	-0.52^{***}	41	-0.27	62	-0.36^{**}	8	-0.47	84	-0.72^{***}	57	-0.61^{***}	12	-0.54	78	-0.57^{***}
Survival																
Adult survival	145	-0.59^{***}	19	-0.74^{***}	19	-0.40	0	*NA*	49	-0.67^{***}	20	-0.19	8	-0.59	30	-0.56^{**}
Niche breadth																
Diet breadth	1650	0.37^{***}	648	0.45^{***}	122	0.41^{***}	129	0.31^{***}	37	0.30	595	0.39^{***}	30	0.15	89	0.14
Habitat breadth	1884	0.24^{***}	698	0.29^{***}	122	0.23^{**}	151	0.00	41	0.29	736	0.29^{***}	34	0.50^{**}	102	-0.18

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. *NA*: Sample size too small to calculate correlation coefficient. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative elevational range used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). All = all realm endemics. Biogeographic realms: Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001).

Table A6.2 Pearson correlation coefficients (*r*) between species-level avian traits and maximum elevation for realm endemics.

	All		**Af**		**Au**		**IM**		**Na**		**Nt**		**Oc**		**Pa**	
	n	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Morphological																
Body weight	5467	– 0.04**	1087	0.11***	705	– 0.25***	496	– 0.07	189	– 0.20**	2594	0.00	53	0.03	343	0.04
Wing length	3082	– 0.10***	953	– 0.03	602	0.07	338	– 0.15**	114	– 0.25**	778	– 0.13***	36	– 0.05	261	– 0.38***
Tarsus length	2846	– 0.11***	928	– 0.17***	590	– 0.05	305	– 0.01	100	– 0.17	657	– 0.05	30	– 0.04	236	– 0.50***
Culmen length	2862	– 0.29***	889	– 0.31***	576	– 0.27***	286	– 0.29***	99	0.01	778	– 0.29***	23	– 0.13	211	– 0.45***
Reproduction																
Clutch size	3929	0.15***	968	0.12***	533	– 0.10*	463	0.05	187	0.45***	1712	0.14***	58	0.08	344	– 0.06
Annual fecundity	949	0.54***	155	0.57***	239	0.49***	30	0.36*	132	0.67***	195	0.49***	23	0.29	175	0.56***
Egg weight	1767	– 0.21***	372	– 0.13*	245	– 0.12	149	– 0.21**	163	– 0.54***	590	– 0.10*	18	– 0.36	230	– 0.38***
Development																
Incubation period	1558	– 0.38***	396	– 0.31***	221	– 0.24***	99	– 0.19	165	– 0.44***	451	– 0.44***	22	– 0.03	204	– 0.40***
Fledging time	1329	– 0.29***	365	– 0.39***	211	– 0.27***	58	– 0.13	148	– 0.34***	372	– 0.22***	20	– 0.08	155	– 0.34***
Age first breeding	423	– 0.51***	56	– 0.24	70	– 0.39***	11	– 0.32	101	– 0.74***	66	– 0.61***	12	– 0.68*	107	– 0.63***
Survival																
Adult survival	177	– 0.51***	27	– 0.62***	21	– 0.44	0	*NA*	57	– 0.59***	25	– 0.28	8	– 0.68	39	– 0.40*
Niche breadth																
Diet breadth	2065	0.33***	912	0.41***	134	0.33***	189	0.40***	54	0.17	642	0.34***	32	0.15	102	0.16
Habitat breadth	2336	0.11***	971	0.18***	136	0.15	216	– 0.05	58	0.15	801	0.11**	36	0.37*	118	– 0.34***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. *NA*: Sample size too small to calculate correlation coefficient. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative maximum elevation used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). All = all realm endemics. Biogeographic realms: Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001).

Table A6.3 Pearson correlation coefficients (r) between species-level avian traits and elevational midpoint for realm endemics.

	All		**Af**		**Au**		**IM**		**Na**		**Nt**		**Oc**		**Pa**	
	n	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Morphological																
Body weight	4308	-0.11^{***}	782	0.00	595	-0.28^{***}	327	-0.10	157	-0.23^{**}	2141	-0.09^{***}	50	-0.04	256	0.06
Wing length	2417	-0.16^{***}	670	-0.12^{**}	522	0.05	237	-0.24^{***}	90	-0.27^{*}	665	-0.16^{***}	35	-0.07	198	-0.47^{***}
Tarsus length	2223	-0.07^{**}	650	-0.16^{***}	511	0.02	215	0.03	77	-0.13	564	-0.03	30	0.01	176	-0.45^{***}
Culmen length	2235	-0.32^{***}	618	-0.36^{***}	495	-0.24^{***}	193	-0.43^{***}	76	-0.03	678	-0.34^{***}	23	-0.10	152	-0.42^{***}
Reproduction																
Clutch size	3083	0.17^{***}	713	0.17^{***}	452	-0.12^{*}	314	0.15^{*}	155	0.50^{***}	1416	0.14^{***}	54	0.07	256	-0.02
Annual fecundity	754	0.55^{***}	107	0.57^{***}	218	0.52^{***}	15	0.64^{**}	114	0.69^{***}	157	0.46^{***}	23	0.26	120	0.57^{***}
Egg weight	1354	-0.20^{***}	256	-0.15^{*}	213	-0.09	95	-0.24^{*}	136	-0.53^{***}	473	-0.05	17	-0.41	164	-0.44^{***}
Development																
Incubation period	1240	-0.38^{***}	287	-0.30^{***}	199	-0.23^{***}	75	-0.24^{*}	139	-0.42^{***}	378	-0.41^{***}	22	-0.06	140	-0.52^{***}
Fledging time	1035	-0.28^{***}	261	-0.39^{***}	190	-0.25^{***}	38	-0.15	123	-0.35^{***}	304	-0.23^{***}	20	-0.12	99	-0.37^{***}
Age first breeding	342	-0.53^{***}	41	-0.31^{*}	62	-0.40^{**}	8	-0.61	84	-0.74^{***}	57	-0.60^{***}	12	-0.74^{**}	78	-0.67^{***}
Survival																
Adult survival	145	-0.56^{***}	19	-0.74^{***}	19	-0.39	0	*NA*	49	-0.56^{***}	20	-0.29	8	-0.67	30	-0.57^{***}
Niche breadth																
Diet breadth	1650	0.28^{***}	648	0.37^{***}	122	0.35^{***}	129	0.33^{***}	37	0.18	595	0.25^{***}	30	0.12	89	0.14
Habitat breadth	1884	0.02	698	0.11^{***}	122	0.09	151	-0.08	41	0.14	736	-0.01	34	0.34	102	-0.35^{***}

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. n = correlation sample size. *NA*: Sample size too small to calculate correlation coefficient. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative elevational midpoint used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). All = all realm endemics. Biogeographic realms: Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001).

Table A6.4 Pearson correlation coefficients (*r*) between species-level avian traits and elevational range for realm non-endemics.

	All		**Af**		**Au**		**IM**		**Na**		**Nt**		**Oc**		**Pa**	
	n	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Morphological																
Body weight	709	– 0.25***	126	– 0.03	193	– 0.28***	444	– 0.21***	226	– 0.21**	203	– 0.27***	48	– 0.63***	473	– 0.12**
Wing length	454	0.01	119	0.00	141	0.10	279	0.07	137	– 0.22	118	– 0.12	40	– 0.20	304	0.00
Tarsus length	433	– 0.08	117	0.15	136	– 0.22*	273	– 0.03	124	0.01	106	0.03	39	0.27	295	– 0.10
Culmen length	426	– 0.21***	116	– 0.17	139	0.33**	270	– 0.23***	120	– 0.16	106	– 0.04	39	– 0.25	289	– 0.26***
Reproduction																
Clutch size	666	0.16***	123	0.26**	185	0.20**	410	– 0.01	221	0.33***	198	0.36***	47	0.55***	442	0.08
Annual fecundity	294	0.61***	91	0.63***	90	0.63***	144	0.55***	139	0.65***	119	0.61***	38	0.65***	172	0.64***
Egg weight	475	– 0.33***	99	– 0.34***	141	– 0.27**	279	– 0.36***	184	– 0.32***	164	– 0.19*	40	– 0.20	299	– 0.45***
Development																
Incubation period	360	– 0.38***	105	– 0.48***	104	– 0.42***	171	– 0.36***	170	– 0.40***	148	– 0.38***	36	– 0.59***	213	– 0.41***
Fledging time	303	– 0.32***	105	– 0.48***	84	– 0.33**	131	– 0.32***	150	– 0.35***	136	– 0.35***	33	– 0.49**	169	– 0.37***
Age first breeding	143	– 0.53***	53	– 0.38**	42	– 0.63***	62	– 0.46***	85	– 0.68***	72	– 0.65***	24	– 0.76***	82	– 0.50***
Survival																
Adult survival	72	– 0.49***	24	– 0.60**	20	– 0.52*	30	– 0.45*	45	– 0.59***	37	– 0.59***	15	– 0.62*	42	– 0.49***
Niche breadth																
Diet breadth	276	0.52***	106	0.57***	81	0.62***	153	0.53***	85	0.49***	82	0.56***	21	0.64**	189	0.51***
Habitat breadth	294	0.25***	105	0.27**	84	0.39***	166	0.31***	88	0.42***	85	0.47***	21	0.64**	200	0.23***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative elevational range used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). All = all realm non-endemics. Biogeographic realms: Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001).

Table A6.5 Pearson correlation coefficients (*r*) between species-level avian traits and maximum elevation for realm non-endemics.

	All		**Af**		**Au**		**IM**		**Na**		**Nt**		**Oc**		**Pa**	
	n	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Morphological																
Body weight	909	– 0.27***	171	– 0.01	228	– 0.28***	588	– 0.21***	254	– 0.27***	228	– 0.34***	53	– 0.61***	644	– 0.14***
Wing length	596	0.05	161	0.08	163	0.11	380	0.11*	151	– 0.22**	129	– 0.09	44	– 0.22	431	0.06
Tarsus length	570	– 0.13**	159	0.13	157	0.11	369	– 0.11*	138	– 0.03	117	0.00	43	0.25	417	– 0.15**
Culmen length	565	– 0.22***	156	– 0.16*	160	– 0.24**	369	– 0.24***	134	– 0.15	117	– 0.04	43	– 0.24	413	– 0.26***
Reproduction																
Clutch size	856	0.07*	167	0.21**	219	0.13	545	– 0.07	248	0.22***	222	0.25***	52	0.52***	606	0.02
Annual fecundity	355	0.55***	108	0.57***	99	0.62***	184	0.49***	153	0.60***	131	0.55***	42	0.65***	222	0.57***
Egg weight	599	– 0.33***	132	– 0.28***	161	– 0.27***	362	– 0.37***	208	– 0.34***	185	– 0.22**	45	– 0.20	401	– 0.42***
Development																
Incubation period	449	– 0.36***	140	– 0.46***	115	– 0.44***	218	– 0.36***	190	– 0.37***	166	– 0.36***	40	– 0.57***	284	– 0.40***
Fledging time	379	– 0.36***	140	– 0.50***	91	– 0.36***	165	– 0.37***	169	– 0.32***	153	– 0.32***	36	– 0.49**	228	– 0.42***
Age first breeding	166	– 0.54***	62	– 0.42***	46	– 0.63***	72	– 0.47***	95	– 0.68***	80	– 0.64***	26	– 0.75***	98	– 0.52***
Survival																
Adult survival	83	– 0.47***	30	– 0.60***	21	– 0.52*	34	– 0.47**	49	– 0.58***	40	– 0.56***	17	– 0.63**	50	– 0.50***
Niche breadth																
Diet breadth	341	0.50***	140	0.58***	86	0.60***	188	0.50***	88	0.47***	85	0.54***	21	0.63**	249	0.49***
Habitat breadth	366	0.19***	141	0.27**	92	0.37***	206	0.22**	91	0.38***	88	0.43***	21	0.63**	266	0.16**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative maximum elevation used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). All = all realm non-endemics. Biogeographic realms: Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001).

Table A6.6 Pearson correlation coefficients (*r*) between species-level avian traits and elevational midpoint for realm non-endemics.

	All		Af		Au		IM		Na		Nt		Oc		Pa	
	n	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Morphological																
Body weight	709	– 0.32***	126	– 0.07	193	– 0.29***	444	– 0.26***	226	– 0.30***	203	– 0.37***	48	– 0.62***	473	– 0.19***
Wing length	454	0.01	119	0.00	141	0.09	279	0.07	137	– 0.21*	118	– 0.09	40	– 0.20	304	0.00
Tarsus length	433	– 0.07	117	0.16	136	0.15	273	– 0.02	124	– 0.02	106	0.02	39	0.23	295	– 0.09
Culmen length	426	– 0.21***	116	– 0.17	139	– 0.22**	270	– 0.22***	120	– 0.18*	106	– 0.06	39	– 0.26	289	– 0.26***
Reproduction																
Clutch size	666	0.11**	123	0.22*	185	0.15*	410	– 0.06	221	0.27***	198	0.30***	47	0.49***	442	0.04
Annual fecundity	294	0.59***	91	0.63***	90	0.65***	144	0.55***	139	0.61***	119	0.56***	38	0.69***	172	0.64***
Egg weight	475	– 0.33***	99	– 0.35***	141	– 0.26**	279	– 0.35***	184	– 0.33***	164	– 0.18*	40	– 0.18	299	– 0.45***
Development																
Incubation period	360	– 0.35***	105	– 0.47***	104	– 0.42***	171	– 0.37***	170	– 0.35***	148	– 0.32***	36	– 0.55***	213	– 0.42***
Fledging time	303	– 0.31***	105	– 0.48***	84	– 0.34**	131	– 0.34***	150	– 0.30***	136	– 0.29***	33	– 0.47**	169	– 0.38***
Age first breeding	143	– 0.53***	53	– 0.39**	42	– 0.63***	62	– 0.47***	85	– 0.70***	72	– 0.65***	24	– 0.77***	82	– 0.51***
Survival																
Adult survival	72	– 0.50***	24	– 0.61***	20	– 0.54*	30	– 0.47**	45	– 0.60***	37	– 0.59***	15	– 0.65**	42	– 0.52***
Niche breadth																
Diet breadth	276	0.48***	106	0.55***	81	0.61***	153	0.50***	85	0.44***	82	0.51***	21	0.64**	189	0.48***
Habitat breadth	294	0.18**	105	0.23*	84	0.37***	166	0.24**	88	0.33**	85	0.38***	21	0.63**	200	0.16*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative elevational midpoint used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). All = all realm non-endemics. Biogeographic realms: Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001).

Table A6.7 Pearson correlation coefficients (*r*) between species-level avian traits and elevational range for restricted-range (lower quartile) species and mountain endemics.

	Lower quartile				Andes				East African Rift				Himalayas			
	Broad		Narrow		Broad		Narrow		Broad		Narrow		Broad		Narrow	
	n	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Morphological																
Body weight	1144	-0.13^{***}	1001	-0.15^{***}	1476	0.06^{*}	625	0.08^{*}	513	0.23^{***}	208	-0.03	402	-0.21^{***}	210	-0.12
Wing length	577	-0.09^{*}	502	-0.05	437	-0.16^{**}	144	-0.21^{*}	493	-0.01	197	-0.23^{**}	265	-0.20^{***}	122	-0.38^{***}
Tarsus length	526	-0.18^{***}	455	-0.18^{***}	359	-0.03	107	-0.29^{**}	484	-0.24^{***}	191	-0.31^{***}	258	-0.25^{***}	116	-0.48^{***}
Culmen length	511	-0.18^{***}	449	-0.16^{***}	470	-0.40^{***}	151	-0.49^{***}	463	-0.38^{***}	181	-0.31^{***}	233	-0.37^{***}	104	-0.55^{***}
Reproduction																
Clutch size	790	0.05	691	0.05	954	0.27^{***}	286	0.34^{***}	464	0.10^{*}	181	0.05	393	-0.12^{*}	198	-0.08
Annual fecundity	129	0.28^{**}	120	0.26^{**}	107	0.72^{***}	17	0.83^{***}	81	0.65^{***}	20	0.50^{*}	85	0.56^{***}	20	0.57^{**}
Egg weight	157	-0.15	137	-0.14	375	-0.05	46	0.12	196	-0.09	41	-0.11	233	-0.37^{***}	98	-0.58^{***}
Development																
Incubation period	188	-0.24^{***}	169	-0.23^{**}	277	-0.52^{***}	43	-0.62^{***}	222	-0.37^{***}	58	-0.38^{**}	128	-0.32^{***}	34	-0.39^{*}
Fledging time	155	-0.04	141	-0.06	226	-0.40^{***}	36	-0.51^{**}	200	-0.50^{***}	56	-0.54^{***}	73	-0.45^{***}	13	-0.35
Age first breeding	52	-0.47^{***}	49	-0.41^{**}	41	-0.68^{***}	11	-0.62^{*}	28	-0.45^{*}	1	*NA*	43	-0.43^{**}	7	-0.14
Survival																
Adult survival	25	-0.17	25	-0.17	12	-0.64^{*}	2	-1.00^{***}	14	-0.73^{**}	4	-0.99^{**}	15	-0.66^{**}	0	*NA*
Niche breadth																
Diet breadth	362	0.18^{***}	320	0.20^{***}	421	0.43^{***}	157	0.29^{***}	480	0.50^{***}	189	0.33^{***}	136	0.19^{*}	52	0.33^{*}
Habitat breadth	520	0.20^{***}	466	0.21^{***}	496	0.28^{***}	203	0.27^{***}	486	0.25^{***}	196	0.18^{**}	150	-0.09	60	-0.39^{**}

* *P*<0.05, ** *P*<0.01, *** *P*<0.001. *n* = correlation sample size. *NA*: Sample size too small to calculate correlation coefficient. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative elevational range used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). Full definitions of ‘broad’ and ‘narrow’ restricted-range (lower quartile) and mountain endemics are given in main body of text (Sections 6.3.1–6.3.2).

Table A6.8 Pearson correlation coefficients (*r*) between species-level avian traits and maximum elevation for restricted-range (lower quartile) species and mountain endemics.

