Novel approaches to inform tropical bird conservation in human modified landscapes

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Thesis submitted for the degree of Doctor of Philosophy in Biodiversity Management
February 2019
Word count: 50,654

Bornean Blue Flycatcher, Simon Mitchell

Dedicated to my Dad, Roger Mitchell whose enthusiasm for birds and wildlife started me on this path.

And to my mum, Marysia Dubeck who has offered unwavering support for everything I do.

(Don't worry guys, this doesn't mean you have to read this whole thing!)

Acknowledgements

My first thanks must go to my supervisors. Matt Struebig has been an incredible academic mentor for the last four year, guiding me through the intricacies of everything from Malaysian immigration, to reviewer comments! I consider myself very lucky to have him as a supervisor and friend. Zoe Davies has offered not only amazingly detailed feedback, thoughtful suggestions and enthusiastic support, but also emotional support at the most challenging times. The general narrative regarding academia seems to be that it’s highly competitive, stressful and cutthroat. However, Matt and Zoe, as well as the rest of the DICE family, have always made it something collaborative, challenging and actually exciting and I sincerely look forward to the possibility of working with them further in future. Huge thanks also to Dave Edwards, for initially suggesting I apply for the PhD position, providing excellent feedback and overall support throughout, and of course opening my eyes to tropical avifauna and ornthiological science to begin with!

Long fieldwork seasons are often a slog, but I feel mine were enhanced immeasurably by the wonderful company of Ryan Grey, Josh Twining, Adeline Seah, Craig Brelsford, Christina Murray, Rosie Drinkwater, Mike Massam, Tor Kemp, Mike Boyle, Joe Williamson, Jess Hightower, Dave Hemrich-Bennet, Jess Haysom, Adam Sharp, Zosia Ladds, Cindy Eva Cosset, Luke Nelson. My fieldwork in Sabah would not have been possible without the amazing SAFE team. Thanks to Jamiluddin “Unding” Jami for coordinating field logistics. Thanks also to all the excellent field assistants: Arnold “Noy” James, Mohd. “Kiky” Shah Nizam Bin Mustamin, Ampat “Anis” Siliwong and Najmuddin “Mudin” Jamal and Sabidee “Didy” Mohd. Rizan.

Many other people were also kind enough to contribute as collaborators, offer helpful pointers or taught me particular techniques or statistical approaches. These include Tom Swinfield, David Milodowski, Joe Tobias, Alex Lees, James Eaton, Marina Jiminez, Alex

Greene, Ross Crates, Eleni Matechou. Special thanks go James Gilroy for giving up his time so generously to teach me two solid days of occupancy modelling techniques!

So many people have made DICE a really great place to be. Foremost amongst are Gwili Gibbon, who has always been there when I need someone to vent to, and Nick Deere who has dropped everything to provide me with help, statistical assistance and a drinking buddy on countless occasions! Even though our PhD have no thematic overlap whatsoever, Nick's *sharp mind has motivated me to achieve more than I thought possible*. I'd also like to extend my gratitude and appreciation to Jess Fisher, Kate Alberry, Alistair Key, Dave Seaman, Jake Bicknell, Gui Braga Ferreira, (Isa)Bela Menezes-Barata, Valeria Boron, Tristan Pett and Lydia Tiller, Simon Tollington, Bob Smith, James Kloda and anyone else I may have failed to mention specifically by name.

Through the trials and tribulations of the last four years also I'd like to thank my old friends Mike Hoit, Keith Langdon, Teegan Dochery, Jacob Best, Jack Stewart, Stephen Hall, Stephen Wagstaff, Tea Basic, Igor Ormus, Helena Nery Alves Pinto, Sara Minarro for their support. Extra special thanks go to Alice Milton, for sticking by me throughout and brightening everything from mist-shrouded rainforests to dismal British winters with her wonderful wit, support and companionship.

Last but not least I would like to thank my brother and sister, and especially my parents. To my dad for creating and nurtuing my passion for the natural world championing my every endeavour and to my mum for always being there to support me in everything.

Author's declaration

The contents of this thesis were written by Simon L. Mitchell with the incorportation of suggestions, feedback and editorial ammendments made by Matthew J. Struebig and Zoe G. Zavies. Associated dataset and code will be made available through NERC EDR and other online repositories at the time of chapter publications.

Chapter 1: SLM wrote the chapter. Comments and feedback were provided by MJS.

Chapter 2: SLM, MJS, DPE, HB and ZGD conceived and designed the methodology; SLM collected, processed and analysed bird encounter data; DC and TJ processed LiDAR data; SLM, led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. This chapter was published in the *Journal of Applied Ecology*.

Chapter 3: SLM conceived the idea undertook all fieldwork. Data analysis was undertaken by SLM, with suggestions from MJS, ZGD, NJD and JG. DC, TS, DM and TJ processed LiDAR data and provided specific measures for each site. SLM produced the figures and wrote the Chapter, with feedback and comments from MJS, ZGD and DPE. NDJ provided comments on the occupancy modelling description incorporated in the methods.

Chapter 4: SLM conceived the idea undertook all fieldwork. Data analysis was undertaken by SLM, with suggestions from MJS and ZGD. SLM produced the figures and wrote the Chapter, with feedback and comments from MJS, ZGD and DPE.

Chapter 5: SLM wrote the chapter. Comments and feedback were provided by MJS.

I hereby declare that there were no competing interests on behalf of all co-authors.

Abstract

In this thesis I utilise a combination of newly advanced methodological and statistical approaches to assess knowledge gaps concerning biodiversity in human-modified tropical landscapes. Specifically, I use cutting-edge LiDAR technology, occupancy modelling and soundscape analysis to document the responses of tropical birds to land-use change in Borneo.

I first evaluate the contribution that riparian reserves – protected natural vegetation around waterways in production landscapes – have in supporting biodiversity. By assessing the avian community structure and richness of riparian reserves I demonstrate that these landscape features can offer significant biodiversity benefits, and support comparable levels of species diversity to logged riparian forests provided they are of sufficient size (>80 m in total width) and habitat quality (>75 tC ha^{-1} of tree biomass). I show that in oil palm estates riparian reserves would need to be >200 m in total width (i.e. 100 m from each riverbank) to preserve comparable numbers of forest specialist bird to logged riparian forest.

I then examine whether responses of species and trait groups to habitat disruption follow linear trajectories or non-linear responses whereby abrupt changes to occupancy and diversity occur once thresholds of disturbance are exceeded. Habitat disruption across a land-cover gradient from intact forest to oil palm plantations was characterised via LiDAR metrics that quantify habitat structure in three dimensions. By scrutinising the individual responses of 171 bird species and 17 different multi-species trait groups to these metrics via hierarchical multi-species occupancy modelling, I show that the majority of species respond to habitat degradation in a non-linear fashion. I demonstrate that thresholds in species response scale up to abrupt changes in trait group richness, particularly those associated with important ecosystem functions such as pollination, seed dispersal and insectivory. I find trait groups exhibit highly varied thresholds from one another. I also highlight how exceeding particular thresholds of degradation in human modified tropical landscapes could result in abrupt changes to ecosystem functioning, thereby making human-modified tropical landscape less resilient to further perturbations.

Last, I seek to test the application of recently developed acoustic approaches for monitoring biodiversity in human-modified tropical landscapes. I assess the performance of five commonly used ‘soundscape’ indices in corresponding to variation in observed or estimated bird diversity from field data. I find that sources of acoustic bias in production landscapes (including human produced noise and the sound of running), make broad application of acoustic monitoring technologies to heavily disturbed habitats such as intensive farmland challenging. I demonstrate that controlling for time-of-day, using noise-reduction algorithms and excluding certain habitat types, improves the capacity of acoustic indices to reflect both observed bird richness, and estimates of species numbers derived from occupancy models.

Taken together, the three studies in this thesis reveal the biodiversity value of riparian areas, the potential for non-linear responses of species to habitat change, and the efficacy of novel monitoring techniques applied to biodiversity monitoring in human-modified tropical landscapes. I offer a number of recommendations and applications of these three sets of findings and explore their implication for biodiversity conservation in tropical regions. By addressing these three knowledge gaps using a combination of newly available innovations I demonstrate not only the importance of the findings themselves, but also highlight how innovations in technology, analytical technique and monitoring approach when used in conjunction can elucidate biodiversity patterns that were otherwise less well known.

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Chapter 1. Introduction

A global environmental and biodiversity crisis

Anthropological degradation of the biosphere continues unabated, with societies continuing to operate beyond the planetary boundaries required to sustain human civilisation (Butler, 2017), 35% of non-human species (Thomas *et al.*, 2004) and potentially human life (Stern Review, U.K Treasury, 2007). Currently, biodiversity loss, climate forcing and nitrogen pollution all exceed what is deemed the ‘safe operating space for humanity’ (Rockström *et al.*, 2009), with levels of ocean acidification and phosphorus pollution also approaching these boundaries (Carpenter & Bennett, 2011; Kawaguchi *et al.*, 2013) The scale of effects on the biosphere are now so pervasive that there is growing concern the planet could become almost uninhabitable to humans in a few generations (Barnosky *et al.*, 2012), especially when overall patterns of resource use and degradation are accelerating (Steffen, Broadgate, Deutsch, Gaffney, & Ludwig, 2015). Increasingly, civil unrest and war (Kelley *et al.*, 2015), famine (Barnett & Adger, 2007) and the rise of authoritarianism (Steinhardt & Wu, 2015) are being driven in part, by societal responses to environmental degradation.

Of the planetary boundaries currently being exceeded, biodiversity loss is occurring at levels furthest beyond those considered ‘safe’ (Rockström *et al.*, 2009). Rates of vertebrate extinction during the last hundred years are at least ~100 times those of the background rate of extinction, suggesting a six major extinction event is already underway (Ceballos *et al.*, 2015). It is estimated that the amount of genetic diversity already lost would take over 200,000 human generations to be regained through evolutionary processes (Myers, 1993). This unprecedented pace of biodiversity loss (Pimm *et al.*, 1995), is eroding the capacity of natural ecosystems to provide goods and services which benefit human wellbeing (Diaz *et al.*, 2006).

Biodiversity underpins the fundamental characteristics of ecosystems, and species losses can compromise ecosystem function and resilience to external perturbations (Cardinale *et al.*, 2006). Species losses worldwide are already having comparable effects upon primary productivity to other forms of environmental change (Hooper *et al.*, 2012). Since 1500 there have been 338 documented vertebrate extinctions (Young *et al.*, 2016). However, the majority of historic and prehistoric extinctions caused by humans probably went unnoticed. Modelled estimates suggest that close to 1000 species of non-passerine land bird went extinct in the Pacific region alone (Duncan *et al.*, 2013). It is projected that a further 130,000 species could become extinct across all taxa by 2060 (Pimm & Raven, 2000). The accelerating crises in biodiversity loss specifically, and environmental degradation more generally, make directing effective and prescient conservation interventions to the most important regions and habitats of the world all the more important.

The degradation and destruction of tropical forests, and implications for biodiversity

Biodiversity is patchily distributed across the planet and highly concentrated in the tropics, where around two-thirds of all life on earth occurs, particularly in humid rainforests (Pimm & Raven, 2000). The tropics in general are hyperdiverse and account for 90% of terrestrial bird species, virtually all shallow-water corals, and over

75% of known amphibians, freshwater fish, ant, terrestrial mammals and flowering plants (Barlow *et al*., 2018). Within tropical regions forests are the most diverse habitats, with about half of the world's known taxa occurring (Scheffers *et al*., 2012). The distribution of these forests largely mirror 25 biodiversity hotspots, where around 30-50% of plant, amphibian, reptile and bird species occur (Pimm & Raven, 2000). However, these same regions have some of the highest human population densities and growth rates globally (Cincotta, *et al*., 2000), as well as the most rapid rates of landuse change (Jantz *et al*., 2015). Since 1990, around five million hectares of tropical forest have been lost per year (Keenan *et al*., 2015). Landuse change in the tropics has been the single greatest driver of biodiversity loss (Baille *et al*., 2004).

Remote sensing analyses reveal 80% of the world's tropical forests to already be somewhat degraded (Potapov *et al*., 2017). Conservation scientists have argued that, in this context, primary forest conservation is paramount, since it is irreplaceable for biodiversity (Gibson *et al*., 2011). Undisturbed forests may be especially important in the context of climate change, given the thermal buffering capacity of forests is compromised by edge effects (Ewers & Banks-Leite, 2013). However, intact tropical forests continue to be cleared at an accelerating rate, with the global extent reduced by 8.4% between 2000 and 2013 (Potapov *et al*., 2017).

Drivers of deforestation and forest degradation vary in terms of their relative importance globally, but 70% of overall forest loss is attributable to direct human land use conversion (Song *et al*., 2018) and agriculture is the strongest driver of tropical forest loss globally (Gibbs *et al*., 2010). Commercial agriculture is a stronger driver than subsistence farming, whilst mining operations, infrastructural expansion and urban development also contribute significantly (Hosonuma *et al*., 2012). Human populations are predicted to continue to expand to around 9-11 billion people by 2050 (Vörösmarty *et al*., 2000) and a 70-100% increase in agricultural production is expected to be necessary in order to satisfy the additional population as well as increases in consumption (Tilman *et al*., 2001; Godfray *et al*., 2010). Projections estimate natural vegetative cover in biodiversity hotspots will be reduced by a further 26-58% by 2100, precipitating hundreds or thousands of extinctions in tetrapods alone (Jantz *et al*., 2015).

In the last decade, the value of degraded tropical forests for biodiversity conservation has become more widely recognised. In part, this is an enforced pragmatic approach on the part of conservation scientists, since the proportion of primary forest is declining, and the alternative to retaining degraded forest is often more intensive agricultural landuse (Lindenmayer & Franklin, 2002; Meijaard & Sheil, 2007). However, the proportion of species from primary forests that persist in heavily logged areas is often substantial, even if those species persist at reduced abundances. Whilst the levels of species numbers retained are highly taxon and region specific (Gibson *et al*., 2011), for twelve out of fifteen taxonomic groups assessed in Amazonia more than half the species found in primary forest persisted in logged forest areas (Barlow, *et al*., 2007). In Borneo, studies have also concluded that >75% of bird and dung beetle species from unlogged forest are still present within forest logged multiple times (Edwards *et al*., 2010). Similarly, research on insectivorous bats showed no definitive effect of logging on site-level richness (Struebig *et al*., 2013). Additional justifications for the conservation and restoration of logged and degraded forests have been offered in terms of the provision of ecosystem services (Chazdon, 2008), including carbon sequestration (Chazdon *et al*., 2016).

Forest degradation in the context of Southeast Asia's biodiversity crisis

Sodhi first highlighted the biodiversity crisis in Southeast Asia in 2004 (Sodhi *et al.*, 2004). The Southeast Asia region has perhaps the greatest degree of endemism of anywhere in the world (Kier *et al.*, 2009). Both current and projected rates of forest loss are higher here than for the global average in the tropics (Laurance, 2007), and the extent of lowland primary forest is vanishingly small. The yield and value of timber in Southeast Asia is higher than anywhere else in the world, resulting in major incentives for the unsustainable logging. In Borneo, in particular, the value of timber extracted between 1980 and 2000 was greater than that of tropical Africa and Latin America combined (Curran *et al.*, 2004), and around 1.6% of forest is lost per year (Wilcove *et al.*, 2013). Modelled estimates suggest that 7-52% of lowland forest bird species and 9-36% of lowland forest mammals are likely to go extinct under business as usual logging scenarios (Wilcove *et al.*, 2013). Biodiversity loss in the region is also compounded by high hunting pressures (Harrison *et al.*, 2016) due in part to geographic proximity to Chinese markets, where demand for rare species causes an 'anthropic allee' for several Southeast Asian taxa (Courchamp *et al.*, 2006). Uniquely for the tropics many bird species are also in high demand, either as pet songbirds or for use in traditional medicine (Nijman, *et al.*, 2018). Southeast Asia is currently one of the regions with most taxa on the IUCN Red List, with 3,319 species listed as Vulnerable, Endangered or Critically Endangered, including 318 species of birds (IUCN, 2018).

In recent years, the expansion of oil palm (*Elaeis guineensis*) agriculture has been one of the leading drivers of deforestation in Southeast Asia. Oil palm is among the most profitable production land uses in the tropics and now covers an estimated

18.7 million ha globally (Meijaard *et al*., 2018). At least 522 Mha of tropical forest was converted to oil palm between 1980 and 2000 (Gibbs *et al*., 2010) and an additional 150 Mha was cleared between 2000 and 2012 (Hansen *et al*. 2013). In Kalimantan, Indonesian Borneo, 90% of oil palm expansion from 1990 to 2010 replaced some type of forest; (47% intact forest, 22% logged forest, and 21% agroforest) (Carlson *et al*., 2012). Demand is expected to continue to increase with a growing global population and affluence (Sayer *et al*., 2012). Expansion to meet this demand could extend the oil palm footprint to 800,000 ha of forest in Colombia by 2020 (Garcia-Ulloa *et al*., 2012), and more than 6.5 million ha by 2080 on Borneo (Struebig *et al*., 2015). Since the climatic niche for cultivating oil palm is similar to that of tropical forests (Pirker *et al*., 2016), oil palm expansion is also likely to continue in other hyper-diverse ecoregions. Therefore, understanding the extent to which biodiversity can be preserved within oil-palm landscapes and how best to manage the competing demands of oil palm production and conservation efforts to maximise both biodiversity protection and human wellbeing is of paramount importance.

Biodiversity in human-modified tropical landscapes

Given that over 40% of the earth’s terrestrial land surface is currently under agricultural management (Perfecto & Vandermeer, 2010), and virtually all tropical habitats are either managed or exploited by people (Kareiva *et al*., 2007) there has been increasing research focus on biodiversity in rural landscapes which undergo active management or modification by people (Gardner *et al*., 2009). Since a mere 10% of tropical forests are formally protected (Schmitt *et al*., 2009), the capacity of reserves to provide adequate protection to tropical fauna and flora is strongly influenced by anthropogenic activities in adjacent land (Wittemyer *et al*. 2008). On this basis, it is argued that conservation science needs to adopt a systematic approach which incorporates the socio-ecological interplay between rural human populations and protected lands in order to offer more holistic solution to problems of biodiversity conservation (Liu *et al*. 2007).

In human-modified tropical landscapes any remaining forest is typically limited to remnants surrounded by agriculture, with such patches comprising native vegetation, secondary regrowth and pioneer vegetation (Laurance *et al*., 2014). The status of biodiversity in these landscapes, and the factors that most affect it, remain poorly understood (Chazdon *et al*., 2009), but a combination of the spatial extent and configuration of remnant natural vegetation are thought to be the main drivers of biodiversity patterns (Ewers, & Didham, 2006), as well as both the intensity of landuse (Tscharntke *et al*., 2012) and the structural and ecological characteristics of crop species (Phalan, 2011). Recent research has highlighted that such landscapes, particularly those that occur along a gradient between undisturbed tropical forest and agriculture, may have comparable levels of alpha (i.e. within site) and beta (i.e. between site) diversity to undisturbed habitats, but distinctly lower levels of gamma (i.e. landscape) diversity (de Castro Solar *et al*., 2015). Biodiversity is thought to be critically important for the maintenance and resilience of ecosystem function in these systems (Lohbeck *et al*., 2016).

The patchwork nature of human-modified tropical forests means research on the responses of biodiversity to fragmentation is highly relevant to understanding these systems fully. However, when trying to address ecological questions over human-modified tropical landscapes holistically, the idea of isolated habitat patches located in an inhospitable matrix may represent an incomplete way of understanding the system. Fragmentation models assume that there is a clear contrast between human-defined patches and the rest of the landscape and that multiple organisms perceive this as suitable habitat, which may not always be the case in landscapes where agriculture or extraction is of low intensity or fragments are also highly degraded (Fischer & Lindenmayer, 2006). The amount and structure of native vegetation, prevalence of anthropogenic edges, degree of landscape connectivity and structure and heterogeneity of modified areas all affect species assemblages in fragmented systems (Fischer & Lindenmeyer, 2007) and these can be useful properties to consider in human-modified landscapes more generally. It is still relevant that the highest levels of biodiversity in agricultural landscapes tend to be in the largest remnant fragments (Heegaard *et al*., 2007) with the greatest degree of structural similarity to continuous undisturbed forests (Decaëns *et al*., 2018), since even landscape-wide conservation interventions should necessarily prioritise the preservation of the areas with the highest levels of richness alongside other management approaches adopted.

Land-sparing and sharing frameworks are also useful when considering the overall efficacy of different approaches to protect biodiversity in human-modified tropical landscapes. Land-sparing approaches focus on attempts to maintain refuges for biodiversity separate from croplands (Fischer *et al*., 2008; Edwards *et al*., 2010; Phalan, 2011), whilst land sharing focuses on employing wildlife-friendly farming methods to enhance (or preserve) biodiversity on productive lands (Clough *et al*., 2011; Pywell *et al*., 2012). The trade-off between two the approaches appears to be mediated by regional context and crop type as land-sparing is fairly successful in preserving biodiversity in coffee and cacao dominated landscapes (Gobbi, *et al*., 2000;

Clough *et al.*, 2001), but generally less successful in oil palm areas (Edwards *et al.*, 2010). The success of land-sharing may also be affected by the type and proximity of surrounding habitats (Gilroy *et al.*, 2014).

Oil palm plantations typically support very low levels of biodiversity. Large reductions in diversity are reported for birds (Edwards *et al.*, 2010); bats in forest (Danielsen & Heergaard, 1995); mammals (Scott *et al.*, 2004) beetles (Chung *et al.*, 2000) and ants (Brul 2001). Among 25 studies comparing biodiversity between logged forest and oil palm, 23 found significant negative effects (Savilaasko *et al.*, 2014). However, the majority of these studies focussed strictly upon plantation areas. When considered as whole landscapes, oil palm estates frequently include remnant forest fragments of varying size. These areas are known to support considerable biodiversity from studies of forest birds (Edwards *et al.*, 2010), bats (Struebig *et al.*, 2008) and ants (Bruhl *et al.*, 2003), for example. A recent multi-taxa synthesis suggested that fragments in oil palm landscapes need to be a minimum of 200 ha in size in order to maintain a 'minimum viable core' area (defined as supporting at least 60% of species found in continuous forest) (Lucey *et al.*, 2017). The landscape-scale differences between industrial and smallholder oil palm agriculture remain uncertain, although the latter appears to have a lower overall negative effect on birds (Azhar *et al.*, 2011).

Understanding the landscape-wide potential for biodiversity conservation in oil palm estates requires ecological valuation of native forests retained not only in 'conventional' fragments, but also in riparian forest remnants. In many oil palm landscapes, riparian forest remnants comprise the majority of natural vegetation (*pers. obs.*), meaning their contribution to landscape-wide patterns of biodiversity in oil palm landscapes is potentially considerable. Whilst riparian reserves may in some ways be considered in the framework of fragmentation as long, linear fragments, the ecology of riparian forests is somewhat distinct from that of non-riparian forest. For example, some taxa are riparian or non-riparian specialists and occur as obligates in their respective habitats (Naiman *et al,* 1998) and the resulting community overlaps with that of the surrounding landscape in terms of species composition, but also contains unique species. The biodiversity value for riparian forest remnants in oil palm landscapes has already been demonstrated for dung beetles, ants (Gray, 2014) and fish (Giam *et al*., 2015), but remains poorly assessed for other taxa.

Birds as biodiversity indicators

Globally, patterns of avian biodiversity mirror those of other taxa, with the greatest biodiversity in the tropics (Jetz, 2012). Global threats facing the birds are also well understood. Of a global estimate of ~10,000 species 1,492 are currently listed as vulnerable, endangered or critically endangered (IUCN, 2018).

Landuse change is the most significant threat to birds around the world. Even in scenarios that assume no additional affects from climate change, at least 400 of 8750 modelled species are projected to experience >50% range reductions by the year 2050 (Jetz *et al*., 2007). The Red List Index for birds, (which provides an indexed metric of the changing levels of endangerment of extinction) showed a 7% worsening in the status of the world birds between 1988 and 2004 (Butchart *et al*., 2004). Disaggregated indices showed deteriorations across all major ecosystems, but the steepest declines occurred in the indices for Sundaic birds (i.e. those found in the

Malay peninsula, Sumatra, Java and Borneo), which were driven by intensifying destruction of lowland forests (Butchart *et al*., 2004).

Birds exhibit many of the features required of biodiversity indicators: they are diverse (Jetz *et al*., 2012); respond to multiple environmental changes in similar patterns to the majority of other taxa; and can be surveyed more cost-effectively than many other taxa (Gardner *et al*., 2008). Birds (alongside mammals) are also the world's best-studied taxonomic group (Costello, 2015), which means new research findings are often more easily contextualised in terms of their broader significance than might be the case for other taxa. However, accurately surveying tropical bird communities is often more difficult than generally appreciated by researchers who do not specialise in these taxa (Robinson *et al*., 2018). The challenge of accurately identifying and counting birds in typically dark, structurally complex rainforest environments where upwards of 95% of species are only encountered aurally, is often underestimated (Robinson *et al*., 2018). Many species have varied acoustic repertoires including multiple short vocalisations, which can lead to difficulty in avoiding false negative detections by non-experts (Robinson *et al*., 2018). The utility of studies with systematic false-negative detections can potentially be compromised (Remsen, 1994).

Survey and monitoring challenges for birds

In the context of the challenges highlighted above, the monitoring and assessment of both temporal and spatial patterns of biodiversity generally, and bird diversity specifically, is increasingly important in conservation. Without adequate monitoring and assessment efforts, predictions of impending species declines, extinctions, and subsequent recommendations for intervention are compromised. Nor is it possible to reliably assess the effectiveness of management practices or conservation efforts without appropriate data for evaluating those practices (Lindenmayer *et al*., 2010). Monitoring biodiversity also provides a potential first warning for the collapse of associated ecosystems, which underpin societal well-being (Rowland *et al*., 2018; Scholes *et al*. 2008). The Aichi Biodiversity Targets specify goals such as "improving the status of biodiversity by safeguarding ecosystems, species and genetic diversity." Evaluations to date show that these global targets have so far been largely missed (Tittensor *et al*., 2014). Implementing new conservation efforts to meet them, necessarily involves biodiversity monitors. Given the available funding for biodiversity conservation globally is insufficient to meet all conservation needs (McCarthy *et al*., 2012), using the most effective methods of monitoring and assessing biodiversity is highly important (Balmford *et al*., 2000). Monitoring efforts should also yield data that are accurate and as ecologically relevant as possible, in order to detect the effects of often cryptic stressors or patterns, which may have profound effects when upscaling study outcomes across large spatial or temporal scales.

In the last 20 years a significant number of innovations have increased our capacity to monitor and assess the responses and patterns of biodiversity in relation to environmental variation in tropical forests, as well as improve the efficiency and cost of monitoring efforts (Pimm *et al*., 2015). Broadly, these fall into categories of new methods and means of capturing biodiversity data, new methods of assessing and measuring environmental variation, and improved analytical approaches for comparing and integrating biodiversity and environmental data. New methods of characterizing biodiversity include autonomous camera traps and acoustic recorders (Steenweg *et al.*, 2017) while environmental DNA monitoring is moving from lab-based to field-based assessment techniques (Thomsen & Willerslev, 2015).

One example of a novel technological approach to biodiversity which has resulted in significant increases in efficiency in capturing species data is that of autonomous acoustic monitoring techniques. These techniques have only become feasible recently on large scales through the reduced cost of recording technology (Hill *et al.,* 2018). Soundscape ecology covers a number of techniques that focus on analysing the interaction of organisms, environmental drivers and human impacts based on their associated acoustic properties (Gasc *et al*., 2013). Such approaches allow the assessment and monitoring of biodiversity in a highly passive manner, with potentially little need for human expertise or effort once autonomous acoustic sensors can be set up.

The means to capture environmental data affecting biodiversity also advanced very rapidly over the last two decades. Freely-available remote sensed datasets were limited to Landsat satellite imagery at the turn of the century (Nagendra, 2001; Wang, *et al.,* 2010). As well as vastly improvement in fine-grain resolution of existing technologies the addition of Synthetic Aperture Radar (SAR) and aerial Light Detection And Ranging (LiDAR) allows the ability to assess structural aspects of vegetation. Advances in drone technology, combined with the algorithms and computing power now also make forest canopy mapping in three dimensions possible via photogrammetry (Saarinen *et al*., 2017).

Perhaps the most notable single advance comes from hyper-spectral LiDAR, which provides the ability to map the fine-scale structure of vegetation in three dimensions and thereby offers the potential to analyse patterns of faunal distribution and association which were previously unachievable. In tropical forests assessing vegetation in three dimensions is especially relevant, since vertical components in these landscapes are inherently important, with up to 70% of species utilising the upper forest strata on a facultative basis (Kays & Allison, 1975). Vertical dimensions are even more important for taxa such as birds and flying insects, and communities often change markedly from terrestrial-feeders to arboreal specialists (Chmel *et al*., 2016; Stork *et al*., 2015). LiDAR-based studies have addressed the effects of habitat extent, canopy height, canopy heterogeneity, vertical canopy distribution, understory density, aspect, elevation, slope and ruggedness have described responses in taxa as diverse as birds, mammals, insects and fish (Davies, *et al*., 2014).

Novel analytical approaches include a vast range of techniques such as improvements in accounting for specific challenges such as imperfect species detection (Jennelle, Runge, & MacKenzie, 2002), advances in meta-analytic approaches to determine effects across multiple systems (Pardo *et al*., 2013), rapid advances in GIS and spatial statistical approaches such as the development of MaxEnt for distribution modelling (Elith *et al*., 2011), the application of deep learning computing techniques in analysing ever larger datasets such as those collected through citizen science (Kelling *et al*., 2013), or to deal with advances in population genetics via environmental DNA (Cordier *et al*., 2017) or classify remote sensed data (Hethcoat *et al*., 2018). Other techniques which have been refined and/or adopted more widely include new ways of conceptualising biotic communities, from approaches such as functional diversity (Cadotte, Carscadden, & Mirotchnick, 2011), to phylogenic diversity (Tucker *et al*., 2017) and the analyses of potential thresholds in species and community responses (Ficetola & Denoe, 2009).

One innovation which could potentially facilitate the detection of far more cryptic responses of species and communities is the increase in data power and error estimation associated with occupancy modelling. Virtually all methods of biodiversity surveying suffer from imperfect detection and complete species surveys are often unfeasible (Iknayan *et al*. 2014). Traditional rarefaction methods have focused on measures which account for the difficulty in detecting rare species by offering the means to assess when communities have been adequately sampled (Chao & Jost, 2012), and extrapolating species accumulation curves to estimate metrics such as species richness and community Hill numbers (Palmer, 1990; Chao *et al*., 2014). Occupancy modelling uses repeat sampling to estimate the probability of false negative detections and then controls for these in overall models (Jennelle, 2002). Concerns have been raised that in some cases gearing study design toward these analyses may result in focusing finite survey effort inefficiently or inappropriately. This is because the amount of data required to obtain 'naïve' estimates is generally substantially lower than that required for estimates which adjust for imperfect detection, when in fact, improved study design can surmount problems of imperfect detection (Banks-Leite *et al*., 2014). Other authors have suggested that although good survey design is fundamental, it will not necessarily solve all detection problems or control for all variation in detectability (Guillera-Aroita, 2017).

Thesis structure

In this thesis I integrate the use of recent advances in biodiversity monitoring in order to address practical knowledge gaps relevant to conservation management in human-modified tropical landscapes. I combine multiple novel approaches to assess the relative biodiversity value of different habitats and provide management recommendations to optimise biodiversity provision in a tropical production landscape, elucidate hitherto unrecognised ecological patterns and refine novel analytical approaches themselves. I focus on Southeast Asia throughout, with a specific research focus in the lowlands of Eastern Sabah, Malaysian Borneo.

In **Chapter 1,** I examine the species diversity present in riparian reserves compared to riparian forest controls. I also determine the proportion of forest-specialist species remaining in these reserves. I use LiDAR derived remote-sensing data to measure the widths and carbon densities of riparian reserves within oil palm estates. Using these data I estimate the optimal riparian reserve widths and carbon densities necessary to support a similar level of species richness to riparian forest controls in continuous forests.

I use **Chapter 2** to focus on the ecological patterns exhibited by the avifaunal community along a continuous gradient of forest degradation using a trait-based approach. I combine a Bayesian occupancy model, parameterised with LiDAR-derived vegetation structure data, with piece-wise regression analyses to assess thresholds in both species and trait group responses to habitat change. Using this approach I infer likely species response thresholds to multiple environmental variables and am able to elaborate on the way particular trait groups have previously been observed to respond to changes in forest structure by identifying points of abrupt change in these responses.

In **Chapter 3** I seek to improve the application of soundscape analysis to biodiversity monitoring by offering recommendations to optimise how well acoustic indices reflect bird communities as measured by conventional point count approaches and species richness as defined by the occupancy model described in Chapter 2. By assessing the influence of controlling for time-of-day and background noise in recordings, and removing habitats where certain indices are non-functional, I am able to offer recommendations as to which indices are most robust for assessing biodiversity in human modified tropical landscapes.

In the Introduction and Discussion sections of this thesis I have adopted a first person singular style. However, given the collaborative nature of the data chapter, I switch to a combination first person plural or passive voice throughout these sections.