	Lower quartile				**Andes**				**East African Rift**				**Himalayas**			
	Broad		**Narrow**		**Broad**		**Narrow**		**Broad**		**Narrow**		**Broad**		**Narrow**	
	n	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Morphological																
Body weight	1263	– 0.21***	1001	– 0.24***	1476	– 0.04	625	0.06	513	0.13**	208	0.04	402	– 0.17***	210	0.09
Wing length	632	– 0.13***	502	– 0.12**	437	– 0.19***	144	– 0.32***	493	– 0.07	197	– 0.28***	265	– 0.28***	122	– 0.47***
Tarsus length	576	– 0.10*	455	– 0.08	359	0.00	107	– 0.29**	484	– 0.19***	191	– 0.35***	258	– 0.23***	116	– 0.52***
Culmen length	565	– 0.10*	449	– 0.10*	470	– 0.42***	151	– 0.54***	463	– 0.40***	181	– 0.33***	233	– 0.41***	104	– 0.66***
Reproduction																
Clutch size	874	0.04	691	0.06	954	0.21***	286	0.37***	464	0.10*	181	0.09	393	– 0.09	198	– 0.03
Annual fecundity	136	0.21*	120	0.18*	107	0.68***	17	0.88***	81	0.64***	20	0.55*	85	0.58***	20	0.70***
Egg weight	169	– 0.21**	137	– 0.20*	375	– 0.05	46	0.01	196	– 0.13	41	– 0.19	233	– 0.40***	98	– 0.60***
Development																
Incubation period	201	– 0.23***	169	– 0.24**	277	– 0.49***	43	– 0.58***	222	– 0.37***	58	– 0.37**	128	– 0.36***	34	– 0.52**
Fledging time	166	– 0.03	141	– 0.05	226	– 0.33***	36	– 0.44**	200	– 0.48***	56	– 0.56***	73	– 0.48***	13	– 0.43
Age first breeding	54	– 0.49***	49	– 0.43**	41	– 0.69***	11	– 0.62*	28	– 0.44*	1	*NA*	43	– 0.54***	7	– 0.43
Survival																
Adult survival	25	– 0.04	25	– 0.04	12	– 0.93***	2	– 1.00***	14	– 0.73**	4	– 0.95*	15	– 0.66**	0	*NA*
Niche breadth																
Diet breadth	384	0.09	320	0.11	421	0.31***	157	0.20*	480	0.47***	189	0.43***	136	0.18*	52	0.38**
Habitat breadth	562	0.02	466	0.01	496	0.02	203	0.04	486	0.15***	196	0.12	150	– 0.21**	60	– 0.48***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. *NA*: Sample size too small to calculate correlation coefficient. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative maximum elevation used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). Full definitions of 'broad' and 'narrow' restricted-range (lower quartile) and mountain endemics are given in main body of text (Sections 6.3.1–6.3.2).

Table A6.9 Pearson correlation coefficients (*r*) between species-level avian traits and elevational midpoint for restricted-range (lower quartile) species and mountain endemics

	Lower quartile				**Andes**				**East African Rift**				**Himalayas**			
	Broad		**Narrow**		**Broad**		**Narrow**		**Broad**		**Narrow**		**Broad**		**Narrow**	
	n	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Morphological																
Body weight	1144	-0.25^{***}	1001	-0.25^{***}	1476	-0.07^{**}	625	0.03	513	0.02	208	0.06	402	-0.14^{**}	210	0.18^{*}
Wing length	577	-0.17^{***}	502	-0.15^{***}	437	-0.21^{***}	144	-0.34^{***}	493	-0.10^{*}	197	-0.29^{***}	265	-0.31^{***}	122	-0.49^{***}
Tarsus length	526	-0.07	455	-0.07	359	-0.01	107	-0.28^{**}	484	-0.16^{***}	191	-0.35^{***}	258	-0.23^{***}	116	-0.53^{***}
Culmen length	511	-0.11^{*}	449	-0.09^{*}	470	-0.42^{***}	151	-0.53^{***}	463	-0.39^{***}	181	-0.32^{***}	233	-0.42^{***}	104	-0.68^{***}
Reproduction																
Clutch size	790	0.04	691	0.06	954	0.18^{***}	286	0.37^{***}	464	0.10^{*}	181	0.11	393	-0.08	198	-0.01
Annual fecundity	129	0.21^{*}	120	0.17	107	0.67^{***}	17	0.85^{***}	81	0.64^{***}	20	0.57^{**}	85	0.59^{***}	20	0.75^{***}
Egg weight	157	-0.22^{**}	137	-0.20^{*}	375	-0.05	46	-0.03	196	-0.15^{*}	41	-0.24	233	-0.41^{***}	98	-0.59^{***}
Development																
Incubation period	188	-0.24^{***}	169	-0.24^{**}	277	-0.48^{***}	43	-0.57^{***}	222	-0.36^{***}	58	-0.36^{**}	128	-0.38^{***}	34	-0.57^{***}
Fledging time	155	-0.02	141	-0.04	226	-0.30^{***}	36	-0.38^{*}	200	-0.47^{***}	56	-0.55^{***}	73	-0.49^{***}	13	-0.48
Age first breeding	52	-0.50^{***}	49	-0.42^{**}	41	-0.68^{***}	11	-0.62^{*}	28	-0.45^{*}	1	*NA*	43	-0.58^{***}	7	-0.56
Survival																
Adult survival	25	-0.05	25	-0.05	12	-0.95^{***}	2	-1.00^{***}	14	-0.73^{**}	4	-0.90	15	-0.66^{**}	0	*NA*
Niche breadth																
Diet breadth	362	0.07	320	0.09	421	0.26^{***}	157	0.17^{*}	480	0.42^{***}	189	0.44^{***}	136	0.17^{*}	52	0.39^{**}
Habitat breadth	520	-0.05	466	-0.05	496	-0.09^{*}	203	-0.04	486	0.09	196	0.09	150	-0.26^{**}	60	-0.51^{***}

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. *NA*: Sample size too small to calculate correlation coefficient. Relative traits used, except for body weight, clutch size and diet/habitat breadth. Relative elevational midpoint used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). Full definitions of 'broad' and 'narrow' restricted-range (lower quartile) and mountain endemics are given in main body of text (Sections 6.3.1–6.3.2).

Table A6.10 Pearson correlation coefficients (*r*) between species-level avian traits and elevational distribution for restricted-range (BirdLife International) species.

	Elevational range		Maximum elevation		Elevational midpoint	
	n	***r***	***n***	***r***	***n***	***r***
Morphological						
Body weight	254	– 0.18**	272	– 0.27***	254	– 0.28***
Wing length	126	– 0.02	136	– 0.14	126	– 0.19*
Tarsus length	121	– 0.23*	131	– 0.16	121	– 0.16
Culmen length	115	– 0.20*	125	– 0.12	115	– 0.13
Reproduction						
Clutch size	146	– 0.02	157	0.02	146	0.02
Annual fecundity	49	– 0.04	50	– 0.16	49	– 0.16
Egg weight	37	0.04	37	– 0.07	37	– 0.10
Development						
Incubation period	52	0.13	52	0.12	52	0.11
Fledging time	50	0.01	50	0.06	50	0.06
Age at first breeding	21	– 0.20	21	– 0.17	21	– 0.17
Survival						
Adult survival	12	0.53	12	0.00	12	0.03
Niche breadth						
Diet breadth	88	0.08	92	0.01	88	– 0.04
Habitat breadth	158	0.27***	167	0.05	158	– 0.03

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. Relative traits were used, except for body weight, clutch size and diet/habitat breadth. Relative elevational distribution used except for correlations with body weight. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). Restricted-range species under the BirdLife International definition are those with a geographical range ≤50,000km^2 (Stattersfield *et al.* 1998).

Table A6.11 Pearson correlation coefficients (*r*) between avian traits and elevational distribution (a: elevational range, b: maximum elevation, c: elevational midpoint) for all realm endemics, across species and phylogenetically independent contrasts (PICs). PICs derived from two independent phylogenetic trees, using the Ericson *et al.* (2006) backbone or the Hackett *et al.* (2008) backbone. Realm endemics defined using the biogeographic realm boundaries in Olson *et al.* (2001).

(a) Elevational range	**Species**		**Ericson**		**Hackett**	
	n	*r*	*n*	*r*	*n*	*r*
Morphological						
Body weight	4306	– 0.02	4302	0.07***	4300	0.04*
Wing length	2716	– 0.07***	2680	0.11***	2687	0.10***
Tarsus length	2483	– 0.01	2473	0.10***	2468	0.03
Culmen length	2492	– 0.09***	2482	0.04*	2476	0.28***
Reproduction						
Clutch size	3359	0.17***	3346	0.22***	3335	0.11***
Annual fecundity	773	0.32***	771	0.23***	761	0.16***
Egg weight	1379	– 0.15***	1369	0.02	1362	– 0.02
Development						
Incubation period	1281	– 0.22***	1264	– 0.12***	1271	– 0.11***
Fledging time	1067	– 0.23***	1057	– 0.08**	1063	– 0.06*
Age at first breeding	348	– 0.36***	340	0.17**	338	– 0.008
Survival						
Adult survival	148	– 0.50***	145	– 0.53***	145	– 0.26***
Niche breadth						
Diet breadth	1816	0.11***	1785	0.21***	1790	0.44***
Habitat breadth	2196	0.30***	2176	0.40***	2172	0.32***

(b) Maximum elevation	**Species**		**Ericson**		**Hackett**	
	n	*r*	*n*	*r*	*n*	*r*
Morphological						
Body weight	5465	– 0.04**	5396	0.08***	5457	– 0.01
Wing length	3441	– 0.08***	3435	0.12***	3441	– 0.02
Tarsus length	3156	0.00	3152	0.09***	3156	– 0.11***
Culmen length	3167	– 0.12***	3163	– 0.03	3164	– 0.01
Reproduction						
Clutch size	4264	0.15***	4243	0.06***	4228	0.34***
Annual fecundity	968	0.27***	964	0.12***	956	0.06*
Egg weight	1798	– 0.11***	1781	0.02	1774	– 0.01
Development						
Incubation period	1604	– 0.19***	1586	– 0.11***	1584	– 0.16***
Fledging time	1365	– 0.19***	1350	– 0.06*	1350	– 0.05
Age at first breeding	429	– 0.30***	419	– 0.03	420	0.04
Survival						
Adult survival	180	– 0.45***	176	– 0.33***	177	– 0.08
Niche breadth						
Diet breadth	2262	0.05*	2241	– 0.03	2241	0.10***
Habitat breadth	2701	0.12***	2696	0.11***	2692	0.08***

Table A6.11 Continued.

(c) Elevational midpoint	**Species**		**Ericson**		**Hackett**	
	n	*r*	*n*	*r*	*n*	*r*
Morphological						
Body weight	4306	– 0.11***	4298	0.03*	4289	– 0.06***
Wing length	2716	– 0.15***	2716	– 0.16***	2706	– 0.14***
Tarsus length	2483	– 0.01	2473	0.02	2472	– 0.05**
Culmen length	2492	– 0.17***	2494	– 0.22*	2476	– 0.20***
Reproduction						
Clutch size	3359	0.10***	3344	– 0.02	3331	0.36***
Annual fecundity	773	0.26***	770	0.04	762	0.03
Egg weight	1379	– 0.14***	1370	0.07**	1360	0.05
Development						
Incubation period	1281	– 0.20***	1268	– 0.08**	1261	– 0.17***
Fledging time	1067	– 0.23***	1056	– 0.004	1053	– 0.01
Age at first breeding	348	– 0.34***	342	0.09	338	– 0.04
Survival						
Adult survival	148	– 0.48***	145	– 0.38***	146	– 0.17*
Niche breadth						
Diet breadth	1816	– 0.02	1783	– 0.10***	1790	– 0.09***
Habitat breadth	2196	0.00	2180	– 0.02	2172	– 0.04

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. Study variables $\log_{10}$ transformed except adult survival (arcsine transformed) and diet/habitat breadth (untransformed). Trait values for both the species and PIC analyses are in their non-residual form.

Table A6.12 Distributional relationships of avian traits for all realm endemics across phylogenetically independent contrasts (PICs), revealed by multiple linear regressions. Independent variables entered into each model were body weight, geographical range, absolute mean latitude (latitude) and elevational distribution (elevation): (a) elevational range, (b) maximum elevation, and (c) elevational midpoint. PICs derived from two independent phylogenetic trees, using Ericson *et al.* (2006) or Hackett *et al.* (2008) backbone. Realm endemics defined using the biogeographic realm boundaries in Olson *et al.* (2001).

Dependent	**Independent**	**PICs (Ericson)**			**PICs (Hackett)**		
		β	***p***	***r²***	**β**	***p***	***r²***
(a) Elevational range							
Body weight	Elevation	0.03	**	0.01	0.05	***	0.01
	Geog. range	– 0.01	*NS*		– 0.02	***	
	Latitude	0.01	**		0.01	*NS*	
		$F_{3,3402} = 6.2^{***}$			$F_{3,3419} = 15.5^{***}$		
Clutch size	Body weight	– 0.04	***	0.15	– 0.02	*	0.14
	Elevation	– 0.01	*		– 0.01	*	
	Geog. range	0.04	***		0.04	***	
	Latitude	0.03	***		0.04	***	
		$F_{4,2522} = 115.4^{***}$			$F_{4,2518} = 110.3^{***}$		
Incubation period	Body weight	0.09	***	0.20	0.08	***	0.16
	Elevation	0.001	*NS*		– 0.003	*NS*	
	Geog. range	– 0.01	***		– 0.01	***	
	Latitude	0.00	*NS*		– 0.002	*NS*	
		$F_{4,1093} = 67.0^{***}$			$F_{4,1092} = 52.7^{***}$		
Adult survival	Body weight	1.70	*NS*	0.24	1.55	**	0.35
	Elevation	– 3.97	*NS*		– 7.39	*NS*	
	Geog. range	– 4.68	***		– 4.78	***	
	Latitude	2.08	*NS*		1.64	*NS*	
		$F_{4,126} = 10.0^{***}$			$F_{4,126} = 16.9^{***}$		
Habitat breadth	Body weight	0.53	*	0.22	0.66	***	0.24
	Elevation	0.83	***		0.98	***	
	Geog. range	1.11	***		0.94	***	
	Latitude	– 0.07	*NS*		– 0.07	*NS*	
		$F_{4,1565} = 113.4^{***}$			$F_{4,1573} = 123.4^{***}$		
(b) Maximum elevation							
Body weight	Elevation	0.05	***	0.01	0.03	**	0.004
	Geog. range	0.00	*NS*		– 0.01	**	
	Latitude	0.01	**		0.00	*NS*	
		$F_{3,4366} = 14.1^{***}$			$F_{3,4395} = 6.0^{***}$		
Clutch size	Body weight	– 0.02	**	0.14	– 0.03	**	0.13
	Elevation	– 0.02	**		– 0.02	**	
	Geog. range	0.04	***		0.04	***	
	Latitude	0.03	***		0.03	***	
		$F_{4,3257} = 135.8^{***}$			$F_{4,3257} = 118.7^{***}$		
Incubation period	Body weight	0.09	***	0.18	0.08	***	0.16
	Elevation	0.01	*NS*		– 0.002	*NS*	
	Geog. range	– 0.02	***		– 0.01	***	
	Latitude	– 0.002	*NS*		– 0.002	*NS*	
		$F_{4,1386} = 75.4^{***}$			$F_{4,1382} = 64.1^{***}$		

Table A6.12 Continued.

Dependent	Independent	PICs (Ericson)			PICs (Hackett)		
		β	*p*	r^2	β	*p*	r^2
(b) Maximum elevation							
Adult survival	Body weight	3.73	*NS*	0.28	2.94	*NS*	0.30
	Elevation	0.26	*NS*		– 2.47	*NS*	
	Geog. range	– 4.94	***		– 5.61	***	
	Latitude	– 4.03	*		– 2.84	*NS*	
		$F_{4,155} = 14.8^{***}$			$F_{4,157} = 16.6^{***}$		
Habitat breadth	Body weight	0.57	**	0.20	0.45	*	0.20
	Elevation	0.73	***		0.78	***	
	Geog. range	1.05	***		1.01	***	
	Latitude	0.02	*NS*		0.06	*NS*	
		$F_{4,1996} = 126.8^{***}$			$F_{4,1986} = 122.9^{***}$		
(c) Elevational midpoint							
Body weight	Elevation	0.07	***	0.02	0.04	***	0.01
	Geog. range	– 0.01	*NS*		– 0.01	***	
	Latitude	0.01	**		0.01	**	
		$F_{3,3398} = 25.2^{***}$			$F_{3,3424} = 14.0^{***}$		
Clutch size	Body weight	– 0.03	**	0.16	– 0.02	*NS*	0.16
	Elevation	– 0.03	***		– 0.03	***	
	Geog. range	0.03	***		0.04	***	
	Latitude	0.03	***		0.04	***	
		$F_{4,3168} = 119.6^{***}$			$F_{4,2519} = 115.9^{***}$		
Incubation period	Body weight	0.09	***	0.18	0.08	***	0.16
	Elevation	0.004	*NS*		0.002	*NS*	
	Geog. range	– 0.01	***		– 0.01	***	
	Latitude	– 0.001	*NS*		– 0.002	*NS*	
		$F_{4,1090} = 59.9^{***}$			$F_{4,1091} = 52.3^{***}$		
Adult survival	Body weight	1.69	*NS*	0.24	2.08	*NS*	0.22
	Elevation	– 3.45	*NS*		– 2.73	*NS*	
	Geog. range	– 4.95	***		– 4.78	***	
	Latitude	2.13	*NS*		2.17	*NS*	
		$F_{4,126} = 9.87^{***}$			$F_{4,126} = 9.1^{***}$		
Habitat breadth	Body weight	0.66	**	0.22	0.79	***	0.23
	Elevation	0.32	*		0.30	*	
	Geog. range	1.28	***		1.08	***	
	Latitude	– 0.11	*NS*		– 0.08	*NS*	
		$F_{4,1564} = 107.5^{***}$			$F_{4,1571} = 114.9^{***}$		

β: multiple regression coefficient (standardised). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. r^2: proportion of variance in the dependent variable explained by retained predictor variables. *NS*: independent variable not significant. Degrees of freedom and F-statistic value for each model also reported. All variables $\log_{10}$ transformed, except adult survival (arcsine transformed) and diet/habitat breadth (untransformed).

CHAPTER SEVEN

Global elevational distribution and extinction risk in birds

7.1 Abstract

Understanding the global geographical distribution of extinction risk and its drivers are key challenges in conservation biology, and central to determining spatial priorities for the focus of conservation efforts. Mountainous regions worldwide are proven hotspots of terrestrial biodiversity (species richness and endemism). In comparison to lowlands, montane regions remain relatively unspoilt by anthropogenic activities. However, many mountain biodiversity hotspots, and high-elevation sites in general, are under increasing threat from human pressures – most notably habitat conversion and climate change. Limits to the taxonomic and geographical extent, resolution and quality of previously available data, have thus far precluded an explicit global assessment for a major taxon of the role of elevational distribution in determining extinction risk. Here, using a global species-level avian database, it is shown that measures of elevational distribution (range, maximum and midpoint) are highly significant negative predictors of avian extinction risk globally – comparable to that of geographical range size. These relationships are maintained within individual biogeographic realms, for species within orders, and across both families and phylogenetically independent contrasts. The consistent findings from this study highlight the role of elevational distribution as a key criterion for categorising extinction risk in birds. Further research is recommended to test for generality across non-avian taxa.

7.2 Introduction

Recent global studies of geographical range sizes have shown that major mountain chains, predominately within the tropics, are the richest areas for terrestrial biodiversity (specifically species richness and endemism), and are therefore of key biodiversity value (Orme *et al.* 2005; Davies *et al*. 2007). Yet, the reasons for this distribution are very poorly understood, as to date, scientists possess limited understanding of the evolutionary and ecological factors that promote hotspots of avian diversity associated with elevational variation. This is due primarily to a lack of focused studies on mountain systems and elevational gradients at large spatial scales (however, see McCain 2009a), and is in stark contrast to the considerable knowledge accrued from numerous studies concerning latitudinal variation in avian diversity (e.g. Rahbek & Graves 2001; Hawkins *et al.* 2003; Storch *et al.* 2006; Davies *et al.* 2007; Hawkins *et al.* 2007). For example, the Andean mountain range, considered to be the undisputed epicentre of global biodiversity and endemism remains one of the least-studied tropical regions on the planet (Pitman *et al*. 2011). However, it should be noted that the number of published studies on elevational diversity gradients, across taxa, has been increasing steadily over the past decade, with a number of theories proposed to explain observed patterns (see Section 1.3 and references within). Furthermore, despite the inherent conservation value of mountain ranges, we know little about the type, distribution and impact of the threats they face, which is essential for the effective prioritisation and implementation of conservation effort.