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Chapter 2. Riparian reserves help protect forest bird communities in oil palm dominated landscapes

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Manuscript published as:

Mitchell, S. L., Edwards, D. P., Bernard, H., Coomes, D., Jucker, T., Davies, Z. G., & Struebig, M. J. (2018). Riparian reserves help protect forest bird communities in oil palm dominated landscapes. *Journal of Applied Ecology 55.6 (2018): 2744-2755.*

Abstract

1. Conversion of forest to oil palm agriculture is a significant and continuing threat to tropical biodiversity. Despite this, little is known about the value of riparian reserves in oil palm and how these conservation set-asides might best be managed to maintain biodiversity.
2. We characterised bird communities of 28 sites in an oil palm-forest mosaic in Sabah, Malaysia using 6104 encounters from 840 point counts. Sites included oil palm riparian reserves of various vegetation quality and reserve widths, which were compared to oil palm streams without a riparian reserve as well as riparian and non-riparian control areas in continuous logged forest.
3. Riparian reserves, oil palm waterways, and control sites in riparian and non-riparian forest supported distinct avifaunal communities. Riparian reserve width, forest quality and amount of forest cover were the strongest predictors of bird species richness. For forest-dependent species, each of these predictors had stronger effect size when compared with all species. On average, reserves held 31% of all species and 30% of forest specialists, whereas riparian forest controls averaged 32% of all species, but 38% of forest species.
4. Riparian reserves with >40 m of natural vegetation on each bank supported similar bird diversity to riparian forest control habitats found in continuous logged forest. However, to support equivalent numbers of forest-dependent species and species of conservation concern, reserves would need to be at least 100 m wide on each bank. The highest numbers of species were found in riparian reserves with above-ground carbon densities exceeding 75 tC ha^{-1},

highlighting the importance of forest quality, as well as width, in supporting riparian bird communities.

5. *Synthesis and applications*. If designed and protected appropriately, riparian reserves in oil palm estates support diverse bird communities, including many species of conservation concern. This can be achieved by designating large reserves (80-200 m total width), but to maximize species numbers forest disturbance should also be minimised prior to conversion as well as during plantation operations.

Key-words: agriculture, riparian buffer, riparian zone, biodiversity, landuse change, fragmentation, landscape configuration, forest management.

Introduction

Human activities are causing unprecedented biodiversity decline (Pimm *et al.* 2014), with agricultural expansion being a primary cause of tropical species loss (Gibson *et al*. 2011). At least 522 Mha of tropical forest was converted between 1980 and 2000 (Gibbs *et al*. 2010) and a further 150 Mha was lost between 2000 and 2012 (Hansen *et al*. 2010). A major contributor to this problem has been oil palm cultivation (*Elaeis guineensis*), which is now one of the most profitable landuses in the tropics, with continued demand (Vijay *et al*. 2016). Meeting this demand will require improved productivity on existing estates, as well as expansion of the crop into new areas.

Tropical production landscapes harbour significantly less biodiversity than native forest (Gibson *et al.* 2011); a pattern documented in many agricultural landuses, including fruit orchards (Round *et al.* 2006), rubber plantations (Warren-Thomas *et al.* 2015), and oil palm under both smallholder cultivation (Azhar *et al.* 2011) and industrial production (Edwards *et al.* 2010). Retaining forest remnants within human-modified tropical landscapes can therefore enhance biodiversity levels (Laurance *et al.* 2018), although crop yields are likely to be reduced as a consequence (Edwards *et al.* 2010). Forest patches are maintained typically on slopes, floodplains, or along waterways.

Waterways and riparian areas are often afforded legal protection in tropical countries to mitigate flooding and sedimentation (Mayer *et al.* 2007). In Malaysia, for example, agricultural companies are required to maintain riparian reserves of between 5 and 50 m from each riverbank, with most being 20-30 m (Government of Malaysia, 2012). In Brazil reserves can be 30-500m wide depending on channel width, but recent policy changes drastically reduce the prescribed widths (da Silva *et al.*, 2017). In addition, oil palm companies that adhere to guidelines under the Roundtable for Sustainable Palm Oil (RSPO), the primary environmental certification scheme for this crop, agree to retain riparian reserves, and there are ambitions to increase the width requirements (Luke *et al.* Submitted).

While the main rationale for protecting riparian reserves is hydrological, these habitats may also be important for maintaining wildlife populations. In Sumatra, riparian reserves in paper-pulp plantations support large-mammal communities comparable to those in continuous forest (Yaap *et al.* 2016), and in Amazonia large and undisturbed riparian reserves retain near-complete mammal and bird assemblages when compared to large forest patches (Lees & Peres, 2008; Zimbres *et al*. 2017). In Borneo, fish (Giam *et al*. 2015), dung beetle and leaf-litter ant (Gray *et al*. 2014, 2016) assemblages in oil palm riparian reserves are more similar to those in contiguous logged forests than the surrounding oil palm matrix in terms of composition, species diversity and functional group diversity.

The species composition of riparian remnants is likely to be influenced by many of the processes associated with habitat fragmentation, such as area, isolation and edge effects (Laurance *et al*. 2018). Area, or width of the riparian remnant, is expected to be a primary determinant of diversity, yet few researchers have documented this in tropical regions, and even fewer provide explicit width recommendations to inform riparian reserve design (Luke *et al*. Submitted). In the Neotropics, riparian zones are reported to extend to 60-250 m for plants (Schietti *et al*. 2014), 100 m for snakes (de Fraga *et al*. 2011) and 140 m for understory birds (Bueno *et al*. 2012), but since these studies were undertaken in forested areas it is unclear whether the same width thresholds would apply in fragmented habitats or agricultural systems, or indeed to other tropical regions (van der Hoek *et al*., 2015).

Here, we explore the relationships between riparian reserve width, forest quality, and the birds present in a modified tropical landscape of Southeast Asia. Specifically, we characterised bird communities in riparian reserves set in forest or oil palm to evaluate the relative value for riparian and non-riparian biodiversity. Reserve width, the main criterion stipulated in environmental policy, is expected to correlate positively with species richness, with more species supported in wider reserves (e.g. Lees and Peres, 2008; Gray *et al*. 2014; Zimbres *et al*. 2017). However, the expected levels of species richness might not be supported if the habitat quality is low (Luke *et* *al*. Submitted). Given the roles of other confounding variables in the fragmentation literature (Laurance *et al*. 2018), it is important to understand how measures of patch size (i.e. width) and quality affect riparian remnant biodiversity in the context of the wider landscape covariates (e.g. elevation, isolation). There is also fundamental policy interest in establishing whether the largest riparian reserves can support similar levels of biodiversity to continuous forest sites, since protecting larger/wider reserves involves a trade-off between conservation interests and making land available for agriculture. We sought to address these questions, while also examining whether riparian reserves are valuable for forest-dependent species and species of conservation concern, since these taxa are the focus of environmental policy in the certification sector.

Methods

Study system

The study was set in and around the Stability of Altered Forest Ecosystems (SAFE) project (117.5°N, 4.6°E) in Sabah, Malaysian Borneo (Fig. 2.1, Ewers *et al*, 2011). The 80,000 ha area comprises both forest and plantations of oil palm and *Acacia*, with all matrix study sites surrounded by oil palm. Most of the remnant forest has been logged two to four times over 30 years and contains few mature trees (Struebig *et al*. 2013), although some parts are less disturbed and are formally protected. The surrounding agricultural matrix comprises multiple oil palm estates with trees planted 8-12 years before the study. Within this matrix, remnants of logged forest are protected alongside watercourses as riparian reserves. Reserves typically extend ca. 50 m on each bank from the river channel, but vary between 10 and 470 m (median=54 m, SD=135 m) across the landscape. Reserves also vary in altitude, topographic ruggedness and substrate (rocky to sandy).

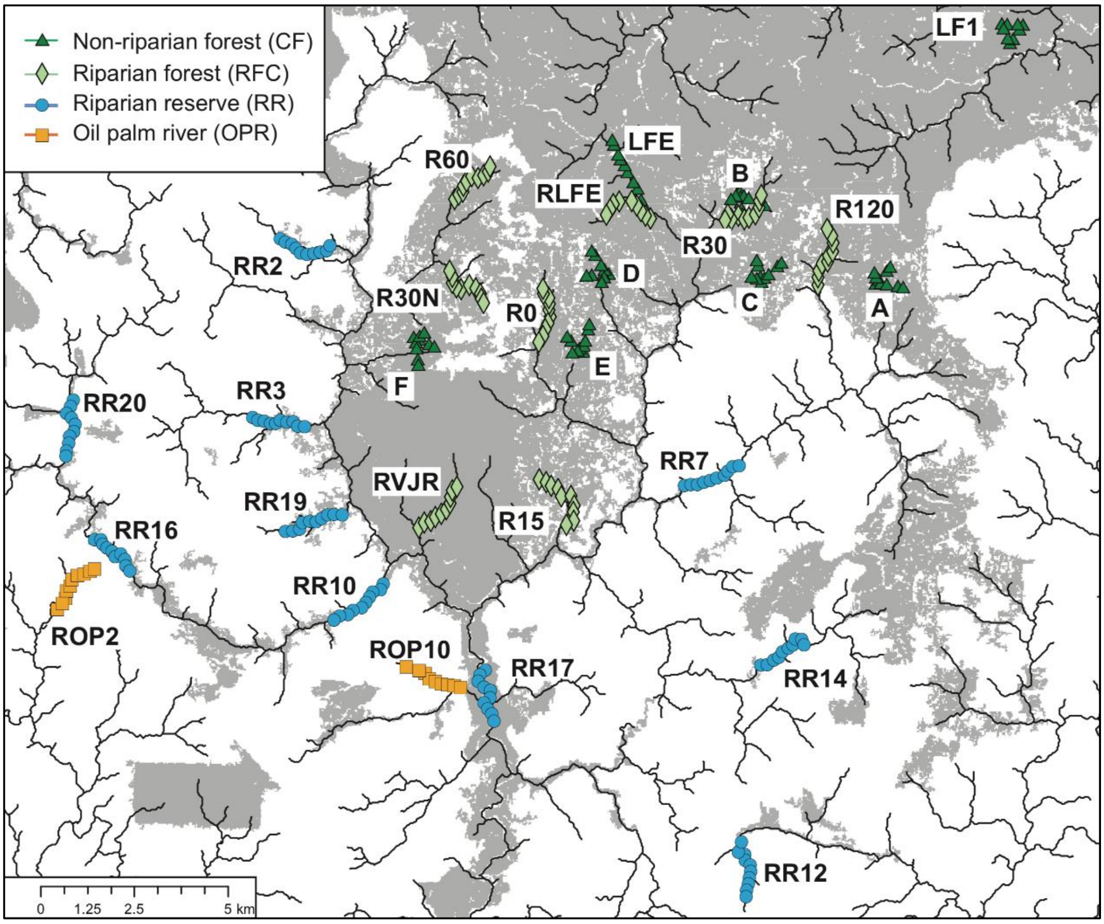

Figure 2.1 Map of the Stability of Altered Forest Ecosystems (SAFE) Landscape. Twenty-eight bird sample sites in riparian (n=20) and non-riparian (n=8) habitat types in the SAFE landscape and surrounding agricultural matrix in Sabah, Malaysian Borneo. A site comprised ten point count stations (indicated by points on the map), each of which were sampled for birds on three separate occasions. Forest is shown in grey; tree plantations (predominantly oil palm), and cleared areas in white. Forest cover was derived from Hansen *et al*. (2013) and updated to represent the landscape in 2014 accurately. Black lines denote the river courses. Names for each site are displayed and correspond to those listed in Fig 2.3.

We sampled bird communities alongside 20 rivers. Ten of the rivers were within oil palm plantation and had riparian reserves (RR), two were in the oil palm with no riparian reserve and were used as controls (OPR), and a further eight rivers were used as controls within the logged forest (hereafter riparian forest control; RFC). The rivers sampled in oil palm were selected to represent the range and distribution of reserve widths present across the study area and plantations elsewhere in Southeast Asia. Larger riparian reserves were scarce and only one site of >100m was available in our study area (RR17, width = 470 m). Forest quality, indicated by above-ground carbon density measured via LiDAR (Jucker *et al*. 2018), also varied substantially across the landscape. Finally, to document any differences between riparian and non-riparian bird communities, we also surveyed eight non-riparian control sites in continuous forest (hereafter forest control; CF), all of which had also been previously logged, reflecting the dominant remnant forest type in lowland Southeast Asia.

Bird sampling

At each riparian site, birds were sampled via ten point counts set at 180-220 m intervals (Euclidian distance) along a 2 km transect following the course of the river. The stations were situated up to 10 m up the riverbank to minimise interference from the sound of running water. During each count, a single experienced observer (SLM) recorded all bird species heard or seen within a 50 m radius of the point for 15 minutes including fly-overs. Average river width ranged between 5 and 13 m, meaning that the detection radius encompassed both terrestrial vegetation and the river. However, the river itself never accounted for more than 5% of the total point count area. Counts were conducted between 05:50 and 11:00 in clear weather, and were repeated on three separate occasions at each site between 2014 and 2016. For non-riparian sites, the ten point counts were spatially configured at comparable distances along access trails. Sites were sampled at mean intervals of 72 days between visits (Table S2.1). Three species of swift (*Aerodramus maximus*, *A. salangana* and *A. fuciphagus*) could not be reliably separated and are considered as *Aerodramus* spp. The bird sampling data from the three surveys were pooled across the ten stations at each site. Taxonomic nomenclature follows Eaton *et al*. (2017).

Environmental predictors of bird community structure

For each site above-ground carbon density (mean values across the ten point counts sites) were derived from remotely sensed data, and used as a proxy for overall forest quality, since lower carbon densities were evident in areas that experienced the most degradation via logging (Jucker *et al*., 2018). Similarly, we also calculated altitude and topographic ruggedness for each site as an average of values extracted within a 50 m radius of each of our ten point stations. Above-ground carbon density was extracted from LiDAR-derived datasets (30 x 30 m), which were gathered in November 2014 using a Leica ALS50-II sensor (Jucker *et al*. 2018). Altitude (30 x 30 m) was estimated from the Shuttle Radar Topography Mission (SRTM; http://www2.jpl.nasa.gov). Likewise, topographic ruggedness was derived using the SRTM, according to Wilson *et al*. (2007). Average values for each raster layer were calculated within the buffer radius of each station using the R 3.2.3 (R Core Development Team, 2015) packages ’raster’, ‘sp’, ‘rgdal’, ‘gtools’ ‘doMC’ and ‘maptools’ (Hijmans & van Etten, 2002; Pebesma & Bivand, 2005; Bivand *et al*., 2016; Analytics Revolution, 2014; Bivand & Levin-Koh, 2013)

For each riparian reserve sampled, we estimated reserve width at each station from the LiDAR canopy height layer (5 m resolution). The width of the river channel was included in this remote measurement as vegetation often obscured the riverbanks. River channel width was recorded in the field, between the high water marks of the two banks, using a laser rangefinder (Leica Rangemaster CRF 1000). Subsequently, this value was subtracted from the reserve width estimate to determine the actual land surface within each reserve. Mean bank reserve width is typically referenced within environmental policy documents, so we use this metric throughout the paper.

As a measure of landscape-scale forest availability, we also calculated percentage forest cover within a 1000 m radius of each point count station, capturing the availability of forest in the landscape without overlapping forest associated with other sample sites. All environmental predictors were average values across the ten point count stations per site.

Statistical analyses

Species accumulation curves were constructed for each site and habitat type, and inspected for being close to asymptote to confirm that sampling was adequate (Fig. S2.1). Rarefied curves, based on 100 iterations, were produced using the ‘vegan’ package in R (Dixon, 2003). We used the number of bird encounters, rather than absolute numbers, to generate curves, as early morning roost flights of Sunda yellow-vented bulbul (*Pycnonotus analis*) occasionally resulted in >100 individuals recorded from a single point. In this case, large numbers of a single species recorded within one visit were treated as a single encounter.

We used a generalised linear modelling (GLM) framework in ‘lme4’ to explore the partitioning of species abundance and richness by habitat type. Spatial autocorrelation was assessed using a Moran’s I test on the residuals of the GLM for richness across all riparian sites to test for unforeseen associations between nearby sites. The package ‘multcomp’ was used to perform Tukey tests between pairwise habitat combinations (RFC vs. CF, RFC vs. OPR, etc.), and the procedure repeated for two subsets of our community: forest-dependent species (defined by consensus of five expert ornithologists in Southeast Asia, Nick Brickle, Frank Rhiendt, Dave Bakewell, Craig Robson and Simon Mitchell), and species of conservation concern (status of near-threatened through to critically endangered, IUCN, 2017).

To visually demonstrate the associations between both carbon density and reserve width, and community structure we plotted the relationships graphically. Community integrity was measured using the Bray Curtis dissimilarity index on an abundance matrix (sensu Banks-Leite *et al.*2014). We used mean differences in species composition between riparian reserves (RR) and each of the riparian forest controls (RFC) to reflect reductions in community integrity.

Ordinations were used to explore bird species composition in relation to habitat type and our environmental predictors. Pairwise Bray Curtis dissimilarity coefficients were calculated between species abundances pooled from across the three visits at each site and non-metric multidimensional scaling (NMDS) ordinations generated using PC-ORD 6.07 (McCune & Mefford 2011), to organise sites by similarity in species composition. The reliability of the ordinations was determined by comparing NMDS solutions produced from 250 runs of real data, with those produced from randomised species-site matrices using a Monte Carlo test. The ordinations were then repeated to ensure that they reflected representative signals in community data and were not being disproportionately impacted by either rare (by removing species recorded only once within the dataset) or highly abundant species (by square-root transformation of all abundances) following Struebig *et al.* (2013). Non-parametric permutations tests (ADONIS, in 'vegan') were used to examine compositional differences between habitat types. We also investigated which species were most associated with particular habitat types using the indicator species analysis INDVAL in PC-ORD (Dufrene & Legandre, 1997).

GLMs were used to determine whether species richness was driven by our potential environmental predictors (river channel width, riparian reserve width, landscape-scale forest cover and above-ground carbon density) at our 20 riparian sites. We selected Gaussian family models, as this best reflected the probability distribution of species richness. All predictor variables were tested for collinearity. As ruggedness and altitude were correlated ($r > 0.18$), ruggedness was retained in the riparian reserve models, because the range of values was greater than for altitude, and altitude was retained in the other models for the same reason.

To examine the influence of the environmental predictors on species composition, we constructed generalised linear mixed effects models (GLMMs) for our two NMDS axes for all habitat types. Habitat type was included as a random variable. Oil palm river communities were excluded from these analyses as species composition was very different from that in other habitat types and this signal obscured any other potential patterns of interest. Parameters were model-averaged across all models within ΔAIC<4 of the best model. The modelling process was repeated for forest-dependent species and species of conservation concern separately.

Results

Species abundance and richness

Across the 28 sites, we detected 8784 individual birds (6104 encounters), of 202 species, including 133 forest-dependent species (3838 encounters, 4939 individuals) and 62 (821 encounters, 1094 individuals) species of conservation concern. Our species accumulation curves approached an asymptote for both site and habitat type, confirming that we had sampled the avifauna well enough to assess differences in richness and community structure between them (Fig. S2.1).

Birds were more abundant in riparian reserves than riparian forest controls and oil palm rivers, but similar to those in non-riparian forest controls (Fig. 2.2a). Riparian reserves supported similar levels of bird species richness to riparian forest controls, and double that recorded in oil palm rivers (Fig. 2.2b).

Forest-dependent species accounted for 65% of all individuals across the whole community, and were significantly more prevalent in both non-riparian and riparian forest controls than in riparian reserves or oil palm rivers (70% in CF; 74% in RFC; 54% in RR; 20% in OPR; Fig. 2.2c). Forest-dependent species richness was highest in both forest control types and significantly lower in oil palm rivers (Fig. 2.2d).

Species of conservation concern comprised 13% of all individuals across the landscape, and formed a larger component of the bird community in riparian (18%) and non-riparian forest controls (16%), compared to those in riparian reserves (11%) and oil palm rivers (2%). There was no significant difference in the number of species of conservation concern found in riparian reserves and riparian forest control sites in terms of either abundance or richness (Fig. 2.2 f, g).

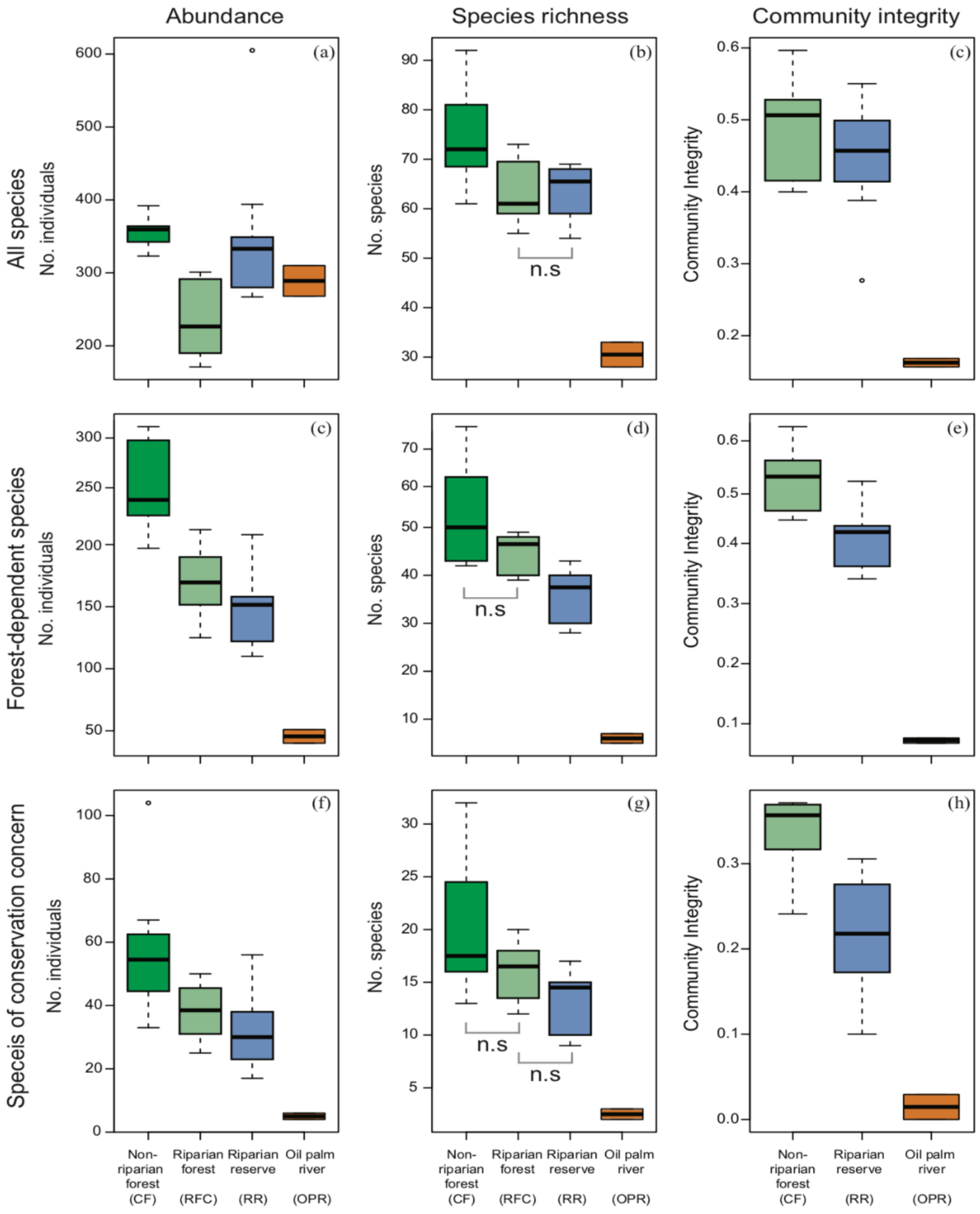

Figure 2.2. Boxplots showing median and inter-quartile values of site-level bird abundance and species richness. Abundance and richness shown across the different habitat types for: all species; forest-dependent species; and species of conservation

concern. General linear model derived linear hypothesis Tukey tests revealed significant differences in richess (*P*<0.05) between all habitat types except for those cases marked non-significant (n.s).

Species richness was not influenced by spatial autcorrelation (Moran's I test; observed = -0.04, *P*=0.80 of GLM residuals for model including habitat type, above-ground carbon density and reserve width).

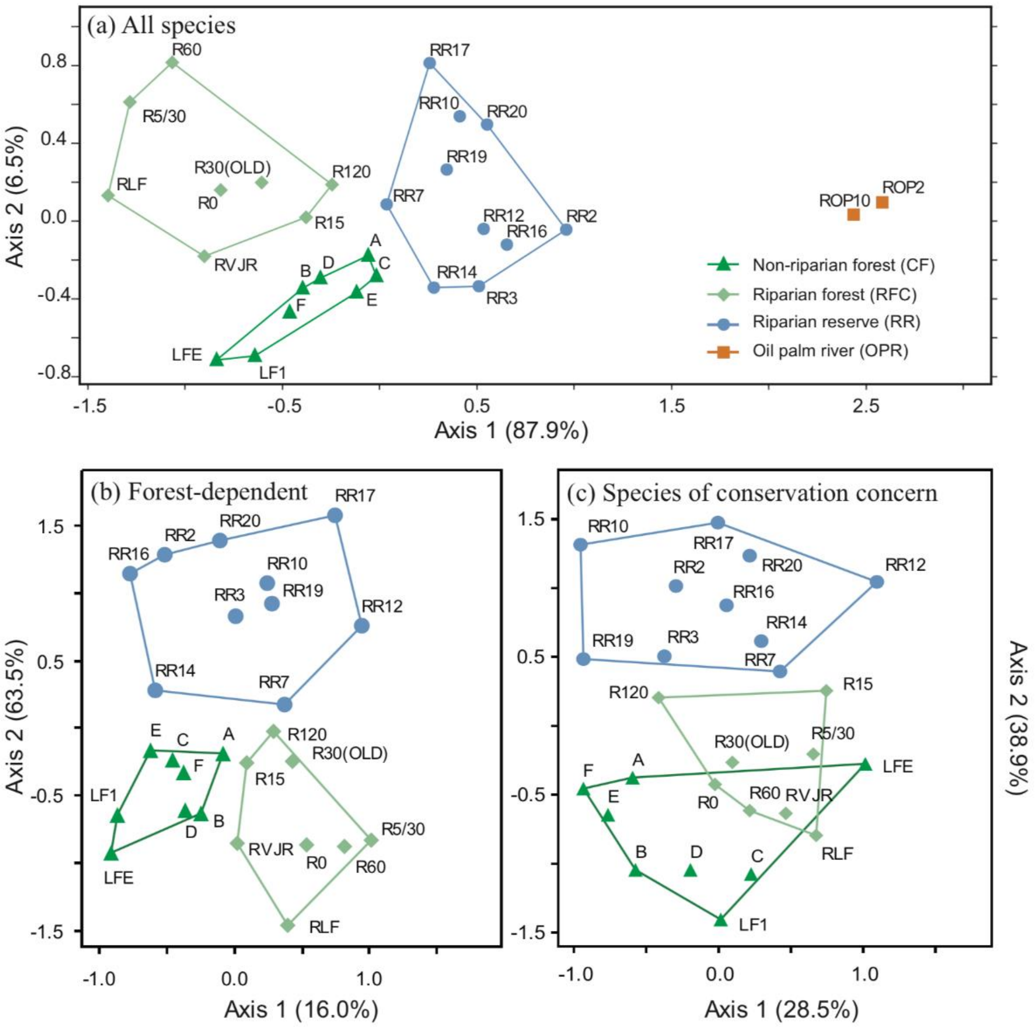

Figure 2.3. Nonmetric multidimensional scaling ordinations of bird community structure. Riparian and non-riparian habitat types are shown. Plots show dissimilarity across (a) all species; (b) forest-dependent species; and (c) species of conservation concern. Oil palm river sites were excluded from (b) and (c) because they included only seven forest-dependent species and three species of conservation concern, and therefore could not be plotted within the same ordination space. Axis scores denote R^2 values. Names for each site are displayed and correspond to those listed in Fig 2.1.

Bird community composition

Our NMDS ordination of community composition performed better than those based on randomised data (Monte Carlo test: observed stress=12.4; simulated stress=28.7; *P*=0.004; Fig. 2.3a), and showed four clear habitat groupings. The most divergent were the oil palm rivers, which supported an almost entirely different bird community to other sites. Communities in riparian reserves were more similar to those in riparian and non-riparian controls, but still distinct from both habitat types in terms of species composition. Since the oil palm rivers had such a strong influence on the landscape-wide ordination, we removed them in our subsequent analyses to better discriminate between the remaining habitat types. Our subsequent NMDS represented 89% of the variation in bird community structure (stress=14.8). None of the models were improved significantly after removal of singletons and square-root transformation of species abundance; as indicated by an increase in stress (16.35).

Species composition was significantly different across all four habitat types (ADONIS: R^2=0.11, *P*=0.01). The same pattern was evident when restricted to just forest-dependent species and species of conservation concern (Fig. 2.3; forest-dependent species: R^2=0.13 *P*=0.01; species of conservation concern: R^2=0.14, *P*=0.01).

Community integrity in riparian sites showed similar patterns to our ordinations, in that riparian reserves were intermediate to riparian forest controls and oil palm rivers (Fig. 2.2c, e, h).

Indicator species analysis revealed 13 significant associations between particular bird species and habitat types, including four species associated with non-riparian forest controls, seven of oil palm rivers, and one each for riparian reserves and the riparian forest controls (Table S2.2).

Environmental predictors of riparian reserve communities

Our GLMMs demonstrated that riparian reserve width was an important predictor of bird species richness and avian community composition (Table 2.1; Fig. 2.4). Reserve width and above-ground carbon density affected bird richness in a consistent manner. None of the other environmental metrics we tested had demonstrable effect in our final models.

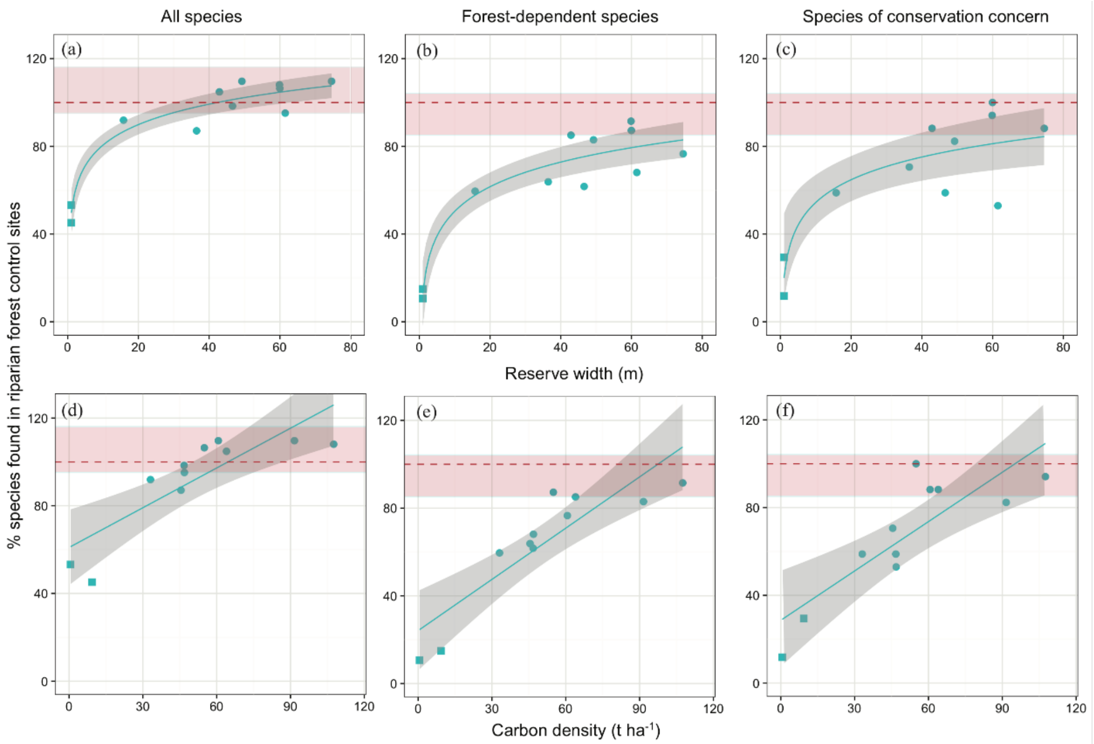

Figure 2.4. Observed species richness for riparian reserves and oil palm river sites. Circles denote riparian reserves and squares denote oil palm river sites in relation to reserve width (on each bank) for all species; forest-dependent species; and species of conservation concern (a,

b, c). Richness values are expressed as percentages of the median richness from the eight riparian forest control (RFC) sites. Observed species richness was also significantly positively associated with above-ground carbon density (d, e, f). Horizontal red shading demonstrates the first and third quartile in the distribution of species richness across all RFC contol sites, with median shown as the black dotted line. Grey shading around trend lines denotes 95% confidence intervals. One riparian reserve (RR17) was excluded from the models because of missing environmental data for the site.

Riparian reserve width, above-ground carbon density and forest cover were all significant positive predictors of observed species richness for the full community (Table 2.1). This pattern was the same for forest-dependent species, though did not apply to species of conservation concern. Across all riparian habitats, above-ground carbon was a significant positive predictor of species richness for both forest-dependent taxa and species of conservation concern. However, our final model for riparian habitats did not reveal any significant predictors across all species. Forest cover was an important predictor of community structure as reflected by the NMDS axis 1 for species of conservation concern. The second axes of our NMDS analyses exhibited no significant relationship with the environmental predictors.