As discussed in Section 1.11.2, it has been widely proposed that climate change will increase extinctions in montane regions, across taxa, principally via the mechanism of upward altitudinal range shifts, with high-montane species frequently labelled as being highly sensitive and vulnerable to warming (e.g. Williams *et al.* 2003; Shoo *et al.* 2005; Sekercioglu *et al.* 2008; La Sorte & Jetz 2010). However, what is the current relationship between extinction risk and elevation? I propose two simplistic yet plausible and contrasting hypotheses to test here, namely:

1) '*Climate change hypothesis'*: extinction risk is positively correlated with elevation, i.e. montane species are at greatest risk of extinction. Species limited to montane areas may be more prone to extinction because of restricted distributions and dispersal capabilities, and small populations.
2) *'Direct anthropogenic pressure hypothesis'*: extinction risk is negatively associated with elevation, i.e. lowland species are at greatest risk of extinction. Species living in lowlands may face more direct human pressures, including habitat destruction and overexploitation. Montane areas in comparison remain relatively unspoilt by anthropogenic activities, due largely to their inaccessibility and steep gradients.

In comparison to numerous papers exploring the relative role of geographical range and latitudinal distribution on extinction risk across taxa (e.g. Manne *et al.* 1999; Orme *et al.* 2005; Grenyer *et al.* 2006; Harris & Pimm 2008), only a few studies to date have investigated elevation as a potential predictor of extinction. Out of these studies, several explicitly analyse species-level elevational distribution as a predictor variable of extinction risk, however, they are spatially and/or taxonomically focused (Manne *et al.* 1999; Manne & Pimm 2001; Gage *et al.* 2004; Keane *et al.* 2005; Krűger & Radford 2008), or lack transparency and a multivariate assessment (Sekercioglu *et al.* 2008). Other research-efforts have been global in extent, but utilise a grid-cell approach to model potential elevational distribution rather than actual recorded elevational limits of the study species (Davies *et al.* 2006; Lee & Jetz 2011). See Section 1.9.4 (and Table 1.3 within) for a more in depth review of existing literature concerning extinction risk and elevation, across taxa.

Understanding the spatial distribution of extinction risk globally is central to determining spatial priorities for the focus of conservation effort, and the world is topographically complex. Consequently, this study uses birds (class Aves) as a model system to addresses this knowledge gap concerning large-scale variation in extinction risk with respect to the third dimension (i.e. elevation). Utilising a comparative macroecological approach, in combination with a global species-level avian trait database, this study investigates if and how present-day extinction risk in birds is influenced by elevational distribution. Analyses are conducted primarily at the global scale across all species with elevational data, but also within biogeographic realms, higher taxonomic subsets, and across phylogenetically independent contrasts. Specifically, the null hypothesis that extinction risk is randomly distributed with respect to elevational distribution is tested.

7.3 Materials and methods

The overall methodology and details on the materials used are described and justified in full in Chapter 3.

7.3.1 Response variable: threat of extinction

The response variable, threat of extinction, was estimated using the IUCN Red List (2012.2 update). All 9,934 extant bird species recognised by BirdLife International have been fully evaluated under the IUCN Red List categories and criteria (IUCN 2001). Threat of extinction was scored on a five-point scale: Critically Endangered (CR) = 4, Endangered (EN) = 3, Vulnerable (VU) = 2, Near Threatened (NT) = 1, Least Concern (LC) = 0. Following Bennett & Owens (1997), threat of extinction was treated as a continuous variable – see Conover & Iman (1981) for a rationale of the use of ranked data in linear models. Species which have recently gone Extinct (EX; n=130 species) or are thought to be Extinct in the Wild (EW; n=4 species) were excluded from all analyses. Species which have been evaluated under the IUCN Red List categories and criteria, but for which insufficient data are available to assign a threat status were also excluded (Data Deficient, DD; n=60 species). A total of 1,239 (13%) of the study-species were deemed to be 'Threatened' (i.e. VU, EN or CR), with the vast majority of species (some 78%) listed as lower risk, i.e. LC. For a summary and breakdown of the response variable used in this study, see Table 7.1.

Caveats surrounding the IUCN Red List were discussed in Section 1.8 and in Purvis *et al.* (2005). However, it is the most comprehensive global assessment of perceived species extinction risk, and for the purposes of this study, the categories are assumed to be equal in width and the criteria equivalent to each other.

Table 7.1 Summary of the response variable, threat of extinction.

IUCN Red List category (abbreviation)		Extinction risk score	No. of species: IUCN Red List	No. of species: avian dataset	% Total
Critically Endangered	(CR)	4	197	181	91.9
Endangered	(EN)	3	389	362	93.1
Vulnerable	(VU)	2	727	696	95.7
Threatened			**1313**	**1239**	**94.4**
Near Threatened	(NT)	1	880	860	97.7
Least Concern	(LC)	0	7677	7632	99.4
TOTAL			9870	9731	98.6

% Total = number of species in the global avian dataset for a given IUCN Red List category divided by the total number of species classified under that category (v.2012.2). Discrepancies between the two values for a given threat category are due to the global avian dataset excluding species recorded as having an elevational range of zero metres (n = 139 species).

7.3.2 Predictors of extinction risk

Elevational distribution was the principal extinction risk predictor in this study – specifically, species-typical elevational range, maximum elevation and elevational midpoint. In order to check the robustness of the methodology used in this study and the potential strength of elevational distribution as a predictor of extinction risk, additional intrinsic predictors were also included. These were selected based on one or more of the following criteria: (1) data availability and sample size, (2) taxonomic and geographic coverage, and (3) if they have been shown to explain variation in extinction risk across birds in previous studies (for comparative purposes). Specifically, a complementary suite of traits were included, reflecting: (a) distribution (geographical range, mean raw latitude, mean absolute latitude), (b) morphology (body weight, sexual dimorphism, wing length, wing-aspect ratio, tarsus length, culmen length), (c) reproduction (clutch size, annual fecundity, egg weight), (d) development (incubation period, fledging time, age at first breeding), (e) survival (adult survival), and (f) niche breadth (diet breadth and habitat breadth). Definitions and descriptions of the included predictors are provided in Section 3.3. For a breakdown of predictor variable sample sizes by IUCN Red List category (2012.2 update) and an indication of data completeness, refer to Table A7.1. Briefly, this table shows that elevational distribution data is not only reasonably well represented within each Red List category (i.e. ≥50%), but relatively comparable across Red List categories – although lowest for CR species.

To better comply with the assumptions of normality, extinction risk predictors were $\log_{10}$ transformed prior to analysis, except adult survival which was arcsine transformed, and raw mean latitude, sexual dimorphism, wing-aspect ratio, diet breadth and niche breadth, which were untransformed (Section 3.4).

7.3.3 Statistical Analyses

Bivariate relationships between extinction risk and predictors: Reduced Major Axis (RMA) bivariate linear regressions were performed between each of the predictors and the five-point extinction risk score at the global scale, firstly across species and then across families. To test for any regional similarities or differences in the global patterns found, bivariate regressions were then conducted for breeding bird species found within each of the biogeographic realms delimited by Olson *et al.* (2001): Nearctic, Palearctic, Neotropical, Afrotropical, Indo-Malay, Australasia and Oceania (excluding Antarctica due to small sample sizes). Specifically, regressions within biogeographic realms were first conducted for all breeding species and then for breeding endemics only (in order to remove wide-ranging/generalist species). Bivariate relationships were also investigated for species found within each of the 23 avian orders, as recognised by Sibley & Monroe (1990). Finally, in order to account for variation in the degree of common phylogenetic association, bivariate relationships between all predictors and extinction risk, at the global scale using all species, were additionally assessed using phylogenetically independent contrasts (PICs) – see Section 3.5.3.

This study is principally investigating global patterns and the generality of any relationships between extinction risk and the study predictor variables (especially elevational distribution). The use of bivariate approaches enables sample sizes to be maximised, in order to maximise statistical power and taxonomic/geographic coverage. It also promotes clarity in the identified trends.

Multivariate relationships between extinction risk and predictors: Stepwise multiple regression models (α-to-enter/remove = 0.05) were performed across species at the global scale, to investigate the relative role of elevational distribution in determining extinction risk, while controlling for confounding variables and known predictors of extinction risk. The five-point extinction risk score was the dependent variable in all models. Due to elevational range, maximum elevation and elevational midpoint being autocorrelated, each measure of elevational distribution was entered as a predictor in separate models. The basal model contained body weight, absolute mean latitude and elevational distribution as predictors. To this basal model, the reproductive and developmental predictors with the largest sample size were entered and removed in turn, namely clutch size and incubation period, respectively. This was repeated for adult survival, diet breadth and habitat breadth. From these models (six per measure of elevational distribution), those predictors that were significant (α < 0.05) were entered into a final model (one per measure of elevational distribution). The three final models were additionally performed using PICs as the units of analysis.

Geographical range was initially included as a predictor in the basal model, and consistently found to be a strong negative correlate of extinction risk. However, geographical range is used in calculating the IUCN Red List Index (IUCN 2001). Therefore, any correlation between geographical range and variation in extinction risk is actually confounded due to non-independence (Purvis *et al.* 2005). Consequently, geographical range was removed as a predictor from all models. It should be noted that a number of studies have sought to resolve this issue of circularity, in order to conduct multivariate analyses, via a variety of methods – principally by: (a) removing species that are threatened due to declines in geographical range, i.e. Criteria B of the Red List (e.g. Lee & Jetz 2011); (b) considering threatened species only if they are listed under Criteria A of the Red List, i.e. population reduction (e.g. Purvis *et al.* 2000b; Cardillo *et al.* 2008); or (c) reclassifying any species whose threat status is dependent on Criteria B to a lower threat category, which could be assigned using only Criteria A and C-E (e.g. Keane *et al.* 2005). However, such approaches not only lead to a reduction in sample size (and consequently statistical power), but geographical range is intrinsically linked (directly or indirectly) to all five of the Red List criteria, e.g. population reduction and small population sizes.

7.4 Results

7.4.1 Bivariate relationships between extinction risk and predictors

Across species globally (Table 7.2a), all three measures of elevational distribution were found to be negative predictors of avian extinction risk, i.e. species with smaller elevational ranges, lower maximum elevational limits and lower elevational midpoints are at greater risk of extinction than species with broader and higher elevational distributions. Out of these, elevational range was the strongest predictor, and the second strongest (after geographical range) of the other 18 predictor variables. Overall, extinction risk was found to be positively associated with morphology, sexual dimorphism, development and adult survival, while negatively associated with measures of distribution, wing-aspect ratio (i.e. poorer flight/dispersal ability), reproduction and niche (habitat) breadth. Only absolute mean latitude and diet breadth were found to be non-significant predictors of extinction risk across species at the global scale. Across PICs, elevational distribution was still found to be a strongly significant negative predictor of extinction risk (Table A7.2).

Table 7.2 Pearson correlation coefficients (r) between extinction risk and predictors at the global scale across (a) species and (b) families.

	(a) Species		**(b) Family**	
Predictor	***n***	***r***	***n***	***r***
Distribution				
Elevational range	5930	-0.41^{***}	140	-0.20^{*}
Maximum elevation	7464	-0.26^{***}	140	-0.20^{**}
Elevation midpoint	5930	-0.20^{***}	140	-0.23^{**}
Geographical range	9242	-0.45^{***}	144	-0.37^{***}
Raw mean latitude	7505	-0.03^{**}	141	-0.27^{**}
Absolute mean latitude	7505	0.01	141	0.15
Morphological				
Body weight	8274	0.18^{***}	144	0.33^{***}
Sexual dimorphism	4066	0.06^{***}	128	0.02
Wing length	5570	0.17^{***}	129	0.25^{**}
Wing-aspect ratio	5054	-0.13^{***}	129	-0.28^{**}
Tarsus length	5135	0.18^{***}	126	0.46^{***}
Culmen length	5082	0.15^{***}	128	0.36^{***}
Reproduction				
Clutch size	6982	-0.11^{***}	143	-0.17^{*}
Annual fecundity	2215	-0.26^{***}	122	-0.21^{*}
Egg weight	3414	0.30^{***}	137	0.41^{***}
Development				
Incubation period	3055	0.27^{***}	131	0.33^{***}
Fledging time	2637	0.28^{***}	125	0.23^{**}
Age at first breeding	1028	0.29^{***}	100	0.20^{*}
Survival				
Adult survival	447	0.21^{***}	66	0.25^{*}
Niche breadth				
Diet breadth	3435	-0.01	113	0.41^{***}
Habitat breadth	4030	-0.30^{***}	122	-0.13

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. n = correlation sample size. Predictors $\log_{10}$ transformed except adult survival (arcsine transformed) and raw mean latitude, diet breadth and habitat breadth (untransformed).

Dividing species up into those that are ‘Threatened’ (i.e. VU, EN and CR) and those that are ‘Not-threatened’ (i.e. LC and NT), at the global scale, both number and proportion of ‘Threatened’ bird species were found to decline with increasing elevational range, maximum elevation and elevational midpoint (Figs. 7.1,7.2). By breaking this binary extinction risk variable up into its constituent threat categories, all three measures of elevational distribution were found to significantly decline with increasing risk of extinction (Fig. 7.3).

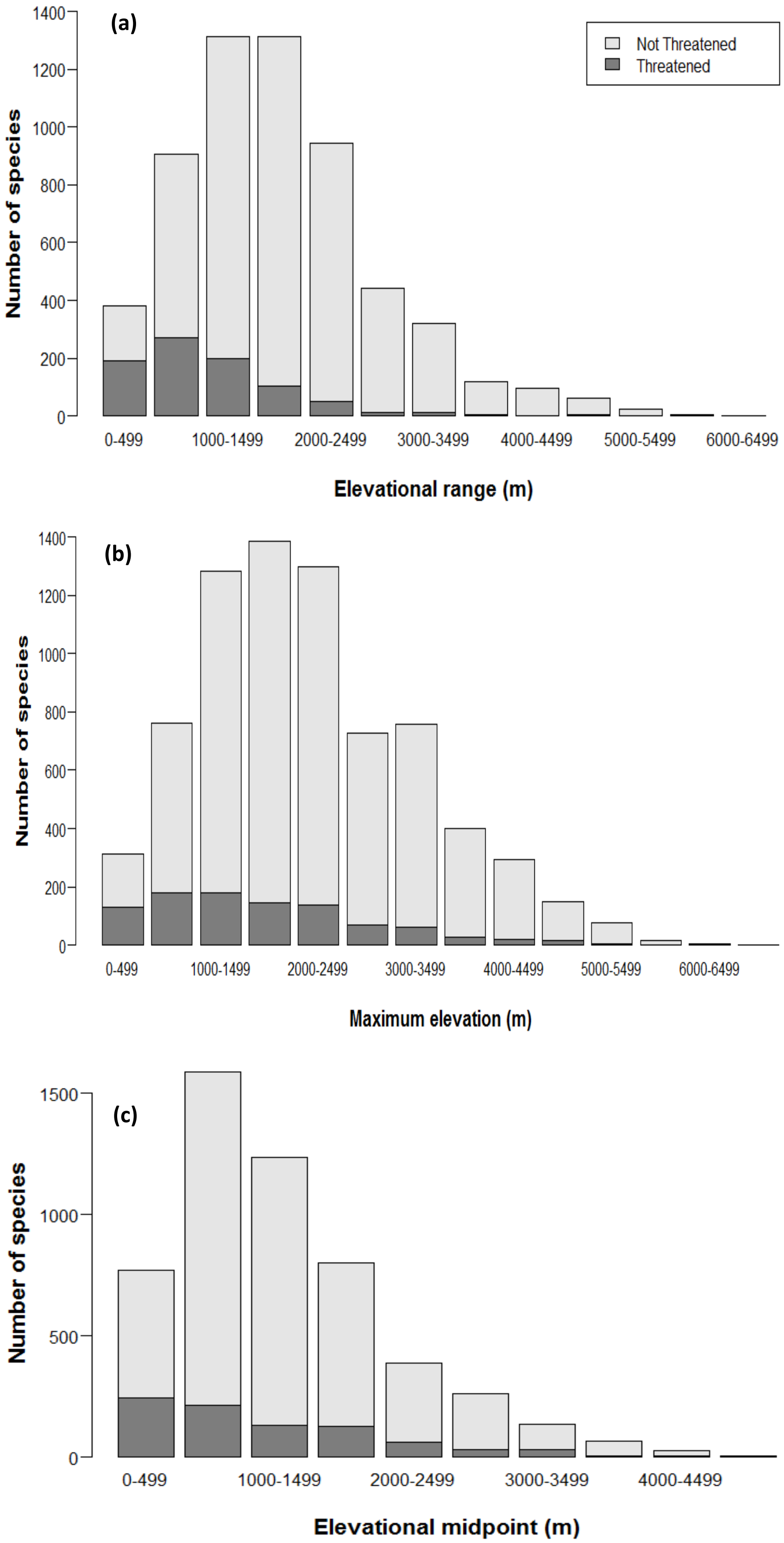


Figure 7.1 Number of 'Threatened' (CR, EN, VU) bird species, as derived from the IUCN Red List (v.2012.2), with respect to (a) elevational range (*n* = 5930 species), (b) maximum elevation (*n* = 7464 species), and (c) elevational midpoint (*n* = 5930 species).

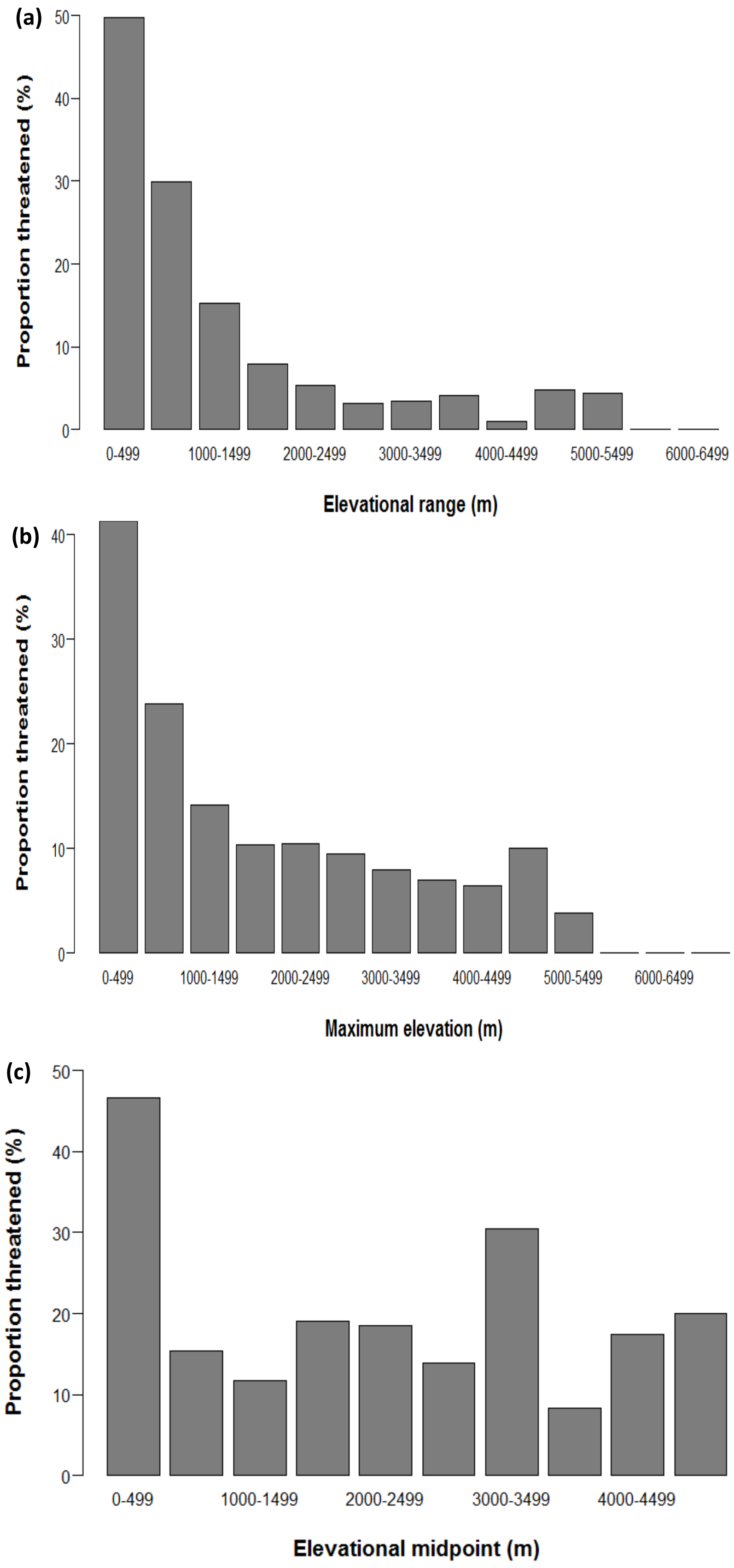


Figure 7.2 Proportion of 'Threatened' (CR, EN, VU) bird species, as derived from the IUCN Red List (v.2012.2), with respect to (a) elevational range (*n* = 5930 species), (b) maximum elevation (*n* = 7464 species), and (c) elevational midpoint (*n* = 5930 species).