Table 2.1. Outputs of generalised linear models (GLM) and generalised linear mixed effects models (GLMM). Model averaged parameter estimates, standard error and confidence intervals for important predictors of observed species richness and community structure are listed. The ΔAIC<4 model set was used to estimate averaged outputs. n represents the number

of sites included in each model. One riparian reserve (RR17) was excluded several environmental predictors were missing for this site.

Predictor	**Parameter estimate**	**SE**	**Lower 95% CI**	**Upper 95 % CI**
GLM: Richness in riparian reserves and oil palm rivers (RR, OPR, n=11)				
All species				
Intercept	63.8	1.1	61.2	66.4
Above-ground carbon density	6.1	2.2	0.9	11.3
Forest cover	8.3	2.3	2.9	13.8
Riparian reserve width	8.6	2.5	2.9	14.3
Forest-dependent species				
Intercept	36.7	1.3	33.6	39.8
Above-ground carbon density	6.6	2.6	0.5	127
Riparian reserve width	10.3	3.0	3.4	17.2
Forest cover	8.9	3.0	1.9	15.9
Species of conservation concern				
Intercept	13.4	0.9	11.4	15.4
GLM: Richness in riparian habitats (RR, OPR, RFC, n = 19)				
All species				
Intercept	59.6	2.5	54.3	64.9
Forest-dependent species				
Intercept	36.1	2.0	31.9	40.3
Above-ground carbon density	156.0	5.3	5.0	27.0
Species of conservation concern				

Intercept	13.3	0.8	11.6	15.0
Above-ground carbon density	5.2	2.6	1.8	10.0
GLMM: Community structure (NMDS axis 1) in all forest or riparian reserve (RR, RFC, CF, n = 26)				
All species				
Intercept	0.0	0.0	-0.1	0.0
Above-ground carbon density	-0.2	0.1	-0.3	-0.1
Forest cover	-0.4	0.1	-0.5	-0.3
Forest-dependent species				
Intercept	0.1	0.4	-0.7	0.9
Species of Conservation Concern				
Intercept	-0.0	0.1	-0.2	0.1
Forest cover	-1.1	0.2	-1.6	-0.7

Community subsets for all species, forest-dependent species and species of conservation concern differed in the reserve width at which richness was equal to that found in riparian forest controls (Fig. 2.4). Trend lines intersected mean richness levels for riparian controls at ca. 40 m when all species were examined. However, for forest-dependent taxa and species of conservation concern, riparian reserves did not reach equivalent richness levels to that found at control sites. The extent of this pattern with above-ground carbon density also varied between community subsets (Fig. 2.4d, e, f). Notably, reserve richness reached equivalent levels to control sites at around 65 tC ha-1 for all species, but at around 100 tC ha-1 for forest- dependent and species of conservation concern subsets.

Discussion

We found that riparian reserves in oil palm, supported comparable levels of bird diversity to sites in continuous forest (both CF and RFC), especially when reserves are wide and comprise high carbon forest. However, these reserves contained fewer forest-dependent taxa and species of conservation concern, which likely require larger tracts of continuous forest for long-term population viability. These results suggest that the mandated reserve width in many tropical countries should be increased. In tandem, forest quality in riparian reserves should be improved: in new plantations by delineating reserves prior to clearance and preventing additional logging within them; in existing heavily degraded reserves via vine cutting and planting with native trees, plus by replanting in areas where crops were planted to river banks and no riparian reserves retained. Our appraisals of forest-dependent taxa and species of conservation concern also demonstrate that not all species are well represented in riparian reserves and it is likely that these taxa require larger tracts of continuous forest for long-term population viability.

Despite a growing number of ecological studies on tropical riparian reserves, there is still little information regarding which features have the greatest benefit for biodiversity (Luke *et al*., 2018.). For birds in oil palm, we find that riparian reserve width is an important predictor of overall number of species, with reserves at least 40 m wide (i.e., 80 m total width) supporting comparable numbers of species to riparian forest controls. Nonetheless, to support equivalent numbers of forest-dependent taxa and species of conservation concern, riparian reserves would need to be much larger - at least 100 m wide (200 m total width), based on extrapolation of observed trend lines (Fig. 2.4b, c). We can only extrapolate, as large riparian reserves are scarce in our study system and oil palm landscapes in general. It therefore remains to be seen whether all forest-dependent taxa and species of conservation concern present in logged forest would actually use riparian reserves even if they were of substantial width and close to continuous forest.

Uniquely for oil palm landscapes, our results demonstrate the influence of forest quality (as measured by above-ground carbon density), as well as reserve width, on the riparian reserve avifauna. These finding suggests that protecting reserves of poor forest quality will offer few conservation gains without habitat restoration. Similar findings have been reported from cattle ranching areas in Amazonia, where riparian reserve width and percentage canopy cover were both positively related to bird and mammal richness (Lees & Peres, 2008; Zimbres *et al*. 2017). This result implies that approaches to restore biodiversity in agricultural areas may be less successful than sparing areas for conversion in the first place, especially because small forest patches, such as riparian reserves, are susceptible to further degradation via edge effects (Laurance *et al*. 2018). Disentangling this relationship is difficult, however, as both larger fragments and reserves tend to be of higher forest quality than smaller ones (e.g. Lees and Peres 2008).

Many previous studies have only compared riparian reserves with the communities of continuous non-riparian forest controls (e.g. Gray *et al*., 2014). We show that, while overall richness remains comparable to non-riparian control sites in continuous forest, bird community composition in riparian reserves is intermediate between that of riparian controls (RFC) and oil palm rivers (OPR) (Fig. 2.2, 2.3). While there were many species shared between riparian reserves and riparian forest habitat, reserves also had some generalist species (e.g *Spilopelia chinensis* [spotted dove], *Geopelia striata,* [zebra dove] *Copsychus saularis,* [oriental magpie robin] and *Pycnonotus analis* sunda [yellow-vented bulbul]) that were rare or absent in both riparian and non-riparian forests controls (i.e. CF and RFC). These matrix-dwelling species are known to be abundant in both industrial oil palm plantations (Edwards *et al*. 2010) and mixed smallholder cultivation (Azhar *et al*. 2011). Riparian reserves also lacked several forest-dependent taxa and species of conservation concern, in accordance with previous studies, which found small forest fragments to support few specialist species (Laurance *et al*. 2018). Across all riparian reserves, we recorded over 70% of the community found in non-riparian forest and over 80% (Fig. S2.1) of the community found in riparian forest control areas. However, the highly different community composition (Fig. 2.3) and lower site-level species richness (Fig. 2.2) suggests that such forest species are found in greatly reduced numbers in riparian reserves.

We found that bird communities around oil palm rivers without a reserve were highly depauperate, consistent with species richness observed in previous oil palm studies (Edwards *et al*. 2010; Azhar *et al*. 2011). Thus, the presence of rivers *per se* appears to have little effect on bird diversity in the absence of significant amounts of natural vegetation. This stark difference was clear even for sites with degraded reserves, highlighting that narrow, low quality riparian reserves can still have a significant positive effect on bird community structure albeit a small one. Crucially, narrow and degraded reserves still held more forest-dependent taxa and species of conservation concern than oil palm on its own, although at much lower numbers than in large riparian forest areas.

It is possible that species recorded in riparian habitats are not part of a viable population and that the reserves are sinks (Gilroy & Edwards, 2017). For example, Weldon & Haddad (2005) demonstrated that indigo buntings (*Passerina cyanea*) in small fragments continued to nest in patches with greater forest edge despite increased mortality. Likewise, small fragmented areas of habitat are far more susceptible to further perturbations and edge effects than large continuous forests (Ewers *et al*. 2007), which can result in extinction cascades long after fragmentation has taken place (Kitzes and Hartle, 2015). Alternatively, riparian reserves could act as movement corridors between larger, higher quality, areas of forest. In the context of landuse change, facilitating species dispersal in this way could be vital in maintaining viable populations in otherwise isolated remnant habitat fragments (Capon *et al*. 2013), particularly for interior forest bird species (Gillies & St. Clair, 2008).

Riparian forest in both riparian controls and riparian reserves held distinct bird communities to other sites. For instance, *Butorides striatus* and *Alcedo meninting* were only recorded in riparian habitats, while *Enicurus ruficapillus*, a species of conservation concern (near-threatened), was identified as an indicator of riparian forest controls (Table S2.2). Microclimate, vegetation structure and prey abundance have been found to differ between riparian and non-riparian habitats in Hong Kong, and these changes correlated with differences in bird species richness and abundance (Chan *et al.* 2008). This emphasises the value of including a riparian forest as a comparator, rather than just non-riparian continuous forest. It also demonstrates that spatial turnover in species composition between riparian and non-riparian sites is greater than that within just one habitat type, indicating that riparian areas have an additional effect on regional species richness (Sabo *et al.* 2005).

Management recommendations

Our results warrant several recommendations for the improved management of riparian reserves in the tropics. These are not mutually exclusive, but each would have different outcomes for bird communities if adopted. First, increasing minimum reserve widths to at least 40 m on each bank would improve bird diversity to levels typical of riparian areas in large forest blocks. In tandem with the vine cutting and replanting of native tree species, this could also benefit forest-dependent species, since reserve width showed a stronger relationship with forest species richness than it did for overall community richness.

Second, the greatest gains in species richness for the smallest loss of cultivated area could be achieved by replanting vegetation in reserves narrower than 30 m to meet existing legislative guidelines. This is because the relationship between reserve width and species richness is non-linear, with the greatest gains in richness occurring at small widths. However, this would only maximise species richness at the level of individual rivers, whereas effects on landscape-scale richness and the benefit to forest-dependent species would be less significant.

Finally, the biodiversity protection of any future riparian reserves could be greatly improved by increasing the quality of reserve habitat. This is not just achieved by restoring degraded habitat in existing plantations, but also by ensuring that contractors follow environmental regulations while forests are being converted. In countries such as Malaysia, these restrictions already exist for conventional logging operations (Forest Enactment for Sabah, 1968). However, narrow riparian reserves are difficult to define and map prior to clearance and may endure opportunistic removal of valuable timber as a result. Once land has been re-designated after logging for plantation, this can result in riparian reserves of substandard forest quality. By improving the enforcement of riparian reserve policy prior to and during conversion operations, riparian areas of higher forest quality could be maintained. This is likely to not only benefit threatened biodiversity, but could also have knock on benefits to other wildlife, hydrological regimes, and water quality downstream.

Supplemental Materials

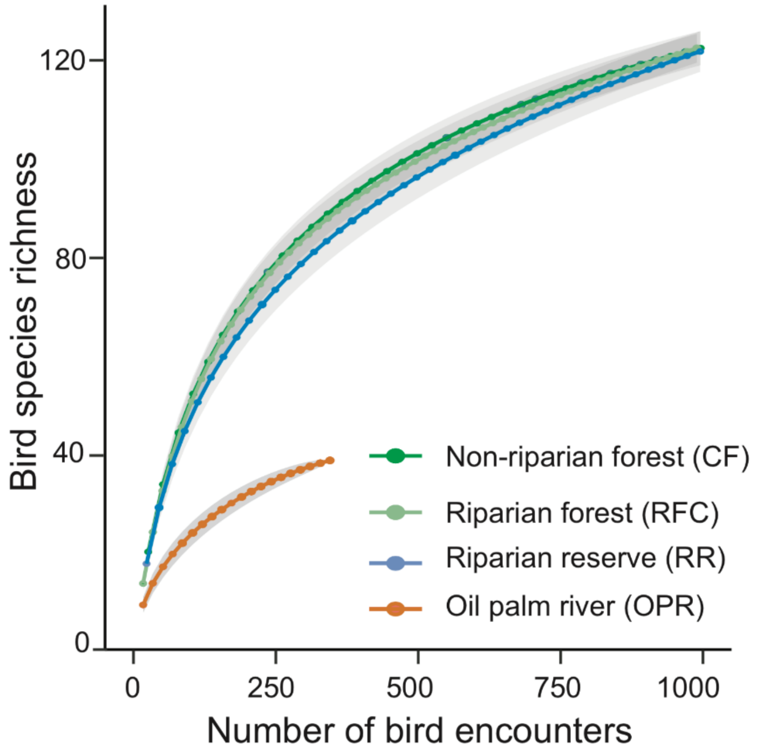

Figure S 2.1. Rarefied bird species accumulation curves for each riparian and control habitatAccumulations for each type based on 100 iterations. Grey buffers denote one 95% confidence intervals either side of mean richness values.

Table S 2.1. Sampling dates and mean intervals for each site.

Habitat	Site	Visit 1	Visit 2	Visit 3
CF	A	09/05/2014	07/07/2014	04/08/2015
CF	B	15/05/2014	05/06/2014	03/03/2015
CF	C	29/04/2014	30/06/2014	16/05/2015
CF	D	07/05/2014	10/06/2014	10/03/2015
CF	E	17/05/2014	12/06/2014	25/06/2015
CF	F	23/05/2014	06/07/2014	23/06/2015
CF	LF1	05/03/2015	24/07/2015	25/07/2015
CF	LFE	15/07/2015	16/08/2015	25/08/2015
RCF	R0	26/05/2014	10/02/2015	19/02/2015
RCF	R120	28/05/2014	17/02/2015	26/02/2015
RCF	R15	21/05/2014	13/02/2015	24/02/2015
RCF	R30(OLD)	06/06/2014	18/02/2015	27/02/2015
RCF	R5/30	27/05/2014	11/02/2015	20/02/2015
RCF	R60	19/05/2014	14/02/2015	23/02/2015
RCF	RLF	01/05/2014	12/02/2015	22/02/2015
RCF	VJR	30/07/2015	11/07/2015	06/08/2015
RR	RR10	29/10/2016	14/11/2016	15/11/2016
RR	RR12	14/07/2015	28/07/2015	03/08/2015
RR	RR14	27/06/2015	30/06/2015	27/07/2015
RR	RR16	28/06/2015	10/07/2015	07/08/2015
RR	RR17	21/11/2016	23/11/2016	24/11/2016
RR	RR19	20/11/2016	05/12/2016	05/12/2016

RR	RR2	22/07/2016	23/07/2016	19/11/2016
RR	RR20	28/11/2016	30/11/2016	02/12/2016
RR	RR3	19/07/2016	20/07/2016	21/07/2016
RR	RR7	06/06/2014	24/05/2015	24/06/2015
OPR	ROP10	27/11/2016	29/11/2016	30/11/2016
OPR	ROP2	16/11/2016	17/11/2016	18/11/2016

Table S 2.2 . Indicator species for each of four different habitat types.Thirteen indicator bird species showing significant associations ($p<0.05$) with different habitat types (continuous forest, CF; logged forest riparian, LFR; riparian reserves, RR; oil palm riparian controls, OPR), according to the INDVAL algorithm (Dufrene & Legrandre, 1997). Relationships with non-metric multidimensional scaling axes (Axis 1=A1, Axis 2=A2) for each species are shown as R^2 and Tau correlation coefficients.

Species	**Habitat**	**IV**	**Mean**	**SD**	**A1 R^2**	**A1 Tau**	**A2 R2**	**A2 Tau**
Malacopteron magnirostre	CF	61.4	29.1	10.43	0.242	-0.48	0.32	-0.46
Pycnonotus simplex	CF	54.7	29.4	9.65	0.015	-0.03	0.31	-0.43
Copsychus pyrropygus	CF	50	20.6	12.46	0.774	0.69	0.003	-0.04
Phaenicophaeus diardi	CF	43.1	21.5	11.66	0.028	-0.15	0.3	-0.44
Enicurus ruficapillus	LFR	61.6	25.1	12.08	0.212	-0.46	0	0.06
Pelargopsis capensis	RR	40	20.7	12.12	0.017	0.22	0.1	0.22
Geopelia striata	OPR	100	16.3	12.43	0.503	0.36	0	0.08
Cinnyris ornatus	OPR	88.9	18.9	13.02	0.279	0.21	0	0.14
Lonchura fuscans	OPR	70.6	27.8	12.99	0.358	0.47	0	-0.14
Egretta garzetta	OPR	41.7	18.8	12.23	0.303	0.37	0.02	0.14
Actitis hypoleucos	OPR	45.5	16.2	12.28	0.252	0.28	0.02	0.16
Chrysocolaptes validus	OPR	46.9	16.7	11.82	0.28	0.3	0.01	0.15
Centropus bengalensis	OPR	40.8	18.9	12.12	0.21	0.26	0.01	0.076

Acknowledgements

This study was funded by the UK Natural Environment Research Council (NERC) (NE/K016407/1; http://lombok.hmtf.info/ and http://bali.hmtf.info; NE/K016377/1), and a Newton-Ungku Omar Fund grant from the British Council and Malaysia Industry-Group for High Technology (MIGHT) (216433953). SLM was supported by a PhD scholarship jointly funded by University of Kent and NERC. We thank the Sabah Biodiversity Council, Sabah Forest Department, Yayasan Sabah, Sime Darby, Benta Wawasan, Sabah Softwoods and Innoprise Foundation for permitting site access. We are grateful to Unding Jami and the LOMBOK research assistant team for their field assistance, and Suzan Benedick, Joseph Tobias and Ryan Gray for facilitating fieldwork.

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Chapter 3. Species traits predict thresholds of nonlinear response to forest change

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Abstract

In the context of rapid environmental change it is import to understand how state-shifts in ecosystems manifest via changes to ecological communities at the species and functional levels. Assessing these patterns may be particularly useful for predicting abrupt thesholds or 'tipping points' in ecological responses after which ecosystems are more vulnerabale to collapse. Here, we assess the responses of 171 tropical birds species to environmental changes associated with forest degradation by applying occupancy modelling to field ornithological data, together with habitat structure information from hyper-spectral LiDAR. Across a land-cover gradient of intact forest to oil palm plantations, we demonstrate that the majority of species respond to habitat degradation in a non-linear fashion. These abrupt responses in species occupancy scale up to abrupt changes to the composition of trait groups associated with ecosystem functions such as pollination, seed dispersal and insectivory. We show that disturbance responses at the trait-group level do not necessarily follow threshold levels of all component species, since many species have idiosyncratic responses. Nonetheless, several trait groups exhibit markedly differing threshold levels from one another, for example the frugivores and nectarivores responded more strongly until canopy height reached 10 – 18 m, whereas both terrestrial and sallying insectivores continued to respond strongly until canopy height reach ~24 m. This suggests that, just as trait-based approaches have proven useful in generalising overall effects in a linear framework, they offer a potentially useful way of generalising non-linear response thresholds and that traditional analyses have masked important species-specific and trait-group responses. These responses demonstrate that passing particular thesholds could result in disproportionate losses of

biodiversity in human-modified tropical landscapes Our findings suggest that the use of non-linear response models offer a framework to reduce false-negative errors in detecting species responses, optimise indicator species used for particular trait groups and understanding fine-scale habitat assocations, especially for highly specialised species.

Introduction

Global environmental changes are causing mass species extinctions (Ceballos *et al.*, 2015) and increasing the vulnerability of ecosystems to collapse (Scheffer *et al.*, 2001; Cardinale *et al.*, 2012). In terrestrial ecosystems, the leading cause of these processes is direct anthropogenic modification of vegetation through landuse change, including habitat conversion, degradation and fragmentation (Ellis, 2011; Newbold *et al.*, 2015). An extensive literature has established links between shifts in ecological communities and landuse change (Gerstner *et al.*, 2014), forest degradation (Gibson *et al.*, 2011) and habitat configuration (Haddad *et al.*, 2015), with many species being reduced in abundance as a consequence of these activities (Phalan, 2011), but a few increasing significantly (Deviktor *et al.*, 2008). Given the enormous global impacts that habitat alterations can have on biodiversity and the functions and services that biodiversity provides, further scrutiny of how land-cover change processes influence species is paramount to conservation.

Functional ecology frameworks allow predictions about how whole groups of species shift by measuring associations between species ecological traits and their responses to environmental change. For example, poorer dispersal capability and larger body size predict range contraction in butterflies (Mattila *et al.*, 2011), and life-history strategies associated with greater specialisation predict greater sensitivity to landuse change for dung-beetles (Barragán *et al.*, 2011), and birds (Newbold *et al.*, 2013), as well as increased extinction risk in birds (Sekercioglu *et al.*, 2007), terrestrial mammals (Davidson *et al.*, 2009), and bats (Jones *et al.*, 2003). Traits have also been shown to mediate the effects of particular drivers of decline, such those induced by the novel the Chytridiomycosis pathogen in amphibians (Murray *et al.*, 2010), or by climate change in amphibians, reptiles (Pearson *et al.*, 2014) and birds (Pacifici *et al.*, 2017). Trait-based approaches are also useful in predicting patterns of ecosystem function (Lavorel & Garnier, 2002). However, to date, trait-based approaches have focussed predominantly on simple linear associations between trait and response (e.g Williams *et al.*, 2010; but see Sasaki *et al.*, 2011) or upon changes in overall functional diversity, which is assessed based on the overall diversity and representation of multiple traits within a community (Magioli *et al.*, 2014). To fully understand the responses of different trait groups, assessments need to take account of both the variation of responses between member species of particular trait groups, and the potential for those responses to be non-linear.

Relationships between changes in environment and subsequent responses of communities and ecosystems are frequently non-linear (Groffman *et al.*, 2006; Andersen *et al.*, 2009). The associated inflection points may constitute critical thresholds beyond which more abrupt, often irrevocable, changes can occur (Scheffer *et al.*, 2001). Such ‘state shifts’ can occur at the ecosystem, community and species levels. For example, sudden transitions between tropical forest and savannah ecosystems, are associated with small changes in precipitation (Hirota *et al.*, 2011); abrupt changes in community-level responses to habitat loss for bats (Muylaert *et al.*, 2016), reptiles (Lindenmayer *et al.*, 2005), amphibians (Riley *et al.*, 2005), mammals

(Silva *et al.*, 2005) and birds (Martensen *et al.*, 2012); and some bird temperate species exhibit thresholds in their response to habitat loss (Radford & Bennet 2004; Betts *et al*. 2007). However, these studies focus either on a few detailed species responses, or in patterns of overall richness. As yet, no assessments have been made that demonstrate the relative contribution of each species response to producing non-linear patterns at the level of the whole community.

Identifying such thresholds in ecological processes and ecosystem responses could have profound implications for the ways the environment is managed. In the context of the global biosphere, exceeding dangerous thresholds may in fact present an existential threat to human civilisation (Rockstrom *et al*., 2009). Furthermore, ecosystems and functions may become difficult or impossible to restore once certain thresholds are crossed (e.g. Carpenter *et al*., 1999). Applying information from thresholds in diversity responses to landscape change has useful applications for conservation planning, as demonstrated for Atlantic forest birds (Banks-Leite *et al*., 2014). However, examining species numbers alone misses important information on ecological processes that tend to manifest at lower hierarchical levels, building from individuals, to species, to communities, to ecosystem processes (DeAngelis 2018). The extent of, and way in which, thresholds in ecological responses scale between these different levels is poorly understood. Understanding non-linear responses at the levels of species, guilds and communities is therefore a vital underpinning of our ability to recognise how species can be maintained at the levels of landscapes to global ecosystems.

There are a number of impediments faced in assessing how species response thresholds scale to functional groups and community richness. Compared to traditional assessments that simply seek to demonstrate the existence and direction of species responses to environmental change, identifying thresholds in these responses requires far larger datasets of a high resolution for each species as well as relevant environmental metrics. Statistical approaches to address this have been proposed (Baker & King, 2010), but remain contentious (Cuffney & Qian, 2013). Occupancy modelling approaches may help overcome data limitations concerning rarer species by controlling for imperfect detection. However, occupancy approaches have been used in very few threshold studies to date (e.g. Betts *et al*., 2010). Traditional remote sensing techniques can expedite the gathering of large datasets on landscape-scale environmental gradients, but in the past have generally been limited to fairly rudimentary two-dimensional landscape-scale measurements. Landscape metrics have been used in the majority of community threshold studies thus far, resulting in a clear emphasis upon responses to landscape configuration and habitat loss within the literature (Melo *et al*., 2018).

Despite the focus on landscape-scale factors, abrupt declines in species richness have also been documented with small increases in habitat disturbance intensity for dung beetles (Franca *et al*., 2017), and in response to changes in nutrient levels and turbidity for aquatic invertebrates (e.g. Evans-White *et al*., 2008), suggesting similar non-linear responses to fine-scale habitat characteristics and structural properties also exist. To better examine tipping points in relation to the structural properties of tropical forests, utilising data from remote-sensed Light Detection and Ranging (LiDAR) offers a promising way forward. Hyper-spectral LiDAR provides the ability to map the fine-scale structure of vegetation in three dimensions and so offers the potential to analyse patterns of faunal distribution and association which were previously unachievable.

Here, we couple occupancy modelling across multiple species with data derived from high resolution LiDAR to examine thresholds in the effects of 3D structure and landscape metrics associated with tropical forest degradation. Where previous studies have focused on single species (Garabedian *et al.*, 2017), we assess thresholds in response at the level of species, trait-groups and entire communities simultaneously. Using a large dataset (n = 1404 point counts) of bird observations as an established indicator taxon (Gardner *et al.*, 2008), we are able to trace how abrupt responses of individual taxa contribute to thresholds among trait groups, ensembles and the community at large. We explore whether each species responses is better predicted with or without a threshold included in the model. The responses of species with shared traits to environmental gradients are often similar, as trait-group members respond similarly to a single underlying mechanism, such as the availability of a particular niche (e.g. Williams *et al.*, 2010). This suggests that species with shared traits will not only demonstrate similar responses to environmental changes, but that where these responses are non-linear, they also exhibit similar threshold levels.

Materials and methods

Study system

Between 2010 and 2017, we sampled bird communities via repeated point counts at 356 localities across a gradient of habitat degradation in the dipterocarp forests of Sabah, Borneo (Fig. 3.1). Old growth forest was sampled at 47 point count localities across three landscapes at Sepilok Forest Reserve (19 localities), Danum Valley (20) and Maliau Basin (8). The majority of point count localities (309) were located around the Stability of Altered Forest Ecosystem (SAFE) project landscape. Of these, 38 were in continuous forest of the Ulu Segama Forest Reserve, which was logged twice since the 1970s, but now protected and recovering. The remaining 156 localities were in the neighbouring SAFE landscape in forest that had been logged several times since the 1970s and salvage-logged ahead of conversion to plantation. A further 115 localities comprised forest remnants within two large oil palm estates surrounding the SAFE project area. This provided respresentative sampling across the complete range of environmental variables we assessed. Sample sites were a minimum of 180 m apart, and grouped into transects of 8-16 point count locations (see Chapter 2; Mitchell *et al*., 2018; Fig. 2.1).

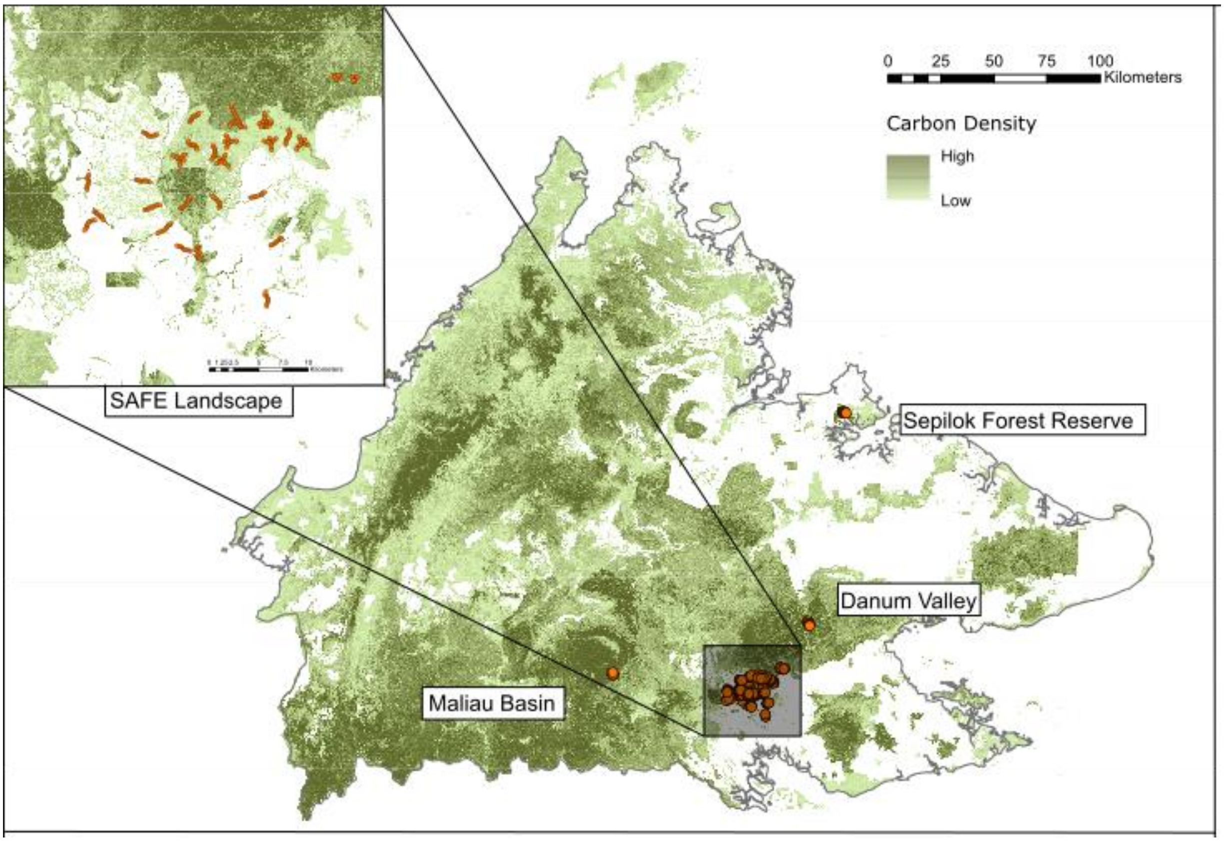

Figure 3.1. Map of Sabah showing four study landscapes. Forest cover is shown in a green. The darkest pixels represent the highest carbon densities (maximum: 303.98), and the palest areas associated with the lowest carbon forest (minimum: 0); plantation areas also are masked in white. Carbon density is derived from Asner *et al*., (2018). The SAFE landscape and surrounding area (inset) show the detailed configuration of points. Red dots indicate sampling locations.

Bird sampling

Each point count locality was sampled three to five times by a single experienced observer (SLM or DPE) who recorded all bird species seen or heard within a 50 m radius of a stationary position for 15 minutes, including fly-overs.

Counts were conducted between 05:50 and 11:00, on mornings without rain or high winds. The 50 m radius around the points comprised a range of habitat types, including both entirely and partly forested habitat, oil palm plantations, rivers channels, bare ground and early regenerating tropical scrub. Counts were recorded and a random sub-sample of recordings later re-checked to ensure species were not overlooked.

LiDAR-based forest structure and configuration predictors

Across all sites we generated five metrics from remotely-sensed data to quantify forest structure and configuration. Four measures were derived from LiDAR point clouds gathered in November 2014 using a Leica ALS50-II sensor (Jucker *et al.* 2018), and reflected mean values within a 50 m radius of each sampling locality. We quantified mean canopy height as well as the standard deviation in canopy height (as a measure of structural heterogeneity). To avoid multicollinearity with canopy height, we included plant area index per metre canopy height, giving an effective measure of vegetation density. We also quantified skewness of the vertical distribution of vegetation density. Finally, as a measure of landscape-scale habitat availability, we included the proportion of forest cover within 100 m radius of each point count, extracted from the forest cover layer produced by Gaveau *et al*., (2014), using the classification of multiple land cover data sources. There was no strong correlation between these five variables - Variance Inflation Factors in relation to canopy height were all below four (canopy heterogeneity, 1.32; plant area density, 1.23; skew, 1.22; forest cover, 1.11).

Occupancy modelling

To model avian responses to habitat degradation, we constructed multispecies hierarchical occupancy models. Community models are comprised of multiple single species occupancy-detection models that hierarchically partition the ecological and sampling processes underpinning the data to differentiate true absence from non-detection (Dorazio & Royle, 2005; Deere *et al.*, 2017). Single-species models were linked via an additional hierarchical component that modelled community-level regression coefficients from a common distribution with estimable hyper-parameters. Consequently, species responses are partially informed by the community average, which provides more robust parameter estimates for rare species that are infrequently detected during sampling (Pacifici *et al.*, 2014). This means that species have similar, but not identical, environmental responses across the community. To reduce model uncertainty, we excluded 35 species that were detected at fewer than three sites, as changes in occupancy and detection cannot be reliably uncoupled when detection data are this sparse, thus resulting in a total community of 171 species (Table S3.1, Supporting information). Whilst this results in the exclusion of the rarest species, community occupancy models necessarily involve a trade off between representing as many species as possible and excluding species for which there is insufficient data to make robust inferences. A further assumption is that variation in abundances do not effect species detection probabilities (Royle & Dorazio, 2008).