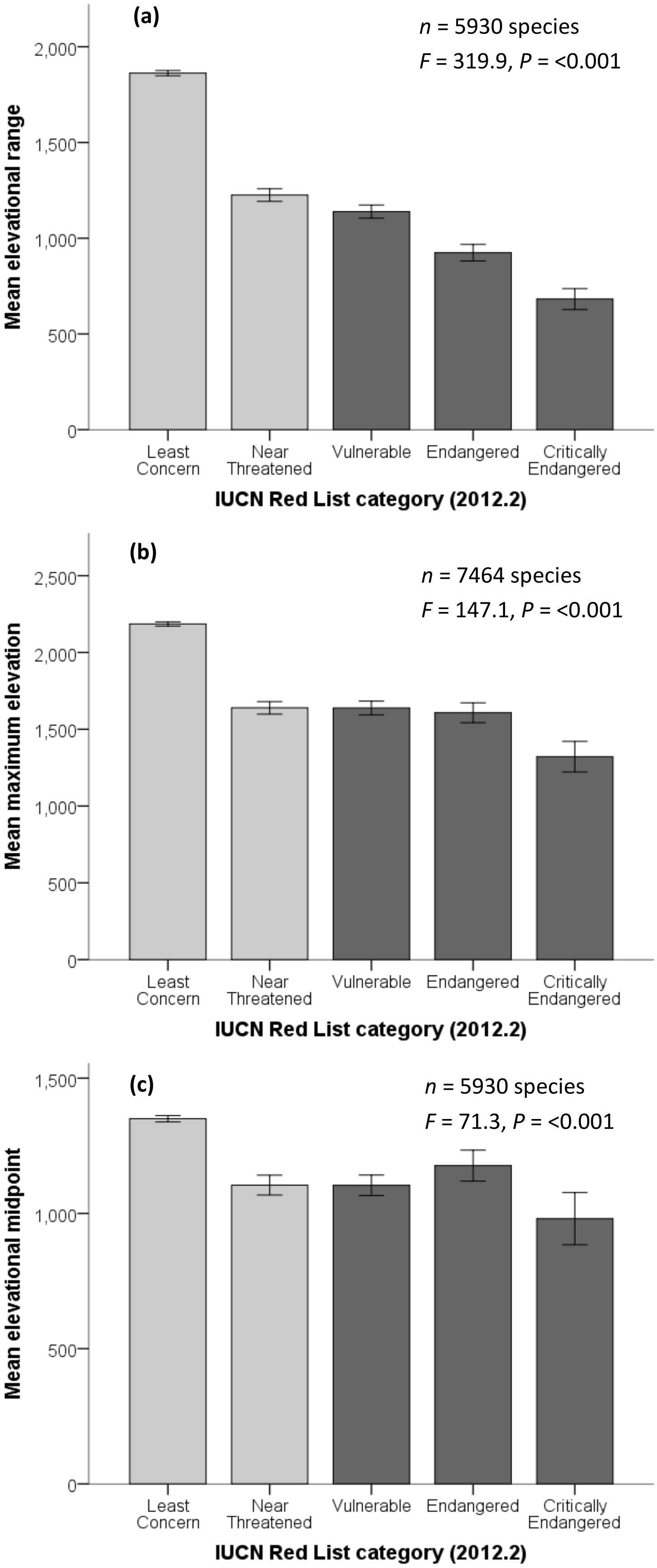


Figure 7.3 Mean (±1SE) elevational distribution for bird species with different levels of extinction risk: (a) elevational range, (b) maximum elevation, and (c) elevational midpoint. ANOVA statistics reported.

Table 7.3 shows that the negative relationship between extinction risk and elevational distribution found at the global scale remains highly significant across all breeding species within each biogeographic realm. The relationship is consistently strongest for those species within the Australasia and Indo-Malay realms, and weakest for Neotropical and Palearctic breeding birds. For biogeographic realm endemics, this significant negative association is also retained, except within Oceania. The strongest correlations were consistently found for Nearctic and Australasia realm endemics. For the equivalent relationships between non-elevational distribution predictors and extinction risk, see Table A7.3.

Extinction risk for species occurring within the 23 taxonomic orders (Table 7.4) was found to be significantly negatively correlated with elevational range (14 orders), maximum elevation (14 orders) and elevational midpoint (11 orders). All significant relationships identified were negative in direction. For the equivalent relationships between non-elevational distribution predictors and extinction risk, see Table A7.4.

Finally, Table 7.2b shows that the negative relationship between extinction risk and elevational distribution seen at the global scale across species is also found across families, although with reduced significance levels. At the family level, elevational midpoint is the strongest predictor of extinction risk out of the three measures of elevational distribution.

7.4.2 Multivariate relationships between extinction risk and predictors

Stepwise multiple regression analysis of the global data, across species, produced models which were qualitatively the same as the outputs from the bivariate tests, but with fewer significant predictors retained (Table 7.5). Elevational distribution was retained as a significant negative predictor of extinction risk in all models (M1-Final), with elevational range consistently found to be the strongest elevational predictor, followed by maximum elevation and elevational midpoint. Adult survival was the only predictor not entered into the final models, due to its lack of significance, and the considerable reduction in sample size it would bring. In the final model containing elevational range, four of the seven extinction risk predictors were significant. Of these, elevational range was clearly the strongest predictor, followed by incubation period, habitat breadth and absolute mean latitude. In the final model containing elevational midpoint, five of the seven extinction risk predictors were significant. Of these, incubation period was the strongest predictor, closely followed by habitat breadth and elevational midpoint. Both clutch size and absolute mean latitude were less significant. In the final model containing maximum elevation, five of the seven extinction risk predictors were significant. Of these, incubation period was the strongest predictor, followed by maximum elevation, habitat breadth, absolute mean latitude and clutch size. The final models explained 25-31% of the total variance in avian extinction risk.

Table 7.3 Pearson correlation coefficients (*r*) between extinction risk and elevational distribution for species breeding within individual biogeographic realms and breeding species endemic to individual biogeographic realms. Realms are ordered in the table from the strongest to the weakest correlation between elevational range and extinction risk.

	Elevational range				**Maximum elevation**				**Elevational midpoint**			
	All		***Endemic***		***All***		***Endemic***		***All***		***Endemic***	
Realm	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Australasia	985	-0.48^{***}	782	-0.47^{***}	1174	-0.39^{***}	934	-0.38^{***}	985	-0.35^{***}	934	-0.34^{***}
Indo-Malay	1012	-0.48^{***}	527	-0.45^{***}	1377	-0.36^{***}	734	-0.31^{***}	1012	-0.33^{***}	734	-0.28^{***}
Afrotropical	1002	-0.46^{***}	875	-0.47^{***}	1368	-0.27^{***}	1195	-0.27^{***}	1002	-0.18^{***}	1195	-0.17^{***}
Oceania	117	-0.46^{***}	69	-0.20	128	-0.32^{***}	75	-0.03	117	-0.23^{***}	75	0.07
Nearctic	389	-0.39^{***}	161	-0.51^{***}	450	-0.29^{***}	194	-0.39^{***}	389	-0.26^{***}	194	-0.35^{***}
Neotropical	2680	-0.35^{***}	2475	-0.35^{***}	3208	-0.16^{***}	2978	-0.15^{***}	2680	-0.11^{***}	2978	-0.10^{***}
Palearctic	793	-0.28^{***}	288	-0.41^{***}	1075	-0.12^{***}	386	-0.22^{***}	793	-0.09^{**}	386	-0.18^{**}

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. All three measures of elevational distribution are $\log_{10}$ transformed. Biogeographic realms as delimited by Olson *et al.* (2001).

Table 7.4 Pearson correlation coefficients (*r*) between extinction risk and elevational distribution for species within each of the 23 orders recognised by Sibley & Monroe (1990). Orders are ordered in the table from the strongest to the weakest correlation between elevational range and extinction risk.

	Elevational range		**Maximum elevation**		**Elevational midpoint**	
Avian order	***n***	***r***	***n***	***r***	***n***	***r***
Turniciformes	15	– 0.76**	15	– 0.76**	15	– 0.76**
Musophagiformes	21	– 0.56**	22	0.09	21	0.28
Strigiformes	197	– 0.54***	221	– 0.41***	197	– 0.30***
Gruiformes	107	– 0.53***	116	– 0.42***	107	– 0.42***
Galliformes	189	– 0.47***	191	– 0.29***	189	– 0.19**
Columbiformes	159	– 0.45***	232	– 0.35***	159	– 0.31***
Coraciformes	86	– 0.45***	105	– 0.43***	86	– 0.43***
Passeriformes	3685	– 0.43***	4790	– 0.22***	3685	– 0.14***
Anseriformes	37	– 0.40*	39	– 0.39*	37	– 0.33*
Ciconiiformes	324	– 0.40***	393	– 0.36***	324	– 0.38***
Craciformes	65	– 0.40***	65	– 0.31*	65	– 0.24*
Piciformes	200	– 0.39***	309	– 0.19***	200	– 0.15*
Psittaciformes	297	– 0.30***	308	– 0.17**	297	– 0.09
Trochiliformes	298	– 0.23***	302	0.02	298	0.07
Struthioniformes	8	– 0.66	10	– 0.65*	8	– 0.66
Tinamiformes	22	– 0.27	31	– 0.18	22	– 0.02
Galbuliformes	37	– 0.25	44	– 0.15	37	– 0.08
Cuculiformes	66	– 0.24	110	– 0.21*	66	– 0.16
Apodiformes	59	– 0.21	71	– 0.20	59	– 0.20
Trogoniformes	31	– 0.15	38	0.01	31	0.16
Bucerotiformes	16	0.03	40	– 0.12	16	0.03
Coliiformes	3	*NS*	4	*NS*	3	*NS*
Upupiformes	8	*NS*	8	*NS*	8	*NS*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. *NS*: sample size and/or variation too small to calculate correlation coefficient. All three measures of elevational distribution are $\log_{10}$ transformed.

When the same three final models were performed using PICs instead of species as the units of analysis (Table A7.5), elevational distribution remained a strongly significant negative predictor of extinction risk. The other significant predictors retained varied depending on the measure of elevational distribution entered into the model, and on the phylogeny used to generate PICs. The final models explained 14-22% and 17-22% of the total variance in avian extinction risk using the 'Ericson backbone' and 'Hackett backbone' phylogenetic trees, respectively.

7.5 Discussion

7.5.1 Distributional predictors of avian extinction risk, with a focus on elevation

This study explicitly assesses the neglected relationship between extinction risk and elevational distribution, using birds, across a variety of taxonomic and geographic subsets, but principally across species at the global scale. The outputs obtained, contribute towards improving our understanding of extinction risk variation with respect to spatial gradients, by investigating the third dimension, i.e. elevation. Such knowledge is vital for aiding the effective establishment of spatial priorities for the focus of conservation efforts.

All three measures of elevational distribution studied here (range, maximum and midpoint) were found to be consistently negatively correlated with avian extinction risk – not just across species globally (Table 7.2a, 7.5), but also within biogeographic realms (Table 7.3), the majority of taxonomic orders (Table 7.4), and across both families (Table 7.2b) and PICs (Tables A7.2, A7.5). Consequently, the null hypothesis that extinction risk is randomly distributed with respect to elevational distribution can be conclusively rejected. These results are in agreement with previous studies that have investigated elevation as a correlate of extinction risk, but that differ from this research by being taxonomically and geographically less representative, or lacking transparency and a multivariate assessment (Manne *et al.* 1999; Manne & Pimm 2001; Gage *et al.* 2004; Keane *et al.* 2005; Sekercioglu *et al.* 2008). Collectively, these findings highlight just how robust and important elevational distribution is as a predictor of avian extinction risk. Accordingly, it should not be neglected in future studies of avian extinction risk correlates.

The negative association between elevational range and extinction risk means that increased elevational range reduces the risk of avian extinction. It has previously been proposed that having a large elevational range raises the chance that a given species will have a large, continuous distribution, which in turn is more likely to provide refuges from the impacts of humans, thus lowering risk of extinction (Gage *et al.* 2004; Keane *et al.* 2005). A somewhat analogous relationship between a species' geographical range and extinction risk has long been known, with small range size proclaimed to be the single best predictor of

Table 7.5 Stepwise multiple regressions of extinction risk against predictors using global species-level data. The table shows the final model and the six models (M1-M6) used to develop it. '*Elevation*' refers to elevational range, maximum elevation and elevational midpoint, respectively, as highlighted at the top of each model column. '*Latitude*' refers to absolute mean latitude of geographical breeding range.

	Predictor	**Elevational range**			**Maximum elevation**			**Elevational midpoint**		
		β	***p***	**r^2**	**β**	***p***	**r^2**	**β**	***p***	**r^2**
M1	Elevation	– 0.32	***	0.15	– 0.20	***	0.09	– 0.15	***	0.07
	Body weight	0.20	***		0.20	***		0.20	***	
	Latitude	0.03	*		0.02	*NS*		– 0.003	*NS*	
		$F_{3,4152} = 239.0^{***}$			$F_{2,5329} = 250.8^{***}$			$F_{2,4153} = 150.0^{***}$		
M2	Elevation	– 0.28	***	0.16	– 0.19	***	0.12	– 0.16	***	0.11
	Body weight	0.24	***		0.24	***		0.24	***	
	Latitude	0.07	***		0.06	***		0.06	***	
	Clutch size	– 0.09	***		– 0.10	***		– 0.13	***	
		$F_{4,3229} = 150.9^{***}$			$F_{4,4163} = 139.3^{***}$			$F_{4,3229} = 97.0^{***}$		
M3	Elevation	– 0.33	***	0.21	– 0.23	***	0.17	– 0.20	***	0.14
	Body weight	0.07	*NS*		0.06	*NS*		0.04	*NS*	
	Latitude	0.04	*NS*		0.05	*		0.03	*NS*	
	Incubation	0.25	***		0.29	***		0.28	***	
		$F_{2,1467} = 189.3^{***}$			$F_{3,1855} = 124.6^{***}$			$F_{2,1467} = 120.0^{***}$		
M4	Elevation	– 0.39	***	0.15	– 0.21	**	0.10	– 0.16	*	0.07
	Body weight	0.02	*NS*		0.06	*NS*		0.05	*NS*	
	Latitude	– 0.12	*NS*		– 0.09	*NS*		– 0.11	*NS*	
	Survival	0.06	*NS*		0.16	*		0.16	*	
		$F_{1,200} = 36.0^{***}$			$F_{2,242} = 12.9^{***}$			$F_{2,199} = 7.9^{***}$		
M5	Elevation	– 0.40	***	0.22	– 0.27	***	0.15	– 0.20	***	0.10
	Body weight	0.21	***		0.24	***		0.24	***	
	Latitude	0.06	**		0.08	***		0.05	*	
	Diet breadth	– 0.06	**		– 0.11	***		– 0.13	***	
		$F_{4,1789} = 124.4^{***}$			$F_{4,2253} = 96.7^{***}$			$F_{4,1789} = 51.6^{***}$		
M6	Elevation	– 0.37	***	0.26	– 0.25	***	0.19	– 0.20	***	0.17
	Body weight	0.18	***		0.20	***		0.19	***	
	Latitude	0.10	***		0.12	***		0.09	***	
	Habitat breadth	– 0.19	***		– 0.24	***		– 0.29	***	
		$F_{4,1905} = 165.2^{***}$			$F_{4,2397} = 143.6^{***}$			$F_{4,1905} = 96.6^{***}$		
FINAL	Elevation	– 0.36	***	0.31	– 0.25	***	0.28	– 0.21	***	0.25
	Body weight	0.001	*NS*		0.01	*NS*		0.01	*NS*	
	Latitude	0.07	*		0.11	***		0.09	**	
	Clutch size	– 0.06	*NS*		– 0.08	**		– 0.09	**	
	Incubation	0.26	***		0.29	***		0.26	***	
	Diet breadth	0.04	*NS*		0.02	*NS*		0.04	*NS*	
	Habitat breadth	– 0.17	***		– 0.18	***		– 0.22	***	
		$F_{4,823} = 90.8^{***}$			$F_{5,1017} = 77.0^{***}$			$F_{5,822} = 54.7^{***}$		

Significance level for a variable to enter/leave each model was $P < 0.05$. β: multiple regression coefficient (standardised). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. r^2: proportion of variance in extinction risk explained by the relevant predictor variables. *NS*: predictor variable not retained in model. Degrees of freedom and F-statistic value for each model also reported. Predictors $\log_{10}$ transformed, except adult survival (arcsine transformed) and diet/habitat breadth (untransformed).

extinction risk for terrestrial bird species (Manne *et al.* 1999; Harris & Pimm 2008). In fact, previous studies have consistently shown geographical range to be a key, if not the main, (intrinsic) correlate of extinction risk across non-avian animal taxa as well (e.g. mammals: Cardillo *et al.* 2008; Davidson *et al.* 2009; amphibians: Cooper *et al.* 2008; Sodhi *et al.* 2008). Chapter 5 consistently found avian elevational range and geographical range to be significantly positively correlated with one another (e.g. globally: n = 5655, r = 0.43, p = <0.001). This implies that species with large geographical extents also occur across a wide elevational range. These two measures of range size are therefore related in terms of how broad a resource base a given species utilises, and both potentially permit a large population size, and act as a buffer against habitat loss.

I disagree with Manne & Pimm (2001), who stated that elevational extent is a '*consistent but relatively unimportant factor in determining threat; abundance and* [geographical] *range size are much more important*'. This study shows, via bivariate regression analysis, that the relationship between elevational range and extinction risk is essentially equivalent in strength to that between geographical range and extinction risk. I therefore instead agree with previous studies that have called for the incorporation of elevational limits into assessments of extinction risk (e.g. Sekercioglu *et al.* 2008; Hall *et al.* 2009), although I appreciate the challenges that such an amendment would entail. Related to this, some studies have shown that after 'trimming' extent of occurrence range maps for birds by their known elevational limits and types of habitat preferred, extents of suitable habitat are often much smaller, especially for species in mountains (e.g. Jetz *et al.* 2007; Harris & Pimm 2008). With considerable advancements in satellite mapping and GIS, such 'refined extent of occurrence maps' could feasibly be adopted widely. However, currently only a proportion of BirdLife International's range maps are based in part on elevation (Schnell *et al.* 2013).

Regarding maximum elevation and elevational midpoint, the results from this study contradict predictions made under the '*climate change hypothesis*', which predicts mountain-top extinctions due to factors including restricted elevation distributions. Specifically, this study highlights the greater vulnerability to extinction of low-elevation species at present, and the conclusion that conservation action may therefore currently be best focused towards low-elevation species and habitats. The findings are therefore instead in agreement with the '*direct anthropogenic pressure hypothesis*'. It is important to note that analysis conducted in Chapter 5 of this thesis found no overarching evidence for restricted ranges at higher elevations. In fact, the global dataset instead identified a positive relationship between elevational midpoint and geographical range (Table 5.1), and a positive relationship between elevational midpoint and elevational range (Table 5.2).

It has been proposed by Manne *et al.* (1999) that lowland continental bird species are more threatened than montane continental species due to 'competitive release' (MacArthur *et al.* 1972), as montane (and island) species tend to be relatively common within their restricted ranges, compared to lowland species, and their greater abundance likely aids in reducing their likelihood of being threatened. Evidence for this explanation has been empirically found (Manne & Pimm 2001). Threatened bird species living at higher altitudes have also been shown to have larger global population sizes than those occurring in lowlands (Blackburn & Gaston 2002), and consequently may be more resilient to human pressures.

These findings also indicate that elevation may be a significant negative predictor of avian extinction risk because it accounts for variation in the intensity of human threats. Anthropogenic pressures occur across elevational gradients (see UNEP-WCMC 2002 and discussion within Section 1.10). However, worldwide human impact (estimated using the 'human footprint index'; Sanderson *et al.* 2002) has been shown to be greatest in lowland regions, declining nearly monotonically with increased elevation (Nogués-Bravo *et al.* 2008). This is likely due to a combination of factors, including montane areas globally, in comparison to low-elevation sites, being characterised by low accessibility, economic potential and human population density (Rodriguez-Rodriguez & Bomhard 2012). Complementing this, Rodriguez-Rodriguez & Bomhard (2012) found that only 6.5% of mountains (outside of Antarctica) are under high direct human influence. However, as stressed by Nogués-Bravo *et al.* (2008), different mountain ranges worldwide have a unique history and present-day anthropogenic influence, with some currently more threatened, and containing more sensitive species, than surrounding lowland areas, e.g. cloud forests of South-east Asia (see discussion in Section 1.10).

Although current evidence suggests that montane bird species are of least conservation concern at present. It is important that we are not complacent about this, as the continued increase in human population levels and natural resource demand means that mountain biodiversity, both avian and non-avian, is under ever-increasing threats from human pressures, most notably settlement sprawl, agricultural conversion and, for tropical montane birds in particular, climate change (Sections 1.10–1.11). As such, we require more in depth investigations and monitoring of the relationship between extinction risk, anthropogenic pressures and elevational distribution, across taxa, in the future.

Related to the above, as discussed in Section 1.12, the world's protected areas are clearly biased towards mountain areas, especially those under the least human influence (Rodriguez-Rodriguez & Bomhard 2012). However, protected area coverage is highly uneven across the world's mountains and inadequate at a range of scales, including areas of particular importance for biodiversity (Rodriguez-Rodriguez *et al.* 2011). As mountains are biodiversity hotspots of species richness and endemism (Orme *et al.* 2005) and threatened species do occur across elevational gradients, there is an inherent need to ensure that existing protected areas are expanded to protect habitat at all elevations, and future montane protected areas placed in regions of greatest need, rather than marginal areas of 'rock and ice'.

It is important to note that both elevational midpoint and maximum elevation were found to be weaker predictors of extinction risk than elevational range. This implies that elevational position has less of an influence on extinction risk than the breadth of a given species' elevational range.

Regarding the pattern between elevational distribution and extinction risk within individual biogeographic realms, the only non-significant relationship was found with respect to those species endemic of Oceania. The Oceania realm is unique in that it is comprises entirely of small oceanic islands, and is the realm where the majority of avian extinctions have occurred since 1500 (Butchart *et al.* 2006; Loehle & Eschenbach 2012; Szabo *et al.* 2012). The reason for a lack of an association is likely due to a combination of factors, including: (1) a lack of power and small sample sizes (i.e. ≤75 species), (2) the majority of species in the subset (72%) being threatened with extinction (i.e. VU, EN, CR), and (3) these threatened species span a wide elevational gradient from 0 to 2100 m.

The avian orders with non-significant species-level relationships between elevational distribution and extinction risk can generally be explained via either very small sample sizes, or being lowland species-rich. However, a lack of an association between elevational midpoint and Psittaciformes (parrots and cockatoos), is better explained due to the relatively even distribution of threatened species with respect to elevation. In contrast, the lack of an association between threat status and both maximum elevation and elevational midpoint for Trochiliformes (hummingbirds) is more complex to account for. However, out of the 32 species deemed to be threatened with extinction, 72% have an elevational midpoint of >1000m. Therefore, nearly three quarters of hummingbird species in this study dataset occur at high elevations. As to why this is the case requires further more detailed studies on this avian order alone. Yet, it is important to note that a significant proportion of these threatened high-elevation species are restricted to the Andes, e.g. *Eriocnemis nigrivestis* (Black-breasted puffleg), *Metallura baroni* (Violet-throated metaltail), and *Aglaeactis aliciae* (Purple-backed sunbeam) – all of which are deemed to be at risk from extensive human-induced habitat loss (BirdLife International 2013).

Despite debate concerning the suitability of phylogenetic comparative methods in studies of extinction risk (Section 3.5.3), this study found the results obtained via species to be qualitatively similar to those derived from PICs. This in turn suggests that observed patterns are independent of phylogenetic relatedness. This makes sense, based on the fact that I found the majority of variation in elevational distribution to occur at the species level (Section 3.5.1).

The relationship between elevational distribution, specifically elevational range, and extinction risk was weaker across families than species. This is likely partially due to reduced sample sizes and, in turn, statistical power. However, it may also be attributed to the fact that species within elevational families often have a wide range of elevational distributions, with both lowland and montane specialists. As mentioned above, this links in with my finding that elevational distribution varies most across species, as opposed to life-history traits that vary most across families (Table 3.1).

The multiple regression analyses conducted here account for no more than a third of the variation in avian extinction risk. This is likely due to the fact that only intrinsic predictors were investigated in this study, which only tell part of the story. They represent the degree to which different species are able to withstand external, predominantly anthropogenic, threatening processes (Cardillo *et al.* 2008). The addition of extrinsic predictors, particularly those relating to contemporary human pressures, would likely increase the variance explained (e.g. Lee & Jetz 2011).

In relation to the final species-level multiple regression models, only a fraction of those species currently classified as LC through to CR by the IUCN Red List are included – final elevational range/midpoint models: 823 species (8.3% of potential species in model); final maximum elevation model: 1017 species (10.3% of potential species in model). The generality of these models, in terms of global and taxonomic representativeness, therefore has to be questioned. There is also the added issue of fluctuating sample sizes based on the predictors added into the models. For example, adult survival has a very small sample size in comparison to the other extinction risk predictors in this study. Its exclusion from the final model was therefore not necessarily due to a lack of an association with extinction risk, but more realistically due to a combined lack of power and geographic/taxonomic representativeness.

It is important to question how representative the findings of this study are, using birds, with respect to other taxonomic groups. It would be worthwhile to expand the analyses conducted in this study to other groups of organisms for which good data on elevational distribution and extinction risk exists. For example, all known extant mammal species (approximately 5,500) have been fully assessed under the IUCN Red List categories and criteria (IUCN 2001). Although for such a comparative analysis to be undertaken would require collation of known mammalian elevational limits into a centralised database.

Although global geographical patterns in extinction risk have been studied on a number of occasions (e.g. Orme *et al.* 2005; Grenyer *et al.* 2006), the inclusion of latitude as an explicit predictor of extinction risk is less common. It is difficult to determine the biological meaning of correlations involving latitude since it is a complex surrogate for a number of environmental variables (Cooper *et al.* 2008). This is evident in this study, whereby the strength and direction of latitudinal correlations with avian extinction risk vary across realms, orders and measure of latitude (i.e. raw or absolute). However, at the global scale, across species, families and PICs (Hackett tree), raw mean latitude of species' geographical range was found to be negatively related to extinction risk. This implies that more species are at risk of extinction in the Southern Hemisphere. Such an association is hard to explain, and the effect size is small. However, one plausible explanation is that both elevational ranges and geographical ranges have been shown, on average, to be smaller in size in the Southern Hemisphere than the Northern Hemisphere (Chapter 5 and Orme *et al.* 2006, respectively).

Although bivariate regression analysis found no relationship across either species or families concerning extinction risk and distance from equator globally (i.e. absolute mean latitude), multiple regression analysis indicates that species (and PICs using the Hackett tree) are more likely to be threatened with extinction with increasing distance from the equator. Cardillo *et al.* (2008) found median absolute latitude of a species' geographical range to be one of the most consistently significant predictors of mammalian extinction risk. They suggested that latitude may be a general proxy for a range of environmental or anthropogenic factors that influence extinction risk. For example, birds of larger body size tend to be found at higher latitudes (Olson *et al.* 2009), while Cardillo *et al.* (2008) suggested that temperate latitudes are often most heavily modified by human activity. However, results from Chapter 5 of this thesis show that life-histories are faster in temperate species compared to those in the tropics (see also Section 2.1.6). As discussed in more detail below (Section 7.5.2), fast life history is a negative predictor of vertebrate extinction risk. To reiterate, without incorporation of underlying environmental and anthropogenic variables, latitudinal variation in extinction risk is too complex an extinction risk predictor to explain with any validity.

7.5.2 Non-distributional predictors of avian extinction risk

Morphology: Bivariate regression analysis found large-bodied birds to be particularly vulnerable to extinction: at the global scale across both species and families (and to a lesser extent across PICs), for species within all realms (except Oceania), and for eight out of the 23 avian orders. The potential reasons for this correlation were discussed in depth by Gaston & Blackburn (1995). This result concurs with previous, taxonomically and geographically restricted, research (e.g. Gaston & Blackburn 1995; Bennett & Owens 1997; Gage *et al.* 2004), and with studies possessing a comparable sample size to that used here (Lee & Jetz 2011).

Similarly, wing length, tarsus length and culmen length (proxies of overall body size) were found to be positive correlates of extinction risk – at an essentially equivalent strength to that of body weight. As with body weight, their effect size was markedly smaller across PICs than species. In fact, wing length was no longer found to be a significant predictor when controlling for phylogeny. These findings imply that phylogenetic non-independence plays a considerable role in driving morphological relationships with threat status in birds.

The exclusion of body weight as a significant extinction risk predictor in the final multiple regression models, across both species and PICs, is at first surprising. This could simply be attributed to the reduction in sample size, and consequently power, when moving from a bivariate (8274 species) to multivariate analysis (823 species). In addition, the relationship between body weight and extinction risk may be weaker, compared to earlier avian studies, due to the subsequent acquisition of knowledge for a considerable number of small-bodied tropical passerines – a number of which are threatened. Bennett & Owens (1997) noted that body size is an extremely difficult variable to interpret and should be treated with caution. This is because large body mass is often, but not consistently, correlated with other extinction-promoting traits, such as larger geographical range (Section 1.9.3). However, geographical range was not entered as a predictor in the multiple regression models, due to confounding issues concerning circularity (Purvis *et al.* 2005), and may therefore help to explain the loss of body weight as a significant predictor in these final models. Finally, further complication arises through the fact that the relationship between body weight and extinction risk varies depending upon the threats faced by a given species (Owens & Bennett 2000), and the fact that, across all body sizes, species can be at risk depending on their specific ecologies (Davidson *et al.* 2009).

Only a few comparative studies have investigated the possible role of pre-mating sexual selection in driving extinction – the majority using birds as their study taxa. To date, the relationship has remained unclear, with several studies supporting the notion that measures of pre-mating sexual selection are associated with increasing extinction risk (e.g. McLain *et al.* 1995; Sorci *et al*. 1998; McLain *et al.* 1999; Doherty *et al*. 2003), while others have found the opposite trend (e.g. Krűger & Radford 2008) or no relationship (e.g. Prinzing *et al.* 2002; Morrow & Pitcher 2003; Morrow & Fricke 2004). In this study, increasing sexual dimorphism was found to heighten extinction risk, but only at the global species level. Across both families and PICs, no evidence was found for a relationship between these factors. These findings are in agreement with Morrow & Pitcher (2003) and Morrow & Fricke (2004), who investigated the global relationship between sexual selection and extinction risk for birds and mammals, respectively. They measured sexual dimorphism and controlled for phylogenetic non-independence using similar methods to mine, although the sample size in my study is four times greater, and so more representative, than that of Morrow & Pitcher (2003). As to why no association was found remains unclear. However, Morrow & Pitcher (2003) found evidence to suggest that threatened bird species experience more intense post-mating sexual selection than non-threatened species. It is therefore possible that the relative costs of traits associated with post-mating sexual selection are considerably greater than those arising from traits associated with pre-mating sexual selection (see discussion in Morrow & Pitcher 2003).

Wing-aspect ratio (i.e. residual wing area), is a quantitative proxy measure of flight (and dispersal) ability. To date, and to the best of my knowledge, no such variable has been incorporated into a study of the correlates of avian extinction risk, but has been requested (Jones *et al.* 2003). Species (families and PICs) with lower wing-aspect ratios (i.e. poorer flight ability) were consistently found to be more threatened with extinction than those with higher wing-aspect ratios (indicative of stronger flight ability). This makes intuitive sense when considering the fact that many of the species driven to extinction since 1500 have been flightless island endemics (BirdLife International 2013), possessing small wings relative to their body weight. Jones *et al.* (2003) investigated two measures of wing morphology as potential predictors of extinction risk in bats globally, namely: (a) aspect ratio (wingspan squared divided by wing area), and (b) wing loading ([body mass times gravity acceleration] divided by wing area). Out of these, they found aspect ratio to be a significant (negative) predictor of bat extinction risk, i.e. species with lower flight efficiencies, higher flight costs, and overall poor dispersal and migratory ability, have heightened risk of extinction. Wing morphology, in both bats and birds, has been shown to be an important predictor of numerous traits, including: ecological foraging niche, dispersal ability, behaviour, and home range area (see references cited in Jones *et al.* 2003). It is therefore likely that wing-aspect ratio is a surrogate measure of ecological traits that are the focus of extinction processes.

Reproduction, development and survival (life history): All three measures of both reproduction (clutch size, annual fecundity, egg weight) and development (incubation period, fledging time, age at first breeding) were found to remain consistently correlated with avian extinction risk globally across species, families and PICs, and within the majority of realms. For species within orders, where a significant relationship was found for these traits, the direction followed those of the full dataset. Birds with a small clutch size were shown to be particularly vulnerable to extinction, concurring with studies including Bennett & Owens (1997) and Krűger & Radford (2008). Similarly, annual fecundity was found to be a negative predictor of extinction risk, even though the sample size was reduced by more than two thirds of that for clutch size. As summarised by Bennett & Owens (2002), this observation may be explained by the fact that low-fecundity populations take longer to recover if they are reduced to small sizes, and are therefore more likely to go extinct if an external force disturbs the natural balance between fecundity and mortality by causing a rapid increase in the rate of mortality. In addition, low fecundity in both birds and mammals has been connected to increased vulnerability to overexploitation (Owens & Bennett 2000; Isaac & Cowlishaw 2004; Price & Gittleman 2007). The trade-off between reproductive output and egg weight (Lack 1967; Blackburn 1991) justifies why egg weight was found to be a positive predictor of extinction risk. Overall, species with ‘slow’ life histories, i.e. low reproductive output, slow growth rates and late sexual maturity, are less able to compensate for increased mortality with increased fecundity and are therefore more vulnerable to extinction (Purvis *et al.* 2000a).

In comparison to the other potential predictors of avian extinction risk investigated in this study, adult survival had the smallest sample size (global species level: n = 447 species). Nevertheless, a positive association with threat status was found for species and families at the global scale. As threatened species were removed from the adult survival dataset that have recently or are currently receiving considerable conservation action, this identified relationship is with respect to ‘natural’ adult survival rates. Such a positive associatation is expected as high survival/low fecundity is a compenent of the slow life-history strategy pattern associated with high extinction risk (Bennett & Owens 2002). The lack of a significant correlation across PICs implies that phylogeny could be partly driving the relationship seen across species. For example, the majority of species with adult survival data are either Passeriformes (51%) or Ciconiiformes (26%), and the majority of Passeriformes appear to have low adult survival rates, whereas the highest rates are found in Ciconiiformes.

Niche breadth: Diet and habitat niche breadth have both previously been found to be negatively correlated with extinction risk (e.g. Norris & Harper 2004; Gage *et al.* 2004; Sekercioglu *et al.* 2004; Krűger & Radford 2008; Lee & Jetz 2011). In this study, bivariate analysis also found habitat breadth to be a negative predictor of avian extinction risk across both species and PICs at the global level (but not across families). However, it only remained significant at the species level in the multiple regressions. As shown by Owens & Bennett (2000), habitat specificity predisposes species to an increased risk of extinction in the face of habitat loss, as loss of habitat disproportionately reduces niche availability in specialists compared to generalists (Norris & Harper 2004). Species with specialist habitat requirements are likely to be less capable of dealing with habitat transformation and fragmentation, as such species tend to be less abundant and widespread than generalists (Brown 1984; Krűger & Radford 2008). In comparison to habitat breadth, diet breadth was found to be a weaker and more ambiguous predictor of avian extinction risk. At the global level, no association was found across species but a significant negative association instead found when controlling for the effects of phylogenetic non-independence. However, across families, a strong positive relationship was found. The degree to which this family-level result is informative is questionable, considering the fact that the majority of variation in diet breadth occurs at the species level (Table 3.1). When incorporated into the final extinction risk models, diet breadth is consistently not retained as a predictor. Yet, it should be noted that at the species level, 'Model 5' (Table 7.5) does retain diet breadth as a significant negative predictor. Overall, based on these findings, it is inferred that habitat breadth is a more reliable and robust predictor of avian extinction risk than diet breadth.

7.5.3 Conclusions

It is important to remember that the elevational patterns found in this study with respect to avian extinction risk are ultimately shaped by underlying variation in both intrinsic avian traits and the natural and anthropogenic environment. Related to this, the key relationship identified in this study, that at the global scale, avian extinction risk is lowest for those species with larger elevational ranges and higher maximum elevations and elevational midpoints, links directly with the main findings of Chapters 4–6 of this thesis. Specifically, the discovery that birds with faster life histories and broader niches have larger and higher elevational distributions globally. These two key findings are interconnected as this study and numerous others across vertebrate taxa have shown both slow life histories and narrow niche breadth to be associated with heightened risk of extinction. The interconnected associations between avian elevational distribution, life history/niche breadth traits, and extinction risk could explain why, although human activities do encroach upon high-elevation sites (e.g. Nogues-Bravo *et al.* 2008), species are less threatened with increasing elevation. Specifically, the overall positive relationship between elevational midpoint and elevational range, life-history pace and niche breadth may be why high-elevation species are found in this study to be generally more resilient than lowland bird species.