Our multispecies model controlled for the effects of date and time-of-day. We applied the R function ‘scale’ (R Core Team, 2014) to standardise our five predictor variables and two detection variables (using root-mean-squares) prior to analysis. This was undertaken to ensure that the influence of different variables upon a species occupancy could be properly compared. Occurrence probabilities were modelled for each species *i* at each point count site *j* via a logit link function:

$$Logit\left(\varphi_{i,j}\right) = \alpha_{i,s} + \beta 1_i \cdot \text{canopy height}_j + \beta 2_i \cdot \text{canopy heterogeneity}_j + \beta 3_i \cdot \text{skew}_j + \beta 4_i \cdot \text{density}_j + \beta 5_i \cdot \text{forest cover}_j$$

Our multispecies model was then fitted to an observation matrix $X_{i,j,k}$. This reflects the number of occasions on which each species *i* was detected at each site *j* on each visit *k* of the total number of visits (*K*). By specifying our observed data as the sum of *K* Bernoulli trials with detection probability $\theta_{i,j,k}$ we estimated true occurrences $z_{i,j}$ as follows:

$$X_{i,j,k} \sim \text{Bern}\ (\theta_{i,j,k} \cdot\ z_{i,j})$$

To account for greater detectability associated with higher avian activity around dawn, we modelled standardised time as influencing detection probability. Similarly, as our study took place across multiple seasons, we included standardised date as a parameter. This also allowed us to model occupancy without directly accounting for potential immigration and emigration of birds to/from sites. Detection probability was modelled for each species θ with a logit link function:

$$Logit\left(\theta_{i,j,k}\right) = \lambda_{i,s} + \beta 7_i \cdot time_{j,k} + \beta 8_i \cdot \text{date}_{j,k}$$

Using a Bayesian framework we specified three Markov chains per parameter, consisting of 120,000 iterations, with a burn-in of 30,000 iterations and thin rate of 10. We assigned diffuse uniform priors for hyper-parameter means and inverse-gamma priors for hyper-parameter variances (Dorazio *et al.* 2006) in order to provide an uninformative start point that made no assumption or use of *a priori* occupancy estimates. Our models were fitted using JAGS v4.3.0 (Plummer, 2017) and called in R with “rjags” (Plummer, 2013), using the wrap-around “jagsUI” (Kellner 2015). We confirmed convergence numerically by inspecting Bayesian P values and lack of fit statistics for each species.

We compared species occupancy probabilities to each of our five environmental variables. Effect sizes of each variable upon each species were assessed in the occupancy model. For community-level effect sizes we measured the community-level hyper-parameter for each metric, which is an averaged effect size informed by all species, weighted according to the number of times they were detected (i.e. abundant species contribute more than rare species).

Testing for thresholds in species response to forest structure and configuration

We identified thresholds in occupancy response to the environmental covariates using the R package ‘segmented’ (Muggeo, 2008), which identifies the point of maximum likelihood of a break in otherwise linear relationships. To test for breakpoints between each species occupancy response and each of our five predictor variables, we used 100 random draws of estimated occupancy probability for each species across all 356 sites. For every species i, we regressed each random draw m of all 356 sites against each of our five independent variables x. For each random draw, we used segmented logistic regression (Muggeo, 2003) to test for a single break point (threshold) φ where $(x-\varphi)_+ = (x-\varphi)_X I(x-\varphi)$. The intercept β_0, slope of left line β_1 and difference between the slopes β_2 were estimated through an iterative process of fitting following the equation:

$$\hat{p} = \exp\left(\frac{\beta_0 + \beta_1 x + \beta_2 (x - \varphi)_+}{1 + \exp(\beta_0 + \beta_1 x + \beta_2 (x - \varphi)_+)}\right)$$

For each draw *m*, we also obtained confidence intervals around the maximum likelihood estimate for each threshold φ, via linear approximation of the ratio of two random variables via the delta method (Muggeo 2003; Betts *et al*., 2003) and derived Akaike Information Criterion (AIC) values to measure the relative quality of each model. We repeated both these processes for 100 samples *M* of each species *i*. This provided us with mean thresholds, mean confidence intervals, and mean AIC of 100 samples for each species:

$$\bar{x}_i = \frac{\left(\hat{p} = \exp\left(\frac{\beta_0 + \beta_1 x + \beta_2 (x - \varphi)_+}{1 + \exp(\beta_0 + \beta_1 x + \beta_2 (x - \varphi)_+)}\right)\right)_m}{M}_i$$

For each sample *m* we also computed a linear regression, which calculated AIC. To determine whether our segmented model represented an improvement, we compared mean AIC of *M* samples between our linear and segmented models. Any species where AIC was not reduced by >4 was considered to be better represented by a model without a break point. Species which did not show thresholds were excluded from further analyses regarding the average level of thresholds (Fig. S3.6), but retained within analyses assessing cumulative trait-group responses (Fig. 3.2 - 3.5). We assumed only a single break-point for each species in order to allow for coherent summarising of threshold patterns to group level. To ascertain cumulative group response thresholds and confidence intervals (and trait group averages – see later), we performed a single segmented linear regression on all samples *M* of all species *I* within each trait group *t*. Since the initial value φ has the potential to influence the value of maximum likelihood of a break-point (Muggeo, 2003), we defined the initial value of

φ as the mean of each environmental metric. We compared this to break-point tests with φ taken via random draws from a uniform distribution of full environmental range, which made no discernible difference. Bayesian piecewise regression (Hutter 2005) could, in theory, be performed within the occupancy model itself. However, nesting a further iterative fitting process to an already computational intensive model was not feasible.

Species trait groups

To assess the responses and non-linear thresholds of different trait groups we employed two approaches. First, we aggregated both the effects and thresholds of all species which showed non-linear responses and estimated the median and quartile distributions for each group (Fig. S3.6). Separately, we added the responses of all species in each trait group (including those with linear responses) and calculated break-points in overall group responses (Fig. 3.2). We used three categories of species groups relating to feeding guilds as well as associations with habitat and vegetation strata. Each species was defined as a member of only one particular group within each category, ensuring maximum differentiation of group. We examined the thresholds associated with 18 ecologically relevant trait groups. Three groups comprised inventories of association with vertical strata following Chapman *et al*., (2017), but were edited with reference to del Hoyo *et al*., (2018) to make groups non-overlapping and reflect only primary associations. Habitat association comprised the same species lists defined for Borneo by Styring *et al*., (2007), whilst feeding guilds were those used by Sheldon *et al*. (2010) (Table S3.3; Supporting Information). These authors used additional trait groups which we also assessed, but we do not report averages or thresholds for groups with fewer than four member species.

Deriving group-level richness from occupancy models

For each site, we calculated the estimated richness of each trait group as the sum of the median occupancy probability from 1000 random draws of estimated occupancy probability for each species in the group. To assess whether the average thresholds of member species within each group, and thresholds for cumulative group richness were associated, we performed correlation tests in R. Thresholds in group richness were calculated using the R package ‘segmented’ (R Core Team, 2014) to assess their relationship to canopy height and forest cover. This followed the same methods as for individual species

Results

Effect sizes of occupancy responses to forest cover and structure

Community-average effects of environmental variables were largest for forest cover (0.379; C.I. 0.217-0.5434), followed by canopy height (0.293; C.I 0.117–0.477), vegetation density (0.174; C.I. 0.05-0.292) and skew (0.158, C.I. 0.054-0.260). Canopy heterogeneity showed no significant average effect across the whole community (0.068; C.I. -0.013-0.147). Of the 171 species included within our occupancy model, we found significant positive effects of forest cover on the occupancy of 36 species (i.e. 21% of the community more prevalent in forest), and significant negative effects for 16 species (9% less prevalent in forest; Fig S3.2).

Occupancy of 44 species (26%) responded positively to canopy height, while 14 (8%) responded negatively (Fig S3.1). Greater vegetation density led to increased occupancy of 20 species (12%), but reduced occupancy for two species (1%; Fig. S3.3), while 14 species were positively affected by canopy vegetation skewed towards greater height, while none responded negatively (Fig S3.4). Three species (2%) exhibited positive effects of canopy heterogeneity, whilst none showed a negative effect (Fig S3.5). Although effect sizes varied greatly between species, we did not detect clear differences between trait groups according to strata-association, feeding guilds or habitat-association (Fig. S3.6).

Group richness effects and thresholds

The effects of canopy height and forest cover on occupancy-derived richness varied between guilds, trait groups and habitat groups (Fig 3.2; Fig 3.3). Canopy height and forest cover had consistently positive effects upon richness for all trait-group, except in the case of *edge species*, for which richness was negatively associated with both.

Table 3.1. Threshold levels in trait group richness. Threshold given for each different strata-association groups, feeding guilds and habitat-association groups in relation to canopy height (within 50 m radius) and forest cover (within 100 m radius) with median (Med) and 95% lower (Lwr CI) and Upper (Upr CI) confidence intervals. ΔAIC values show the reduction in AIC from linear models to segmented models.

	Mean Canopy Height in 50 m radius	Proportion forest cover in 100 m radius

	Group	Med	Lwr CI	Upr CI	**Δ**AIC	Med	Lwr CI	Upr CI	**Δ**AIC
Strata	*Canopy*	9.75	7.05	12.46	12.26	0.84	0.72	0.95	4.66
	Understorey	25.61	21.70	29.52	21.03	0.62	0.53	0.71	49.23
	Ground	25.33	19.94	30.74	9.13	0.81	0.69	0.92	8.45
Feeding guilds	*Arboreal frugivore*	18.83	15.81	21.86	37.10	0.74	0.66	0.82	42.18
	Arboreal gleaning insectivore	22.71	19.23	26.20	22.52	0.78	0.63	0.94	5.51
	Arboreal gleaning Insect / frugivore	29.41	21.64	37.19	4.10	0.78	0.73	0.84	55.90
	Sallying insectivore	25.32	22.46	28.19	40.50	0.78	0.68	0.89	16.17
	Terrestrial insectivore	25.33	21.69	28.98	24.20	0.79	0.65	0.93	6.86
	Terrestrial insectivore. / frugivore	42.75	33.37	52.14	6.18	0.78	0.62	0.94	5.15
	Nectarivore / insectivore/ frugivore	10.08	8.209	11.96	20.85	0.79	0.66	0.91	10.58
	Insectivore / pescivore	35.45	29.39	41.51	17.67	0.74	0.68	0.81	56.05
	Raptor	9.94	9.125	10.76	94.50	0.09	0.07	0.11	243.2
Habitat associations	*Forest-specialist*	22.61	16.52	28.71	4.81	0.78	0.70	0.87	26.85
	Edge-tolerant forest	25.52	19.70	31.34	7.51	0.77	0.69	0.85	30.49
	Edge species	20.09	18.24	21.94	87.30	0.81	0.63	0.99	1.16
	Open species	31.78	26.40	37.16	16.69	0.89	0.79	0.99	2.11
	Generalist species	36.15	28.69	43.61	10.85	0.79	0.72	0.87	27.58

For canopy height and forest cover, trait groups demonstrated markedly different response thresholds in richness (Table 3.1). For example, thresholds in group richness differed between strata-association groups in relation to both canopy height and forest cover (Fig. 3.2). *Canopy* species had the lowest threshold with canopy height (median 9.75 m, C.I 7.05 m-12.46 m), followed by *Ground* species (25.33 m, C.I 19.94 m–30.74 m) and *Understorey* species (25.61 m, C.I 21.70 m-29.52 m). The change in the magnitude of response (i.e. the change in the steepness of the lines), was also markedly different. *Canopy* species went from a rate for increase of ~1 additional species per metre (spp./m) below the threshold to ~0.24 additional spp./m above the threshold, *Understorey* species ~0.25 spp./m below the threshold to ~0.03 spp./m above the threshold and *Ground* species went from ~0.25 spp./m below the threshold to ~0.09 spp./m above (Fig. 3.2). Richness thresholds of different guilds also varied in relation to canopy height (Fig. 3.3). However, group richness thresholds in relation to forest cover were consistently around 73-78% of forest cover for feeding guilds (with the exception of raptors; Table 3.1). Groups of species associated with different habitat types exhibited somewhat differing thresholds in response to canopy height, but either did not differ, or did not exhibit thresholds, in relation to forest cover (Table 3.1).

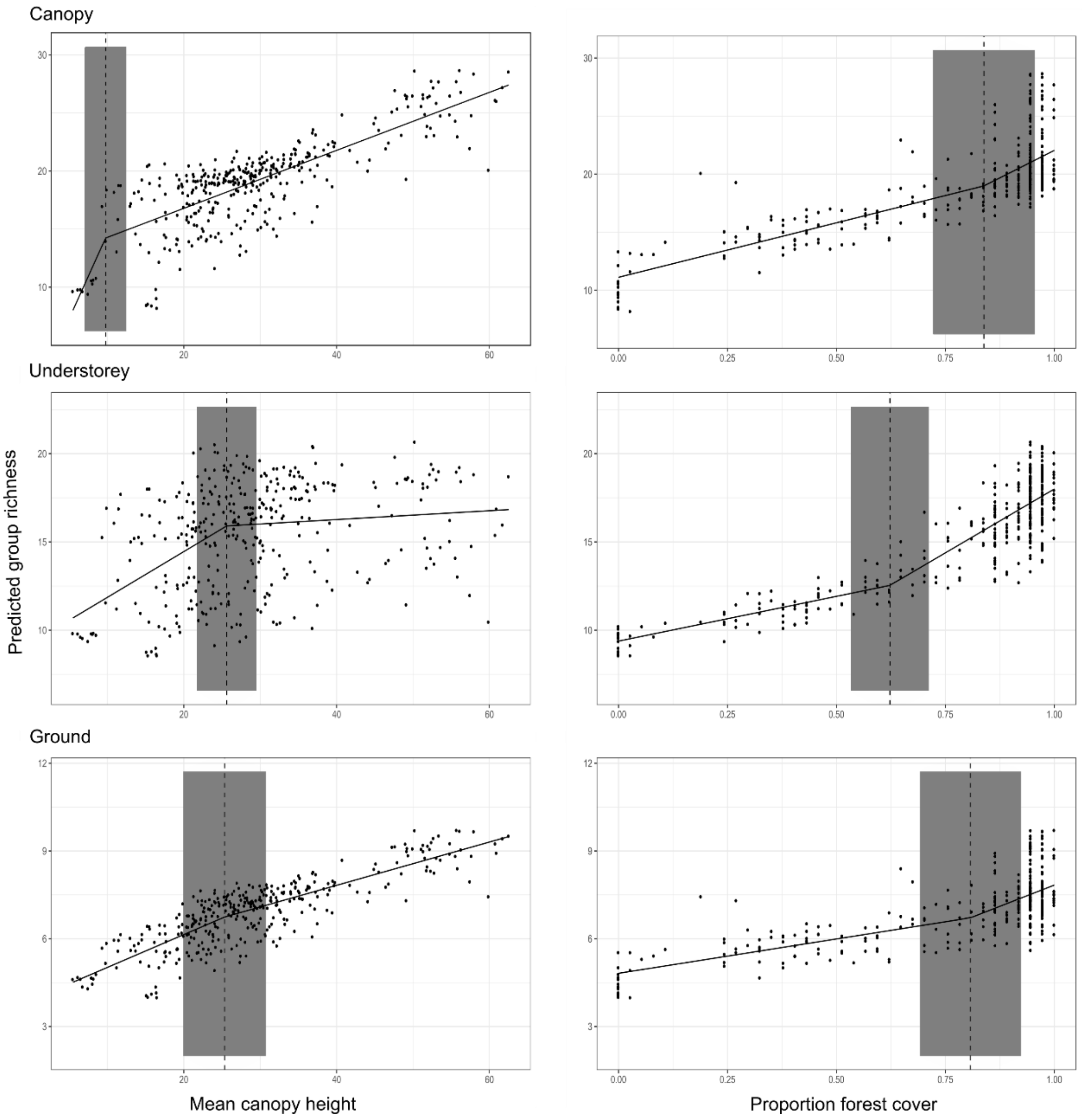

Figure 3.2. Species richness predicted by the segmented models for strata associations. Three different groupings of species are reported depending on strata associations and related to both mean canopy height and proportion of forest cover. Median occupancy values of each species are used. Thresholds displayed are calculated from median values, with confidence intervals (shaded) calculated by the segmented package in R. All segmented relationships are ΔAIC>4 improvement from linear models.