7.6 Appendix: Supplementary tables

Table A7.1 Breakdown of predictor sample sizes (*n*) and data completeness by IUCN Red List category (2012.2 update) for species with data on both minimum and maximum elevational limits.

	CR		**EN**		**VU**		**Threatened**		**NT**		**LC**		**Total**	
Predictor	***n***	**% total**	***n***	**% total**	***n***	**% total**	***n***	**% total**	***n***	**% total**	***n***	**% total**	***n***	**% total**
Distribution														
Elevational range	98	49.7	264	67.9	488	67.1	850	64.7	498	56.6	4582	59.7	5930	60.1
Maximum elevation	98	49.7	264	67.9	488	67.1	850	64.7	498	56.6	4582	59.7	5930	60.1
Elevational midpoint	98	49.7	264	67.9	488	67.1	850	64.7	498	56.6	4582	59.7	5930	60.1
Geographical range	81	41.1	233	59.9	450	61.9	764	58.2	469	53.3	4420	57.6	5653	57.3
Raw mean latitude	45	22.8	143	36.8	329	45.3	517	39.4	313	35.6	3777	49.2	4607	46.7
Abs. mean latitude	45	22.8	143	36.8	329	45.3	517	39.4	313	35.6	3777	49.2	4607	46.7
Morphological														
Body weight	63	32.0	169	43.4	362	49.8	594	45.2	364	41.4	4152	54.1	5110	51.8
Sexual dimorphism	18	9.1	62	15.9	136	18.7	216	16.5	130	14.8	1995	26.0	2341	23.7
Wing length	52	26.4	149	38.3	302	41.5	503	38.3	242	27.5	2242	29.2	3187	32.3
Wing-aspect ratio	37	18.8	110	28.3	245	33.7	392	29.9	190	21.6	2293	29.9	2875	29.1
Tarsus length	47	23.9	140	36.0	275	37.8	462	35.2	215	24.4	2249	29.3	2926	29.6
Culmen length	39	19.8	119	30.6	249	34.3	407	31.0	196	22.3	2328	30.3	2931	29.7

Table A7.1 Continued.

	CR		EN		VU		Threatened		NT		LC		Total	
Predictor	***n***	**% total**	***n***	**% total**	***n***	**% total**	***n***	**% total**	***n***	**% total**	***n***	**% total**	***n***	**% total**
Reproduction														
Clutch size	54	27.4	148	38.0	277	38.1	479	36.5	254	28.9	3399	44.3	4132	41.9
Annual fecundity	22	11.2	54	13.9	78	10.7	154	11.7	39	4.4	873	11.4	1066	10.8
Egg weight	21	10.7	50	12.9	122	16.8	193	14.7	84	9.5	1576	20.5	1853	18.8
Development														
Incubation period	32	16.2	74	19.0	123	16.9	229	17.4	94	10.7	1323	17.2	1646	16.7
Fledging time	24	12.2	63	16.2	94	12.9	181	13.8	64	7.3	1130	14.7	1375	13.9
Age first breeding	14	7.1	32	8.2	48	6.6	94	7.2	28	3.2	369	4.8	491	5.0
Survival														
Adult survival	6	3.0	10	2.6	19	2.6	35	2.7	7	0.8	176	2.3	218	2.2
Niche breadth														
Diet breadth	48	24.4	122	31.4	289	39.8	459	35.0	165	18.8	1475	19.2	2099	21.3
Habitat breadth	92	46.7	238	61.2	428	58.9	758	57.7	203	23.1	1537	20.0	2498	25.3

% total = number of species in avian dataset for a given predictor and IUCN Red List category (with data on elevational limits), divided by the total number of species classified under that category (IUCN Red List 2012.2 update).

Table A7.2 Pearson correlation coefficients (*r*) between extinction risk and predictors using phylogenetically independent contrasts (PICs) for the global avian dataset. PICs derived from two independent phylogenetic trees, using: (a) Ericson *et al.* (2006) backbone, and (b) Hackett *et al.* (2008) backbone.

	(a) Ericson		**(b) Hackett**	
Predictor	***n***	***r***	***n***	***r***
Distribution				
Elevational range	5817	– 0.44***	5825	– 0.36***
Maximum elevation	7318	– 0.24***	7327	– 0.22***
Elevation midpoint	5807	– 0.17***	5823	– 0.15***
Geographical range	9058	– 0.49***	9039	– 0.49***
Raw mean latitude	7321	0.00	7359	– 0.03**
Absolute mean latitude	7323	0.00	7349	– 0.03**
Morphological				
Body weight	8110	0.03**	8126	0.02*
Sexual dimorphism	3998	0.02	4014	– 0.03
Wing length	5452	0.00	5462	– 0.02
Wing– aspect ratio	4969	– 0.09***	4962	– 0.07***
Tarsus length	5030	0.08***	5041	0.05***
Culmen length	4986	0.04**	4501	0.00
Reproduction				
Clutch size	6841	– 0.15***	6831	– 0.09***
Annual fecundity	2162	– 0.17***	2174	– 0.17***
Egg weight	3357	0.09***	3342	0.17***
Development				
Incubation period	2988	0.13***	2988	0.10***
Fledging time	2583	0.17***	2574	0.34***
Age at first breeding	1006	0.14***	1007	0.09**
Survival				
Adult survival	436	0.06	435	0.05
Niche breadth				
Diet breadth	3386	– 0.25***	3396	– 0.23***
Habitat breadth	3949	– 0.31***	3975	– 0.33***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n* = correlation sample size. Predictors $\log_{10}$ transformed except adult survival (arcsine transformed) and raw mean latitude, diet breadth and habitat breadth (untransformed).

Table A7.3 Pearson correlation coefficients (*r*) between extinction risk and non-elevational distribution predictors for species breeding within individual biogeographic realms and breeding species endemic to individual biogeographic realms.

	Af		**Af (endemic)**		**Au**		**Au (endemic)**		**IM**		**IM (endemic)**	
Predictor	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Distribution												
Geographical range	1897	– 0.48***	1640	– 0.50***	1657	– 0.40***	1351	– 0.39***	1560	– 0.42***	818	– 0.32***
Raw mean latitude	1582	– 0.07**	1333	– 0.05	1346	– 0.18***	1055	– 0.10**	1331	– 0.21***	612	– 0.02
Abs. mean latitude	1582	0.12***	1333	0.14***	1346	– 0.07**	1055	– 0.06	1331	– 0.17***	612	0.06
Morphological												
Body weight	1773	0.12***	1518	0.14***	1374	0.26***	1079	0.28***	1290	0.33***	597	0.36***
Sexual dimorphism	1220	0.05	1018	0.05	831	0.02	659	0.00	497	0.13**	182	0.10
Wing length	1653	0.13***	1415	0.15***	1273	0.15***	1046	0.19***	965	0.26***	492	0.29***
Wing-aspect ratio	1556	– 0.08**	1320	– 0.07**	1136	– 0.14***	914	– 0.13***	847	– 0.23***	390	– 0.25***
Tarsus length	1604	0.17***	1373	0.19***	1202	0.14***	990	0.17***	895	0.28***	443	0.33***
Culmen length	1522	0.10***	1298	0.12***	1192	0.13***	973	0.15***	880	0.26***	426	0.29***
Reproduction												
Clutch size	1626	– 0.11***	1379	– 0.11***	1173	– 0.03	883	0.02	1276	– 0.20***	588	– 0.10*
Annual fecundity	428	– 0.24***	260	– 0.33***	682	– 0.10**	527	– 0.08	291	– 0.36***	41	– 0.59***
Egg weight	782	0.32***	577	0.38***	634	0.27***	416	0.28***	633	0.36***	196	0.41***
Development												
Incubation period	805	0.26***	597	0.32***	603	0.29***	431	0.34***	432	0.34***	137	0.41***
Fledging time	761	0.28***	554	0.34***	553	0.30***	407	0.36***	307	0.31***	83	0.29**
Age first breeding	201	0.23**	97	0.34***	220	0.18**	144	0.20*	120	0.43***	16	0.56*
Survival												
Adult survival	77	0.29**	33	0.48**	90	0.20	53	0.15	45	0.31*	0	*NS*
Niche breadth												
Diet breadth	1511	– 0.01	1312	0.01	352	– 0.05	238	0.11	536	– 0.13**	294	– 0.01
Habitat breadth	1610	– 0.21***	1410	– 0.21***	412	– 0.42***	291	– 0.38***	626	– 0.31***	362	– 0.17**

Table A7.3 Continued.

	Na		Na (endemic)		Nt		Nt (endemic)		Oc		Oc (endemic)		Pa		Pa (endemic)	
Predictor	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Distribution																
Geographical range	721	– 0.46***	308	– 0.54***	3448	– 0.45***	3138	– 0.44***	225	– 0.64***	148	– 0.52***	1461	– 0.33***	565	– 0.40***
Raw mean latitude	680	0.02	287	– 0.21***	2705	– 0.05**	2398	0.01	208	0.03	133	0.36***	1327	0.14***	466	0.06
Abs. mean latitude	680	0.05	287	– 0.20***	2705	– 0.02	2398	– 0.01	208	0.15*	133	0.23**	1327	0.11***	466	0.05
Morphological																
Body weight	723	0.09*	312	0.13*	3237	0.13***	2928	0.15***	172	– 0.10	94	– 0.08	1379	0.28***	523	0.33***
Sexual dimorphism	502	0.07	204	0.05	1160	0.04	959	0.03	87	0.06	35	– 0.06	791	0.12***	314	0.15**
Wing length	484	0.05	209	0.05	1241	0.14***	1051	0.15***	143	– 0.22**	77	– 0.26*	1032	0.21***	416	0.25***
Wing-aspect ratio	480	– 0.08	207	– 0.10	1123	– 0.13***	935	– 0.11***	123	– 0.23**	57	– 0.18	991	– 0.15***	388	– 0.21***
Tarsus length	451	0.04	192	0.09	1049	0.08**	877	0.09**	123	0.08	62	0.06	971	0.24***	376	0.33***
Culmen length	426	0.04	187	0.03	1172	0.03	1007	0.02	108	0.00	47	– 0.07	924	0.22***	341	0.34***
Reproduction																
Clutch size	714	– 0.11**	308	– 0.21***	2276	– 0.09***	1974	– 0.07**	192	– 0.12	115	0.16	1380	– 0.04	533	– 0.15***
Annual fecundity	522	– 0.18***	231	– 0.28***	439	– 0.27***	242	– 0.31***	102	– 0.25*	36	0.13	664	– 0.22***	290	– 0.33***
Egg weight	628	0.06	274	0.10	950	0.29***	694	0.34***	99	– 0.05	30	– 0.20	944	0.34***	367	0.44***
Development																
Incubation period	609	0.05	275	0.16**	780	0.23***	542	0.28***	98	– 0.15	36	– 0.47**	785	0.27***	335	0.36***
Fledging time	549	0.05	246	0.13*	667	0.22***	446	0.27***	96	– 0.08	38	– 0.46**	630	0.25***	259	0.38***
Age first breeding	365	0.14**	170	0.36***	211	0.32***	89	0.29**	55	0.01	15	– 0.30	384	0.22***	183	0.38***
Survival																
Adult survival	201	0.01	92	0.09	88	0.17	30	0.06	35	0.33	10	0.47	179	0.10	65	– 0.08
Niche breadth																
Diet breadth	226	– 0.20**	88	– 0.22*	914	– 0.10**	796	– 0.04	95	– 0.39***	69	– 0.07	507	0.06	155	0.20*
Habitat breadth	233	– 0.31***	93	– 0.33**	1189	– 0.41***	1068	– 0.40***	114	– 0.56***	88	– 0.32**	578	– 0.20***	207	– 0.19**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n*: correlation sample size. *NS*: sample size and/or variation too small to calculate correlation coefficient . Predictors $\log_{10}$ transformed except adult survival (arcsine transformed) and raw mean latitude, diet breadth and habitat breadth (untransformed). Biogeographic realms: Af = Afrotropical, Au = Australasia, IM = Indo-Malay, Na = Nearctic, Nt = Neotropical, Oc = Oceania, Pa = Palearctic (Olson *et al.* 2001).

Table A7.4 Pearson correlation coefficients (*r*) between extinction risk and non-elevational distribution predictors for species within each of the 23 orders recognised by Sibley & Monroe (1990).

	Anseriformes		**Apodiformes**		**Bucerotiformes**		**Ciconiiformes**		**Coliiformes**		**Columbiformes**		**Coraciformes**		**Craciformes**	
Predictor	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Distribution																
Geographical range	152	– 0.55***	95	– 0.47***	56	– 0.58***	894	– 0.49***	6	*NS*	299	– 0.50***	147	– 0.48***	68	– 0.47***
Raw mean latitude	143	0.06	81	0.02	47	0.24	784	– 0.09*	4	*NS*	242	0.03	129	– 0.05	55	– 0.02
Abs. mean latitude	143	0.11	81	0.15	47	0.22	784	0.08*	4	*NS*	242	0.02	129	0.02	55	0.03
Morphological										*NS*						
Body weight	150	– 0.12	74	– 0.26*	51	0.46***	825	0.24***	6	*NS*	220	0.25***	125	0.11	58	0.30*
Sexual dimorphism	144	0.00	29	– 0.02	38	– 0.04	558	0.09*	5	*NS*	83	0.17	92	– 0.09	30	– 0.10
Wing length	152	– 0.13	35	– 0.31	45	0.33*	770	0.19***	6	*NS*	110	0.25**	128	– 0.05	69	0.32**
Wing-aspect ratio	150	– 0.10	32	0.42*	41	– 0.41**	703	– 0.19***	6	*NS*	98	– 0.31**	111	– 0.31**	58	– 0.14
Tarsus length	145	– 0.09	30	0.00	41	0.29	732	0.14***	6	*NS*	104	0.39***	122	0.08	67	0.22
Culmen length	137	– 0.06	32	– 0.06	45	0.33*	594	0.16***	4	*NS*	97	0.33***	124	0.03	23	– 0.20
Reproduction										*NS*						
Clutch size	151	– 0.17*	67	– 0.15	49	– 0.30*	827	– 0.24***	6	*NS*	229	– 0.07	114	– 0.26**	59	– 0.19
Annual fecundity	106	– 0.17	17	– 0.32	12	– 0.70*	527	– 0.30***	2	*NS*	47	– 0.08	41	– 0.03	13	– 0.04
Egg weight	148	– 0.06	29	– 0.07	21	0.41	656	0.33***	4	*NS*	90	0.29**	58	0.02	39	0.16
Development										*NS*						
Incubation period	145	0.02	27	– 0.09	26	0.27	617	0.34***	4	*NS*	79	0.28*	34	0.08	29	0.56**
Fledging time	124	0.05	29	0.08	27	0.35	556	0.40***	4	*NS*	70	0.25*	40	– 0.27	0	*NS*
Age first breeding	115	– 0.06	3	*NS*	3	0.79	305	0.31***	4	*NS*	10	0.30	8	0.05	8	0.07
Survival										*NS*						
Adult survival	42	0.19	2	*NS*	1	*NS*	118	0.25**	1	*NS*	5	– 0.81	4	*NS*	0	*NS*
Niche breadth										*NS*						
Diet breadth	84	– 0.01	61	– 0.13	43	– 0.41**	434	– 0.17***	4	*NS*	89	0.03	126	– 0.06	25	– 0.24
Habitat breadth	86	– 0.21*	67	– 0.16*	43	– 0.30	510	– 0.25***	4	*NS*	117	– 0.39***	128	– 0.43***	33	– 0.53**

Table A7.4 Continued.

	Cuculiformes		Galbuliformes		Galliformes		Gruiformes		Musophagiformes		Passeriformes		Piciformes		Psittaciformes	
Predictor	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Distribution																
Geographical range	139	– 0.42***	51	– 0.32*	210	– 0.53***	179	– 0.56***	23	– 0.73***	5527	– 0.47***	346	– 0.41***	343	– 0.52***
Raw mean latitude	113	0.02	42	– 0.09	164	– 0.06	153	0.19*	20	0.15	4400	– 0.04*	290	– 0.02	269	0.01
Abs. mean latitude	113	– 0.16	42	0.09	164	– 0.17*	153	0.19*	20	0.15	4400	– 0.01	290	0.00	269	– 0.01
Morphological																
Body weight	126	0.12	48	– 0.15	208	0.19**	148	0.33***	22	– 0.14	4945	0.05**	322	0.08	309	0.28***
Sexual dimorphism	101	0.03	6	– 0.02	168	0.00	92	0.22*	18	– 0.44	2076	0.02	196	– 0.04	60	0.34**
Wing length	135	0.14	1	*NS*	208	0.13	75	0.33**	23	– 0.27	2821	0.02	344	0.09	352	0.21***
Wing-aspect ratio	123	– 0.06	1	*NS*	204	– 0.17*	67	– 0.45***	22	– 0.27	2559	– 0.08***	318	– 0.09	309	0.00
Tarsus length	133	0.30***	0	*NS*	156	0.20*	74	0.36**	23	– 0.24	2631	0.09***	302	0.14*	343	0.26***
Culmen length	133	0.28**	16	0.11	61	0.35**	70	0.41***	23	– 0.19	2745	0.03	311	0.11	344	0.21***
Reproduction																
Clutch size	62	– 0.08	23	– 0.19	183	– 0.26***	156	– 0.36***	22	– 0.16	4006	– 0.12***	223	– 0.12	261	– 0.09
Annual fecundity	12	*NS*	13	0.24	50	– 0.42**	56	– 0.56***	0	*NS*	1072	– 0.22***	62	– 0.23	72	– 0.28*
Egg weight	67	0.03	6	*NS*	105	0.35***	100	0.51***	7	– 0.31	1627	0.04	151	0.11	106	0.25*
Development																
Incubation period	21	0.13	5	0.41	132	0.21*	76	0.54***	16	– 0.01	1440	0.11***	97	0.14	148	0.18*
Fledging time	23	– 0.12	6	0.11	15	– 0.33	45	0.42**	14	– 0.83***	1329	0.05	94	0.08	134	0.27**
Age first breeding	6	*NS*	0	*NS*	41	0.29	37	0.63***	0	*NS*	349	0.26***	30	– 0.15	60	0.53***
Survival																
Adult survival	4	*NS*	0	*NS*	14	– 0.18	4	*NS*	0	*NS*	229	0.16*	7	0.32	3	*NS*
Niche breadth																
Diet breadth	66	– 0.21	37	– 0.20	146	– 0.24**	139	0.00	20	– 0.27	1558	– 0.06*	199	– 0.01	169	– 0.03
Habitat breadth	69	– 0.18	42	– 0.10	162	– 0.28***	159	– 0.37***	21	– 0.37	1929	– 0.37***	221	– 0.17*	136	– 0.34***

Table A7.4 Continued.

	Strigiformes		**Struthioniformes**		**Tinamiformes**		**Trochiliformes**		**Trogoniformes**		**Turniciformes**		**Upupiformes**	
Predictor	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***	***n***	***r***
Distribution														
Geographical range	273	– 0.48***	10	– 0.63	46	– 0.26	315	– 0.48***	39	– 0.26	15	– 0.69**	9	*NS*
Raw mean latitude	231	– 0.01	10	– 0.40	37	0.03	238	– 0.03	34	0.17	11	– 0.29	8	*NS*
Abs. mean latitude	231	– 0.12	10	0.35	37	0.04	238	– 0.24***	34	– 0.29	11	0.26	8	*NS*
Morphological														*NS*
Body weight	234	– 0.06	11	– 0.48	34	0.02	300	– 0.06	36	0.11	14	– 0.26	8	*NS*
Sexual dimorphism	142	– 0.06	8	– 0.60	24	0.01	151	0.15	27	– 0.12	12	0.52	6	*NS*
Wing length	174	– 0.15	2	*NS*	46	0.08	11	– 0.87***	39	0.03	15	0.32	9	*NS*
Wing-aspect ratio	147	– 0.20*	2	*NS*	34	0.02	11	– 0.92***	36	– 0.06	14	0.37	8	*NS*
Tarsus length	146	0.07	10	– 0.70*	37	0.05	0	*NS*	9	– 0.56	15	0.07	9	*NS*
Culmen length	141	– 0.05	10	0.59	46	0.29	103	– 0.17	7	0.21	7	*NS*	9	*NS*
Reproduction														*NS*
Clutch size	200	– 0.09	11	– 0.71*	30	– 0.15	250	*NS*	31	– 0.55**	15	– 0.22	7	*NS*
Annual fecundity	67	– 0.14	7	– 0.45	4	*NS*	21	– 0.64**	4	0.55	8	– 0.43	2	*NS*
Egg weight	85	0.06	10	– 0.49	19	0.17	51	*NS*	28	0.19	3	*NS*	4	*NS*
Development														*NS*
Incubation period	76	0.03	10	0.55	17	– 0.02	31	0.55**	11	– 0.45	11	0.40	3	*NS*
Fledging time	70	– 0.04	3	– 0.92	1	*NS*	32	0.56***	12	0.62*	6	*NS*	3	*NS*
Age first breeding	22	0.48*	9	0.02	1	*NS*	10	*NS*	3	*NS*	2	*NS*	2	*NS*
Survival														*NS*
Adult survival	5	*NS*	1	*NS*	0	*NS*	6	– 0.87*	0	*NS*	0	*NS*	1	*NS*
Niche breadth														*NS*
Diet breadth	130	– 0.10	11	– 0.13	27	0.00	23	– 0.53**	30	– 0.17	6	0.13	8	*NS*
Habitat breadth	156	– 0.33***	11	0.16	46	– 0.21	44	– 0.59***	31	– 0.07	7	0.78*	8	*NS*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. *n*: correlation sample size. *NS*: sample size and/or variation too small to calculate correlation coefficient . Predictors $\log_{10}$ transformed except adult survival (arcsine transformed) and raw mean latitude, diet breadth and habitat breadth (untransformed).

Table A7.5 Multiple linear regression of extinction risk against predictors using phylogenetically independent contrasts (PICs) for the global avian dataset. '*Elevation*' refers to elevational range, maximum elevation and elevational midpoint, respectively, as highlighted at the top of each model column. '*Latitude*' refers to absolute mean latitude of geographical breeding range. PICs derived from two independent phylogenetic trees, using: (a) Ericson *et al.* (2006) backbone, and (b) Hackett *et al.* (2008) backbone.

Predictor	**Elevational range**			**Maximum elevation**			**Elevational midpoint**		
	β	***p***	r^2	**β**	***p***	r^2	**β**	***p***	r^2
a) Ericson									
Elevation	– 0.93	***	0.22	– 0.69	***	0.14	– 0.67	***	0.17
Body weight	0.14	*NS*		0.07	*NS*		0.14	*NS*	
Latitude	0.02	*NS*		0.02	*NS*		0.02	*NS*	
Clutch size	– 0.58	**		– 0.67	***		– 0.92	***	
Incubation	0.77	**		0.97	***		1.24	***	
Diet breadth	0.01	*NS*		0.00	*NS*		0.001	*NS*	
Habitat breadth	– 0.01	*NS*		– 0.002	*NS*		– 0.02	*	
	$F_{7,802} = 32.1^{***}$			$F_{7,991} = 22.5^{***}$			$F_{7,800} = 23.4^{***}$		
b) Hackett									
Elevation	– 0.75	***	0.22	– 0.60	***	0.17	– 0.55	***	0.18
Body weight	0.21	*		0.12	*NS*		0.15	*NS*	
Latitude	0.09	***		0.07	**		0.11	***	
Clutch size	– 0.69	***		– 0.81	***		– 0.99	***	
Incubation	0.74	*		0.86	**		0.91	*	
Diet breadth	0.008	*NS*		0.00	*NS*		0.001	*NS*	
Habitat breadth	– 0.007	*NS*		– 0.003	*NS*		– 0.01	*NS*	
	$F_{7,801} = 31.9^{***}$			$F_{7,989} = 28.1^{***}$			$F_{7,800} = 24.6^{***}$		

β: multiple regression coefficient (standardised). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. r^2: proportion of variance in extinction risk explained by the relevant predictor variables. *NS* indicates predictor variable not retained in the model. Degrees of freedom and F-statistic value for each model also reported. Predictors $\log_{10}$ transformed, except diet breadth and habitat breadth (untransformed).

CHAPTER EIGHT
Conclusions

The empirical findings of this thesis were presented and discussed in detail within the respective data chapters (i.e. Chapters 4–7). The aim of this chapter is therefore to provide a brief yet critical synthesis and evaluation of the key findings and discussions arising from this research. Emphasis is placed on the broader picture, including highlighting the implications of this study for both large-scale ecology and biodiversity conservation. To end with, potential study biases and limitations are identified, and suggestions made concerning useful avenues along which future research should proceed.

8.1 Synthesis of key results

This thesis arose from the realisation that although both regional and global scale studies conclusively show that mountains are hotspots of not only terrestrial species richness but also endemism (and so of inherent biodiversity conservation value), the underlying reasons for this distribution are poorly understood (Section 1.3). The principal aim of this thesis was therefore to highlight and address fundamental knowledge gaps in our current understanding of interspecific variation in morphology, life history, ecology, and ultimately extinction risk with respect to elevational distribution.

I first conducted novel and extensive reviews of existing peer-reviewed literature relating to research conducted at all spatial scales and across taxa on: (a) trait biogeography, (Section 2.1), and (b) elevational distribution as a predictor of extinction risk (Section 1.9.4). Although limitations and biases of existing studies specific to each of the literature reviews conducted were revealed, three common shortfalls were also identified. Specifically, both reviews collectively showed that research on trait and extinction risk variation with respect to elevational distribution are: (1) greatly outnumbered by similar studies focusing on latitudinal gradients and geographical range sizes, (2) taxonomically and/or geographically restricted, and (3) lack transparency and/or a multivariate assessment. In other words, it was clear that a global elevation-focused assessment of both trait and extinction risk variation was missing – at the global scale and that covered a broad taxonomic range. The recognition of this existing knowledge gap and comprehension of the importance of addressing it shaped the overarching research aim of this thesis and corresponding broad research questions, which for reasons outlined in Section 3.1, were addressed using all extant birds as a model system.

Collectively, one of the main results of this research was that, at the global scale, bird species with larger elevational ranges and higher maximum elevations and elevational midpoints display traits characteristic of fast-living species (i.e. high reproductive output, fast development, low survival rates and broad niche breadth), and is largely discussed in relation to elevational gradients of environmental variability and harshness (Chapters 4–6). As shown in this research and in the existing literature, for both avian and non-avian taxa, species possessing faster life histories have consistently been shown to be less at risk of extinction than slow-living species (Chapter 7). In conjunction with both of these results, global avian extinction risk was found to be greatest in lowland species and those with small elevational ranges (Chapter 7), in turn potentially implying that species with larger and/or higher elevational distributions are more resilient to anthropogenic threats. Importantly, when all of the aforementioned relationships were analysed at the family level, across PICs, and within taxonomically and geographically restricted subsets (i.e. biogeographic realms and endemic/restricted-range subsets), these findings were found to largely remain robust, via both bivariate and multivariate analytical techniques.

Table 8.1 provides a summarised comparison of my global-scale results investigating avian trait and extinction risk variation with elevational distribution with those from previous less representative avian studies. It also highlights how the relationships identified for elevational midpoint and elevational range compare with those of latitude and geographical range size, respectively. Many of the relationships studied in this thesis are novel, having not been previously studied at any spatial scale or taxonomic range, let alone at the global scale across all bird species with available data. For example, variation in niche-breadth with elevational distribution and trait/extinction risk variation with maximum elevation are previously unstudied in birds (and vertebrate taxa as a whole). The later being a surprising omission due to the importance of maximum elevational limits in terms of both physiology and geometric constraints. Differences are clearly highlighted between the results I found for trait variation with elevational midpoint and those in previous studies (discussed in Section 4.5). An interesting finding from this thesis is that trait patterns for elevational midpoint and elevational range mirror those found for absolute latitude and geographical range size, respectively – in both previous studies and this research. Finally, my results for extinction risk variation with elevational range are in agreement with previous studies and mirror those for geographical range size. Surprisingly, before this research, only one study explicitly investigating elevational midpoint as a predictor of extinction risk could be found (Krüger & Radford 2008).

It is important to note that Table 8.1 does not include the four morphological traits investigated (i.e. body weight, wing length, tarsus length and culmen length). As discussed throughout the data chapters, morphology (in particular body weight) is a complex variable to investigate in such a large-scale study, with a variety of trends found, as has also been the

Table 8.1 Comparison of global scale results from this thesis investigating avian trait and extinction risk variation with elevational distribution (across species and phylogenetically independent contrasts) with those from previous avian studies (at any spatial scale and taxonomic range). In addition, a comparison is provided of my results for elevational midpoint and elevational range with those found for absolute mean latitude and geographical range size, in both previous studies and this thesis.

	My elevational distribution results versus previous studies			**My results for (a) elevational midpoint and (b) elevational range versus absolute mean latitude and geographical range size, respectively, in both previous studies and this thesis**	
	Elevational range	**Maximum elevation**	**Elevational midpoint**	**(a) Absolute mean latitude**	**(b) Geographical range size**
Life history traits[*] *(Sections 2.1.6 and Chapters 4–6)*	Not previously studied.	Not previously studied.	Opposite to previous studies that found life history to shift from a high reproductive strategy at low elevations to a high survival strategy at high elevations.	Same (i.e. higher reproductive output, faster development and lower survival with increasing elevation/latitude).	Same (i.e. higher reproductive output, faster development and lower survival with larger ranges).
Niche breadth traits[*] *(Sections 2.1.6 and Chapters 4–6)*	Not previously studied.	Not previously studied.	Not previously studied.	Mirrors latitude-niche breadth hypothesis (i.e. positive trend).	Same (i.e. positive trend).
Extinction risk *(Section 1.9.4 and Chapter 7)*	Same (i.e. negative trend).	Not previously studied.	Disagrees with non-significant finding of Krüger & Radford (2008), but agrees with dichotomous studies finding lowland species to be more threatened than montane species.	Not previously studied. My results show elevational midpoint to be more strongly and consistently (negatively) correlated with extinction risk than absolute mean latitude.	Same (i.e. negative trend).

[*] For a list and description of all life-history and niche breadth traits studied, see Section 3.3.

case in previous studies (Sections 2.1.4–2.1.5). In fact, the morphological traits were the only traits found to consistently vary in trend direction with respect to elevational distribution when using species/families and PICs as the study units (see Section 8.4.4 for a discussion of the limitations of the phylogenetic analyses conducted in this thesis).

8.2 Conservation implications

8.2.1 Conservation utility of desktop-based comparative studies of extinction risk

Although increasingly popular in recent years, the relevance of desktop-based comparative studies of species extinction risk for conservation policy, planning and practice has been debated (e.g. Fisher & Owens 2004; Kerr *et al.* 2007; Cardillo & Meijaard 2012). This 'big-picture' approach to conservation science broadly aims to discover and describe generalisations about patterns and processes in the decline or threat status of species, and I believe that such studies, in conjunction with in-the-field research, are often necessary prerequisites for effective biodiversity conservation. In fact, the recent creation and rise of conservation biogeography as a sub-discipline of biogeography and branch of conservation biology (Section 2.1.2), provides clear evidence of the growing realisation that conservation focused at small scales is not sufficient for the task at hand (Richardson & Whittaker 2010).

Desktop-based conservation science can undoubtedly contribute to a general accumulation of knowledge and development of theory concerning the ecology of decline and extinction under global anthropogenic change, which has the potential to guide conservation practice if communicated effectively. They can focus conservation efforts on the ground by providing the basis for both species- and area-based conservation prioritisation, which given the scarcity of funds available for conservation, needs to become increasingly systematic and quantitative. For example, both this thesis and previous studies have identified non-random taxonomic and geographical distributions of extinction risk, hotspots of threatened species richness, and priority areas for extinction risk reduction opportunity (Section 1.9; Di Marco *et al.* 2012). The prevailing mindset of conservation is as a reactive, crisis discipline, however, a particular strength of the comparative approach is in its ability to guide proactive and preemptive actions to prevent increases in extinction risk among currently unthreatened species (e.g. in the case of my research, high-elevation bird species with narrow elevational ranges).

Cardillo & Meijaard (2012) states that one of the principal reasons that comparative studies fail to inform and influence conservation practice is that there are few clear messages that have emerged from such studies to date. They claim that results arising from comparative studies are often '*vague, inconsistent, complex and clouded by uncertainty*', which in turn does not provide a robust guide for developing policy. However, it should be highlighted that my research did unambiguously find elevational distribution to be a strong predictor of avian extinction risk, across all units and data subsets studied. In fact, I believe that there are two key conservation implications arising from the results of this thesis, as outlined in the following two subsections (Sections 8.2.2–8.2.3).

8.2.2 Refining distribution maps using knowledge of species elevational limits

One of the principal contributions made by science for systematic conservation prioritisation and practice is to provide the baseline data needed to assess the current threat status of species, e.g. IUCN Red List (IUCN 2001). Conservation practitioners are heavily reliant upon the IUCN Red List and the current extinction risk status conferred to species, and therefore on the underlying baseline data – especially the distribution maps. Such maps therefore need to be as closely representative of a given species' range as both knowledge and technology permits. However, studies have shown Extent of Occurrence Maps (EOO) to be prone to overestimation, particularly for range-restricted and threatened species (see Jetz *et al.* 2008b). This study has highlighted the importance of elevational distribution as a predictor of avian extinction risk, at the global scale and within a variety of taxonomically and geographically restricted data subsets (Chapter 7). Consequently, this research greatly adds to existing evidence (Section 1.9.4) in support of extending and incorporating the knowledge of species' vertical ranges into the IUCN Red List assessment (Section 7.5). As previously mentioned by Schnell *et al.* (2013), only a small proportion of BirdLife International's range maps are based in part on elevation, yet I believe that both the knowledge and technology are available for developing such 'refined extent of occurrence maps' for the vast majority of bird species.

8.2.3 Conserving mountain biodiversity and the full elevational gradient

The value of mountains for terrestrial biodiversity is conclusive (Section 1.3). Although mountains are currently reported to be well represented by the protected area network (Section 1.12), it is important to question how many of these are conserved based on their remoteness and low value to humans, i.e. those that are residual 'rock and ice' protected areas. Also, how many of these montane protected areas are simply 'paper parks', with minimal active management? It is now more important than ever to promote the efficient and effective conservation and protection of mountainous regions. For example, mountains located in wilderness areas and that are examples of comparatively 'pristine' habitat, especially within the tropics, are of considerable value and their active conservation would be both proactive and preemptive. An important point to make with regards to mountain protected areas is that it is vital to not only monitor and conserve the low-elevation parts of mountains, which typically hold the greatest number and proportion of threatened species and also the greatest levels of overall human impact – at present. Instead, it is necessary to promote connectivity and protect across entire elevational gradients, for three main reasons: (1) currently threatened and range-restricted species are found at both low and high elevations (Chapters 6–7), (2) mountain biodiversity will continue to be increasingly vulnerable to anthropogenic pressures encroaching up mountain sides, such as habitat degradation and associated fragmentation (Section 1.10), and (3) climate change has the potential to shift and contract species' ranges, create local extinctions and alter community assemblages (Sections 1.11).

8.3 Phylogenetic versus grid-cell approach

One of the main impetuses for the methodological design of this study (i.e. primarily adopting an 'individual species focus') was that previous global-scale research on spatial variation in traits and extinction risk have utilised a grid-cell approach, e.g. all work performed under the ADHoC (Section 3.2.1). A main critique of grid-cell studies is that their relatively coarse scale degrades the underlying raw data and obscures crucial patterns, most importantly the data concerning where species occur, and particularly in topographically complex regions (e.g. mountains). In addition, conservation decisions typically take place at scales much finer than those used for global analyses that evaluate diversity patterns and identify priority areas for conservation, which have tended to be conducted at a cell resolution of 10,000km^2 (e.g. Orme *et al.* 2005; Grenyer *et al.* 2006; although see Jenkins *et al.* 2013). It is also important to note that species still remain the fundamental units of conservation, yet, in comparison to interspecifc comparative studies, there is a disconnection between the species and their associated data when using a grid-cell approach. Related to this, interspecific studies allow actual elevational limits to be used, whereas grid-cell approaches to date instead rely on the average elevational range for a given cell, derived from a digital elevation model (e.g. Davies *et al.* 2007; Gaston *et al.* 2007; Olson *et al.* 2009).

Concerning visualisation of data, planimetric grid-cell studies do enable maps to be produced with relative ease. Mapping can provide more information about possible driving forces of spatial patterns than depicting such relationships using an interspecific, bivariate scatter-plot approach (see discussion in Ruggiero & Hawkins 2006). Elevational relationships are difficult to map at large spatial scales, and it is difficult to envisage how a grid-cell approach could be adapted for large-scale elevational studies – although see Fig. 4.4 for an attempt at mapping global clutch size variation within discrete elevational bands. In addition, although the multivariate analyses conducted in this research incorporated spatial coviariates in two dimensions (i.e. elevation and latitude), there is a need to develop three-dimensional mapping techniques in order to obtain as realistic a picture as possible of species diversity (i.e. richness, endemism and threat) and traits in space.

To conclude, large-scale ecological studies adopting either an individual species or grid-cell approach both have strengths and weaknesses, and value for informing biodiversity conservation decisions. Future studies might therefore benefit from utilising both methods.

8.4 Potential study biases and limitations

Every effort was made to ensure that the data within the GADB and the statistical framework employed in this study were as robust as possible. However, in any research, it is essential to acknowledge and understand the limitations of both the data and methodologies used. Although largely addressed within Chapter 3, additional discussion on this matter is provided in the following subsections.

8.4.1 Biodiversity informatics: caution needed when using big data for big questions

Recent advances in biodiversity informatics have seen a rise in the development of large datasets detailing taxonomic, trait, ecological and environmental information, at a variety of taxonomic and geographic levels. These valuable resources have consequently generated an increase in the amount of biodiversity research being conducted at large spatial and temporal scales (Section 1.1). For example, the GADB used throughout the entire of this thesis has previously been used in a number of high-impact global-level research studies (Section 3.2.1). Nevertheless, it is important to be transparent and highlight the existing limitations of large species-level trait datasets.

Concerning the GADB, the main issue surrounding the associated data is its representativeness with respect to: (a) study variables, (b) geography, and (c) taxonomy. This was investigated and discussed in Section 3.8, but it is important to highlight here the main areas that need to be addressed in the future, relating to identified knowledge gaps. Specifically, we need more detailed knowledge regarding:

1) Species exact elevational distributions (to match that of existing geographical range data);
2) The life history and ecology of tropical species;
3) Traits that are difficult to measure in the field or require collection of data over a period of time (e.g. adult survival).

Related to the above, some species have only a single data-entry for a given trait, whereas others have many (i.e. uneven sampling effort and associated sampling bias). Common, widespread and well-studied bird species are much more likely to possess multiple data entries for a given trait than rare, elusive and little-studied species. It is difficult to know how representative the data in the GADB are for a given species and trait.

There is a real need to develop and incorporate approaches with which to explore the consequences of these existing biases and limitations surrounding large biodiversity datasets. Nevertheless, despite these issues, it is important to emphasise the great value of such datasets in terms of the recent advances made in both large-scale biogeography and macroecology. What is important is that large datasets are treated as dynamic resources that need to be regularly updated, both in terms of new data and concerning the techniques used with which to manage and assess their quality. Finally, I agree with Beck *et al.* (2012), who see an urgent need for establishing and strengthening cooperation between practitioners of large-scale ecology and bioinformatics in order to facilitate data finding and sharing, and the associated filling in of data gaps and transparency (see also Section 8.5).

8.4.2 Integrating historical information into analyses

A limitation of this study is that the methodology does not extensively incorporate the past (i.e. both spatial and historical temporal elements). Such an approach would improve our understanding of the identified trends found throughout this research. This analytical gap was highlighted in Section 6.5.3 in relation to endemic species (but in fact applies to all species) and a framework outlined with which to address it.

8.4.3 Testing for 'natural' patterns of spatial trait variation

In essence, most research investigating interspecific trait variation with respect to spatial covariates is interested in determining the evolutionary (i.e. 'natural') patterns, outside of any anthropogenic influence. Human activities are likely to have influenced some, if not most, of the distributions (both latitudinal and elevational) of extant bird species. Specifically, humans are likely to have had varying degrees of influence via directly or indirectly driving range contractions, expansions and shifts. However, in this study (as with the majority of others), no explicit account for this was made, except for the geographical range maps of well-known invasive/alien species excluding areas where they have been introduced. In principle, this problem can best be overcome by working with data for historical (i.e. pre-human impact) species ranges, but greater levels of uncertainty inevitably surround their actual magnitude, and the likely biases are difficult to evaluate. There are simpler steps that can be taken, such as determining the influence of the inclusion and exclusion of threatened species, whose ranges have commonly been most strongly influenced by human activities (i.e. species classified as threatened under 'Criteria B' of the IUCN Red List), although this has seldom been employed (however, see Gaston *et al.* 2005). Due to the size of the dataset used in this study and the robustness of the trends found across all units and data subsets analysed, the removal of a few hundred threatened species seems unlikely to greatly influence the results. Neverthless, it would still be of value to test.

8.4.4 Statistical limitations

The statistical framework used in this research was selected based on its simple yet robust approach that produced biologically meaningful and intelligible results. However, regarding limitations surrounding the statistics used here, I can think of two main areas for future refinement and improvement, as outlined below.

1) As has already been mentioned in the discussions of both Chapters 4 and 5, the results obtained in this research across PICs should be interpreted with caution. Not only was the directionality of some relationships found to disagree with those found at both the species- and family-level, but were also shown to vary with respect to the specific phylogenetic tree being used (i.e. Ericson versus Hackett tree). It is important to remember that the phylogeny and associated trees being used in this research (Section 3.5.3) are new and have not been tested much at all. Further investigation is therefore needed in order to clarify whether or not the relationships identified using these PICs are valid. The fact that the family-level relationships were found to support those at the species-level, implies that further refinement of the PIC method used is necessary. Fortunately, the field of phylogenetics and associated comparative methods is rapidly developing, and this research would benefit in the future by comparing the results from more trees and phylogenies (e.g. Sibley & Ahlquist 1990), utilising model averaging techniques, and analysing PICs at the family level.
2) Throughout this research, some evidence for non-linear relationships between avian elevational distribution and traits, extinction risk and spatial covariates was found. For example, a hump-shaped trend between elevational midpoint and habitat breadth (Fig. 4.2h), and a decline in elevational range at the highest elevations (Fig. 5.3) were identified. Therefore, future studies should also explore incorporating nonlinear (i.e. quadratic or cubic) terms, in order to compare how they may or may not improve variance explained in the bivariate and multivariate models produced.

8.5 The push for open data

Large-scale ecology and conservation science are inherently collaborative and multidisciplinary research areas, amplifying their need for open access to data. Unfortunately, only a very small proportion of ecological data ever collected is currently readily accessible and in a usable condition (Reichman *et al.* 2011). There is a large literature concerning the call for scientists to make data freely and publicly available (and a push for 'open science' in general), which is beyond the scope of this thesis to discuss in any detail. However, it is important to note that, although heavily debated, the benefits of online data publication to all participants in research (from the individual scientists as a data creator, through to funding agencies, governments and society at large) outweigh the challenges and often unjustified concerns voiced (see Costello 2009).

The GADB has been in existence for over 15 years (since Bennett 1986). Its unquestionable value for science was outlined in Section 3.2.1 and by the research conducted in this thesis. I believe that the next logical step with respect to the database is to scope and prepare it for being made publicly available online. For example, via the Dryad digital data repository (http://www.datadryad.org/), which assigns a permanent identifier to the dataset that must be cited when reused. It is appreciated that this will take time and effort to achieve, due to factors including: tidying of metadata and references, format standardisation, ensuring transparency, and establishing an efficient and effective maintenance and editing system. However, doing so, will in turn: (1) enhance the credibility and repeatability of research conducted using it, (2) enable it to be synthesised with other datasets to create new data resources and for use in meta-analyses, and (3) overall aid in enhancing and accelerating scientific progress.

8.6 Future research

Due to the scale, novelty and conservation implications of this research, there are numerous directions to potentially take in terms of future related work - several of which I consider to be the most interesting and worthwhile ideas are outlined below in turn.

8.6.1 From patterns to processes, and the need for focused regional studies

This thesis predominantly involved conducting novel research to identify global-scale patterns in both avian trait and extinction risk variation with respect to elevational distribution. The associated underlying processes driving the identified patterns were proposed in the discussions of the individual data chapters, and not explicitly studied. As highlighted in Section 1.1, there is a gap between our knowledge of large-scale ecological patterns and their respective drivers. Therefore, the next logical step with regards to this research is to expand the existing methodological framework in an attempt to identify and understand the large-scale patterns found. However, among other factors discussed below, the inherent complexity of environmental variation with respect to elevation (Section 1.4) makes this challenging to achieve.

It is relatively straightforward to conduct global-scale grid-cell based studies (Section 8.3) investigating geographical (i.e. planimetric) variation in species richness diversity (e.g. Storch *et al.* 2006; Davies *et al.* 2007; Thomas *et al.* 2008) and traits (e.g. Jetz *et al.* 2008a; Olson *et al.* 2009), that incorporate environmental data layers with which to model potential underlying drivers in the spatial patterns found. In fact a variety of GIS-derived data layers have been used as independent variables in such studies to date, for example: normalised difference vegetation index (NDVI: a measure of productive energy availability), mean annual temperature (measure of ambient energy availability), annual precipitation, degree of seasonality, topographic heterogeneity, and both actual and potential evapo-transpiration (measures of water-energy balance/productivity and ambient energy, respectively). Measures of human impact have also been incorporated into such studies investigating planimetric variation in extinction risk, including: human population density, economic activity (e.g. GDP), and land-use modification (e.g. extent of agricultural and urban land-area) – see Davies *et al.* (2006) and Lee & Jetz (2010). However, it is difficult to envisage how such a grid-cell approach could be translated for investigating drivers of elevational variation in both traits and extinction risk, especially at the global scale.

One potential way could be to still use a planimetric grid-cell approach, but at the highest resolution possible, in order to account for variation in elevation and large, complex mountainous regions. To achieve this, the above data layers would need to be available at a fine (i.e. ≤1km^2) spatial resolution. With satellite data quality ever-increasing and the discipline of GIS continuously advancing, such an approach could be possible in the near future. For example, WorldClim data and the GTOPO30 digital elevational model are currently available at a spatial resolution of 1km^2. However, the development and use of three-dimensional environmental data layers in ecological studies has yet to be seen.

Related to the above, numerous studies have focused on diversity, trait and threat variation along single elevational gradients, or at a regional level. At these scales it would be far easier to investigate the underlying processes driving patterns found. It might therefore be worthwhile conducting focused regional in-the-field studies for different mountain ranges across the world – ensuring a consistent methodology was applied (potentially using elevational bands), where both dependent and independent data could be collected first-hand if neccessary. A more detailed, refined and regional approach has been recommended by both Fisher & Owens (2004) and Cardillo & Meijaard (2012) with respect to the conservation value of comparative studies of extinction risk. Alternatively, a similar approach to that used by Christy McCain when investigating elevational diversity gradients at the global scale could be adopted for studying trait and extinction risk variation (e.g. McCain 2009a).

Ultimately, it is important that studies concerning patterns and processes of elevational variation in diversity, traits and threat-status are not only conducted at a variety of spatial scales, but understood to be complementary to one another and so looked at collectively.

8.6.2 Future traits to investigate

It is important to emphasise that for the purpose of this thesis, only a select number of avian traits were studied, selected based on criteria outlined in Section 3.3. A large proportion of available species-level traits in the GADB were therefore not analysed here with respect to how they vary with elevational distribution, or incorporated as independent variables in multivariate models. A few of the traits omitted from this study that would be desirable to examine in the future are listed and briefly discussed below.

Additional ecological traits: The two ecological traits included in this research were diet breadth and habitat breadth. It would be informative to expand upon these to include, for example, measures of social mating system (i.e. monogamy, polygyny, polyandry, polygynandry), nest type, parental care (i.e. female, male or both) and developmental mode (i.e. altricial through to precocial).

Migratory behaviour: Migration is among the best studied of animal behaviours, yet it is a highly complex variable, and difficult to incorporate into large-scale interspecific comparative studies such as this. Individual birds within a population may be resident or migrant, and different populations within a species may show varying degrees of migratory movement. The migratory categories currently in the GADB are unavoidably arbitrary to a certain degree: short-distance, long-distance, altitudinal and resident. In an attempt to investigate the relationship between migratory behaviour and elevational distribution, species-typical behaviours should be used, with those species possessing highly variable movement behaviours either omitted from analyses or added as a fifth category (i.e. labelled as ‘variable’). In addition, once a suitable species-level migratory behaviour dataset has been compiled, this categorical trait should be entered as an additional predictor to the multivariate models performed in this research.

Focusing on altitudinal migration, although it is purported to be a common strategy of birds occupying mountainous areas (particularly within the tropics), no extensive literature on the subject exists. Empirical studies documenting the existence and causes of such movement behaviour are scarce and taxonomically and geographically restricted (e.g. Boyle 2008; Mackas *et al.* 2010 – and references within both). Specifically, altitudinal migration involves relatively short distance annual movements of all or part of a population uphill to breeding areas and downhill to nonbreeding areas (Mackas *et al.* 2010). Such a behaviour may be advantageous because it allows migrants to exploit temporal or spatial variation in food resources, minimise the risk of nest predation, escape extreme climatic conditions that impact physiological function, or could in fact be a conditional strategy used by subordinate birds (see Boyle 2008; Mackas *et al.* 2010). In addition to investigating variation in general migratory behaviour with elevational distribution, it would be novel and informative to collate existing data documenting bird species that undergo altitudinal migration and to assess evidence, patterns and underlying drivers of such behaviour, as has already been done for bats (McGuire & Boyle 2013). In connection with this, the underlying traits of such species should be identified and could potentially be compared to those species that are resident, in an attempt to better understand this elusive behaviour.

Sexual dichromatism and plumage colouration: As discussed in Section 2.1.6, several studies have examined variation in sexual dichromatism for a small number of bird species with respect to elevational range (Badyaev & Ghalambhor 1998; Tobias & Seddon 2009) and elevational midpoint (Badyaev 1997a), finding a positive and negative trend, respectively. Currently, the reasons for these identified relationships are not well understood, and their generality unknown. Therefore, following standard methodology (e.g. Owens & Bennett 1994), such an analysis should be taxonomically expanded.

Related to the above, no study has yet investigated interspecific variation in plumage colouration with respect to elevational distribution in birds or any other taxa. This could be investigated with regards to Gloger's rule (Gloger 1833), i.e. endothermic animal species in warm and wet regions should be more heavily pigmented and typically darker than those in cool dry areas. Although this hypothesis was formulated nearly 200 years ago, it has not been well tested, with existing studies of birds and mammals at both the inter- and intraspecific levels to date having produced varied results (see James 1991; Kamilar & Bradley 2011).

Physiology: Much ambiguity still exists as to the factors responsible for the variation in avian basal metabolic rates (BMR). With respect to spatial variation, BMR has been shown to be higher in temperate than tropical birds, and has been connected to their contrasting life histories (see Wiersma *et al.* 2007; Williams *et al.* 2010; Section 2.1.6). Based on this finding, does a similar trend exist with elevation? Limited studies have found montane birds, particularly those in the tropics to possess higher BMR than their lowland counterparts (e.g. McNab 2009). However, such studies use a simplistic dichotomous measure of elevation (i.e. species endemic or non-endemic to elevations above 1000m), and do not investigate variation with respect to elevational range. In collaboration with Dr Peter Bennett, I have been collating existing avian BMR data for which it would be possible to undertake a more detailed analysis of the above. In general, current understanding of interspecific variation in physiological traits is limited with respect to elevational variation and demands further study. Another candidate trait whose variation has never been investigated with respect to elevation and for which data is available (albeit for a limited number of species), is white blood cell count – a measure of immune function.

8.6.3 Beyond birds

Although briefly mentioned in the data chapter discussions of this thesis (specifically Chapters 4 and 7), it is important to emphasise the value of investigating the wider generality of the relationships identified here for birds with respect to other major taxa. For example, I consider there to be real potential for conducting similar research on mammals. Although at present, elevational distribution data is not explicitly included in the global mammal trait database PanTHERIA (Jones *et al.* 2009), a proportion of the records are georeferenced to a reasonable precision (Nick Isaac, personal communication). This means that it would be feasible to extract corresponding elevation information from a digital elevation model (DEM) and import into the database. Further data collection from primary sources and online databases such as the Global Biodiversity Information Facility (GBIF: http://www.gbif.org/) would also be necessary to attain confidence of possessing a decent taxonomic coverage. Alternatively, there are maps associated with each known extant mammal species accessible via the IUCN Red List website (http://www.iucnredlist.org /technical-documents/spatial-data#mammals). From these it would be relatively straightforward to derive elevational limits via ArcGIS (Kate Jones, personal communication). However, this would only provide a measure of potential (rather than known) elevational limits. I believe elevational distribution to be one of the main variables missing from PanTHERIA at present, and one that would greatly enrich its utility as a resource for comparative ecological research and conservation.

8.6.4 Three-dimensional ranges

As discussed in Section 2.2.4, only a handful of ecological studies to date could be found utilising non-planimetric species range sizes that attempt to merge geographical and elevational distribution into one parameter (e.g. Smith *et al.* 2007; La Sorte & Jetz 2010; Recio *et al.* 2010). It would be both informative and innovative to use recent advances in 3D GIS (such as the ArcGIS 3D Analyst extension, which can calculate parameters including surface area, volume, slope and aspect) to obtain simplified measures of non-planimetric range sizes for bird species in the GADB with both geographical and elevational distribution data available. These values of surface area range size could then be directly compared with geographical range sizes to test for differences and similarities.

Studies have discussed and shown that the species-area relationship is more apparent in flat areas than in mountains (e.g. Vetaas & Grytnes 2002; Nogués-Bravo *et al*. 2008; Vetaas & Ferrer-Castan 2008, but see Nogués-Bravo *et al*. 2006; Triantis *et al.* 2008). A related and interesting thought experiment, is to imagine that if a given mountain range (e.g. Andes) were to be 'flattened out', one may find that species diversity is either very similar or actually lower than the surrounding lowlands (e.g. Amazon basin), contrary to current understanding (Section 1.3). In other words, if a 'flattened' mountain range and adjacent lowland were to be compared, which would be found to have the greatest diversity levels in terms of species richness (per unit surface area)? This question is one that should be explored at a regional scale with respect to birds, potentially utilising the mountain range boundaries delineated in Chapter 6, and a lowland definition of terrestrial regions ≤300m (UNEP-WCMC 2002).

8.6.5 Utility of museum specimens in detecting historical elevational range shifts

In addition to the need to conduct informed field excursions to collect primary data, macroecologists must also make better use of existing data (Beck *et al.* 2012). Natural history museum (NHM) collections are a valuable but highly underused resource for avian ecological- and conservation-focused research (see discussions in Collar *et al.* 2003; Suarez & Tsutsui 2004; Gill 2006; Joseph 2011). For example, NHM collection data can (and has) been used to detect temporal range shifts, providing novel insights into how the natural world has responded to past environmental change, and how it might respond in the future (see Shaffer *et al.* 1998; Tingley & Beissinger 2009). It is undeniably true that a number of inherent issues surround the utility of NHM collection data for documenting range shifts, namely: (a) error – including error in taxonomic identification and spatial error; (b) bias – primarily the geographical and environmental biases associated with *ad hoc* data collection, and (c) presence only versus presence–absence data, which influences the type of modelling algorithm that can be used. However, considerable methodological advancements accounting for these problems (and others) are continuously being made (see Tingley & Beissinger 2009).

Historical range change studies to date have been focused at the two-dimensional (planimetric) level. I am interested in investigating the feasibility of and potentially developing a novel methodology for reconstructing historical ranges and studying range contractions (and to a lesser extent expansions) at the three-dimensional level, by focusing on elevational range change over time. Intermittently during the course of this PhD (and ongoing), I have been scoping the possibility of conducting such a study for the Psittaciformes (parrots and cockatoos) of eastern Australia, where the Great Dividing (mountain) Range lies, between the period of European settlement (220 years ago) up to the present day, with the aid of museum specimen records, species distribution maps, trait data from the GADB, and underlying environmental layers. To date, I have been compiling a database of location and collection date data of relevant specimen records acquired from museums worldwide, via: (1) freely accessible online composite databases, such as the Online Zoological Collections of Australian Museums (OZCAM, www.ozcam.org.au/); (2) digitised specimen records (online and private) from individual museums, and (3) museum visits to collect non-digitised data (e.g. NHM Tring). The next few steps would be to continue with data collection, undertake retrospective georeferencing where necessary, and validate the data whilst checking for spatial and temporal biases (using a method similar to that used in Boakes *et al*. 2010).

8.7 Concluding thoughts

This thesis establishes that consistent and robust relationships occur between elevational distribution and both traits and extinction risk, for extant birds at the global scale. Consequently, this research has considerably added to our current understanding of large-scale ecology, trait biogeography, and conservation biology. Ultimately, I hope that this thesis, in conjunction with associated future research, will: (a) assist in the incorporation of an elevational perspective into terrestrial biogeography and macroecology theory and conservation practice, and (b) further highlight the importance of mountains as hotspots of terrestrial biodiversity and regions to be protected and conserved.

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