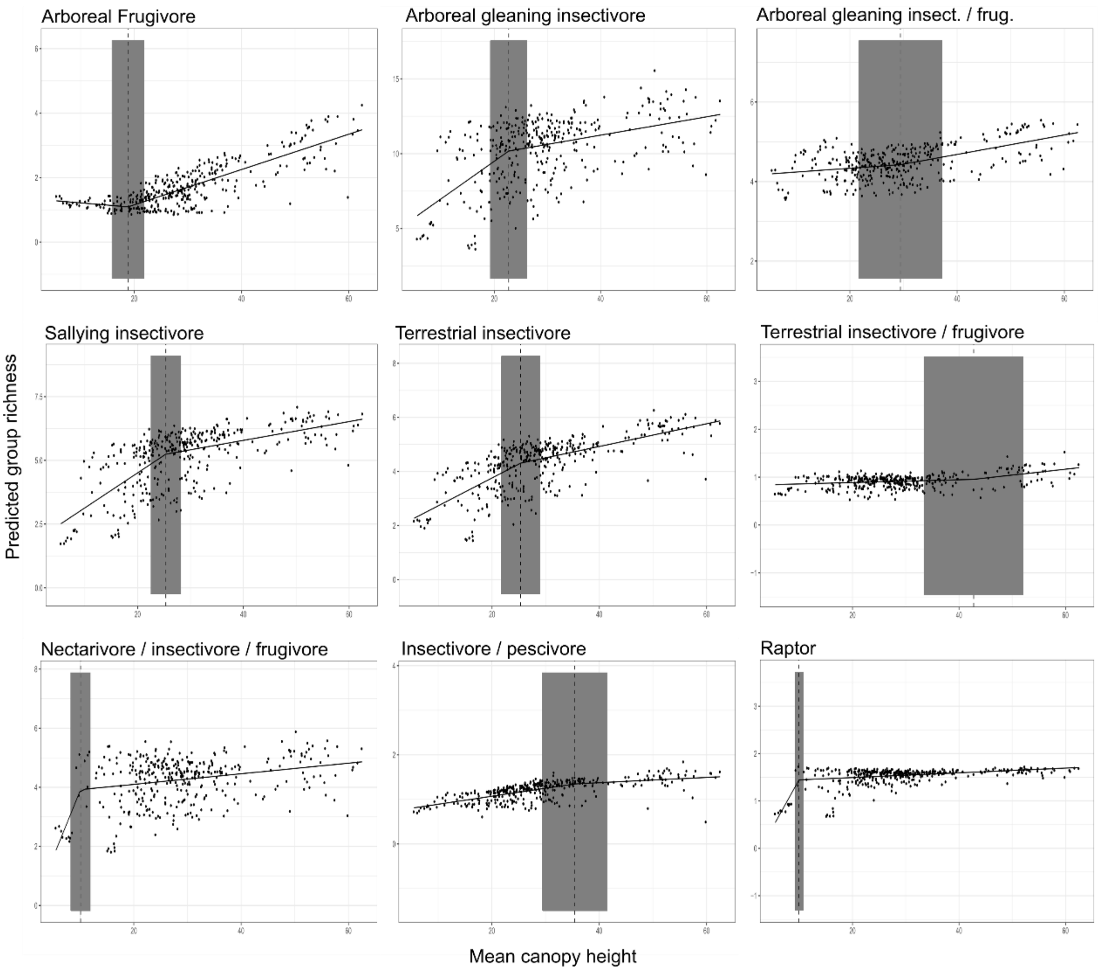

Figure 3.3. Species group richness predicted by the best segmented models for nine avian feeding guilds. Richness reported in relation to mean canopy height. Median occupancy values of each species are used. Thresholds are calculated from median values, with confidence intervals (shading) calculated by the segmented package. All segmented relationships are ΔAIC>4 improvement from linear models.

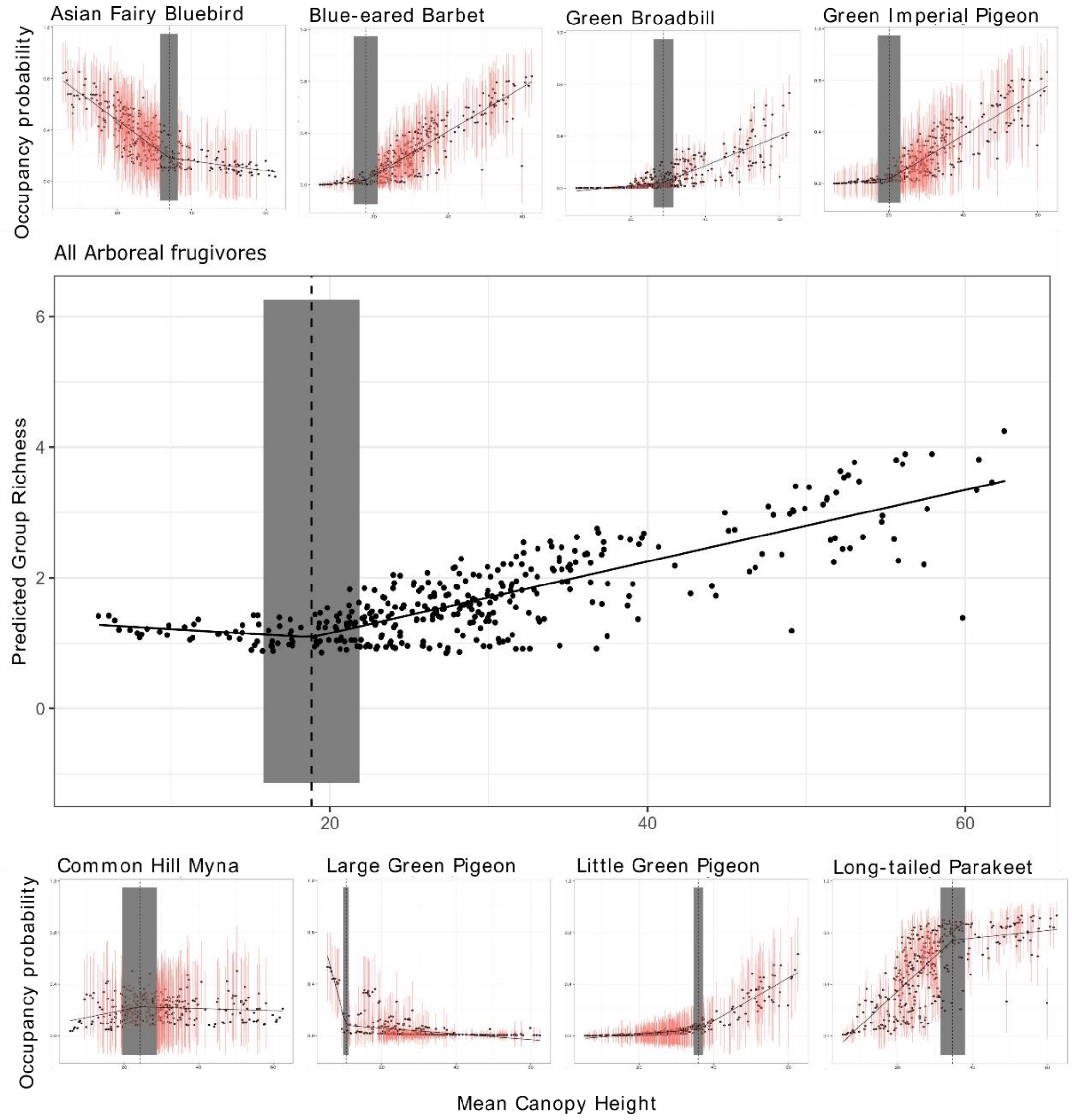

Figure 3.4. Segmented models for different species of the arboreal frugivore feeding guild. Occupancy probability responses to mean canopy height, together with predicted richness resulting from all eight species. Vertical lines denote species 95% Bayesian credible intervals. Median occupancy values of each species are used for predicted richness. Thresholds displayed calculated from median values, with

confidence intervals (shading) calculated by the segmented package. All segmented relationships are ΔAIC>4 reduction from linear models.

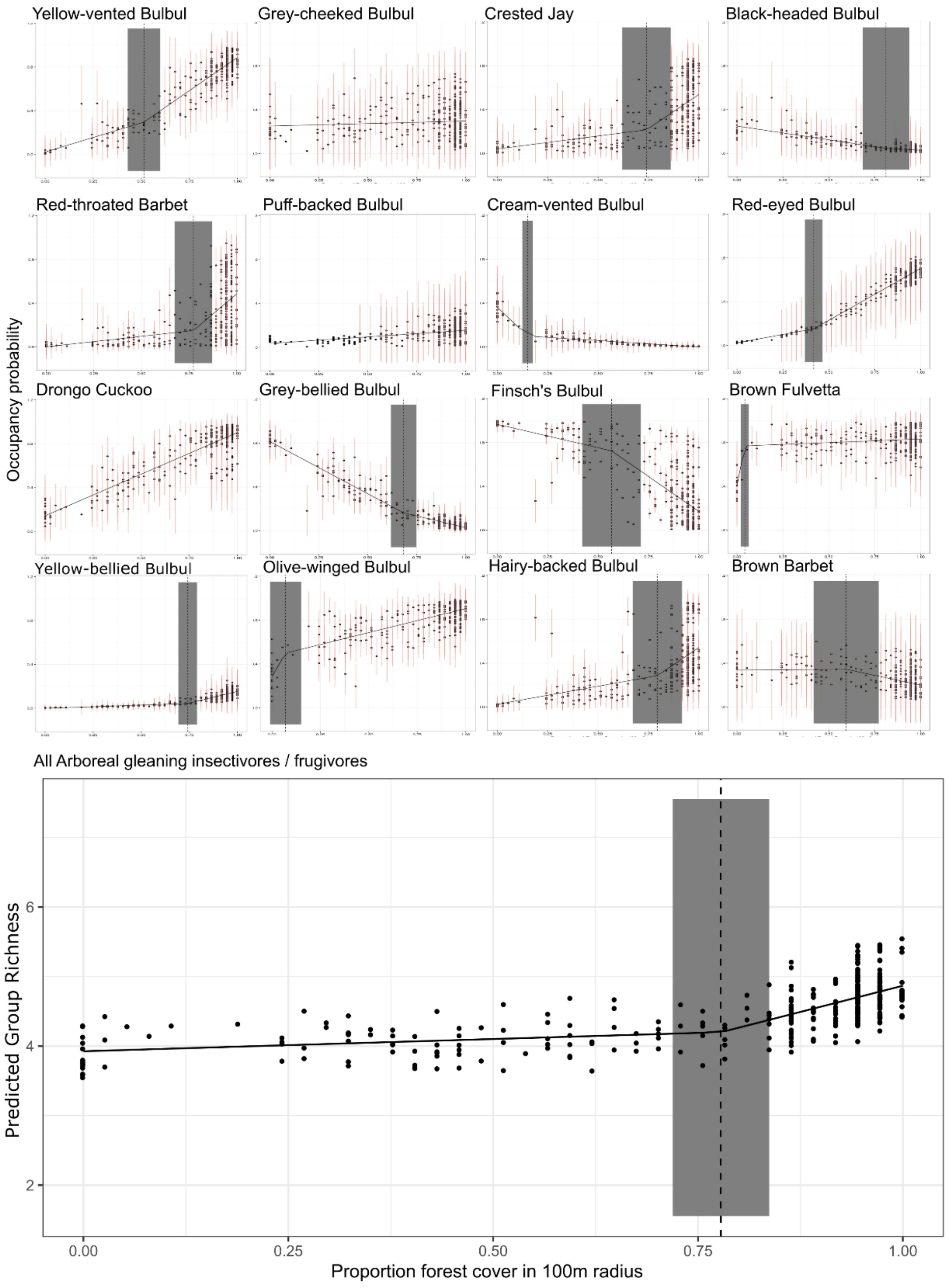

Figure 3.5. Segmented model for different species within the arboreal gleaning insectivores / frugivores guilds. Occupancy reponses shown in relation to proportion of forest, together with predicted richness resulting from all twenty species.

Vertical lines denote species 95% Bayesian confidence intervals. Median occupancy values of each species are used for predicted richness. Thresholds displayed calculated from median values, with confidence intervals (shading) calculated by the segmented packaged. Segmented relationships are ΔAIC>4 reduction from linear models.

Species thresholds

Occupancy changes in relation to environmental covariates were better explained by segmented models than linear ones. Associations between species occupancy (derived from our model) and forest cover were better explained by segmented models with a single breakpoint than by linear models for 139 species (i.e. for 139 of 171 species the segmented model yielded a reduction of >ΔAIC=4 compared to the linear model for the same dataset). The same was true for 166 species for canopy height, 129 species for vegetation density, 120 species responses to skew, and 151 species for canopy heterogeneity (Table S3.3). Average reductions in model AIC were 54.6 for forest cover, 86.4 for canopy height, 33.1 in density, 17.6 in skew and 56.6 in canopy heterogeneity.

Between groups, the average threshold levels in the responses of member species (i.e., thresholds in each species response to a given environmental variable, taken as the median across all group member species) did not differ significantly between the various strata groups, feeding guilds or habitat groups. Separating member species of trait groups into further sub-groups depending on whether their overall response was positive or negative, or whether they showed increasing or decreasing strength of response, did not highlight any significant variation between trait-groups or sub-groups (Fig. S3.6; Table S3.5).

Thresholds of richness in relation to canopy height differed significantly between different trait groups (Fig. 3.3), but were not correlated with the average thresholds of the species within those groups (p=0.69). Nor were group richness thresholds for forest cover associated with the median values for member species thresholds (p=0.51).

Discussion

Our study demonstrates both variation and similarity in thresholds of species responses to changes in forest cover and three dimensional structure - features known to shift following tropical forest degradation. While the concepts of tipping points (Folke *et al*., 2004) and non-linear responses (Meron, 2015) to environmental change are fairly well established in the ecological literature, most observational studies address these on broad scales, such as in the functioning of entire ecosystems (e.g Nobre & Bourma, 2009), or changes of overall species richness or community integrity (e.g. Banks-Leite *et al*., 2014). Our data on palaeotropical birds reveal a number of tipping-points which appear to be common across multiple trait groups, but also highlight idiosyncratic threshold levels for other species groups. We examined the responses of almost every species in the bird community individually to discern where unexpected responses of particular taxa might otherwise be overlooked by grouping species together. Previous assessments that have tracked individual species thresholds to their contribution to community-level effects either focussed on very simple communities (Dieleman *et al*., 2015), selected groups of species (Betts *et al*., 2010), or used species abundance (Suarez-Robio & Lookingbill, 2016) or naïve occupancy (Bergman *et al*., 2004) as their response measure. Our study reveals how thresholds in the responses of trait groups manifest, by examining how the differences in thresholds between up to 48 different member species contribute to overall group thresholds in richness. This multi-level examination allows us to address the efficacy of applying the concept of thresholds to species trait groups.

Pervasive non-linear responses to habitat change in the tropical bird community

We found relationships between most species occupancy and environmental variables were better described by models that included non-linear thresholds. Whilst previous studies found individual species respond in a non-linear manner to two-dimensional landscape scale changes (e.g. Betts *et al.*, 2010), we assessed the thresholds of responses to structural vegetation metrics, captured in three dimension using hyperspectral LiDAR. Thresholds at the species level were most common in responses to canopy height (Table 3.1). A few species also showed response thresholds to explicitly three dimensional forest structure characteristics of skew and vegetation density. For example, Blue-throated Bee-eater, *Merops viridis* increased in occupancy probability with increased skew (vegetation density skewed towards the higher vegetation strata). This was of a greater magnitude once skew increased above a threshold of 0.9. Blue-throated Bee-eaters specifically hunt for insects from perches on tall trees (del Hoyo *et al.*, 2019), and prefer areas of mixed forest or open habitat where vegetation is concentrated to higher canopy strata, since this maximises the area of open storey where they predominantly forage. Conversely, other species (e.g. Cream-vented Bulbul, *Pycnonotus simplex*) were only recorded in areas where skew was below a threshold of 0.5. This species is described as favouring “lower and middle storeys along forest trails, especially in more open areas” (del Hoyo *et al.*, 2019), which suggests that the species tolerates a maximum level of upwards vegetation skew. The use of LiDAR data allows us to reveal several relationships like these across a whole community for the first time.

Patterns in trait-group responses to forest disturbance

We found differing threshold levels in the 18 different trait groups we assessed, both as member species-averages (Fig. S3.6), and when assessed as whole-group (Fig. 3.3; Fig 3.4). For example, principally nectarivorous species exhibited lower thresholds in their response to canopy height than solely insectivorous guilds, both in terms of member species averages (Fig. S3.6), and in the responses of group richness derived from cumulative predicted occupancy (Fig. 3.3). Elsewhere on Borneo, Cleary *et al*. (2007) demonstrated terrestrial insectivores to be more strongly negatively affected by logging activities than nectarivores and frugivores, a finding associated with reduced canopy height. We are able to elaborate on this assertion more specifically by demonstrating that increases in canopy height from only 5 m to 10 m result in an increase of 2-4 species detected (i.e. 0.4 additional species per metre height). Once the canopy reaches 10 m in height, species richness gains are quite minor: for example, an average of one nectarivorous bird for the next 50 m of additional gain in canopy height (0.02 additional spp/m) (Fig. 3.3).

Contrary to this pattern, terrestrial insectivores increased at rate of 0.11 additional spp./m between 5 m and 25 m in canopy height (a much higher threshold than nectarivores) after which only an average rate of 0.04 additional spp./m between 25 m and 60 m was observed (Fig. 3.3). Terrestrial insectivores have previously been found to be largely absent from heavily logged forests (which are characterised by reduced canopy height), apparently due to associated changes in microclimate and leaf-litter (Stratford & Stouffer, 2012). By contrast, many principally nectarivorous or frugivorous species are more abundant in logged forests (Cleary *et al.*, 2010; Edwards *et al.*, 2009). Further to these basic ecological patterns, we can reveal specific, contrasting cut-off points in canopy height below which terrestrial insectivores and nectarivores decline at a more rapid rate.

Thresholds in the responses of feeding guilds to forest cover were remarkably consistent, with eight out of nine feeding guilds showing abrupt changes in response to forest cover at between 73% and 79%. Whilst this is higher than most previous thresholds in the relationship between forest cover and overall community richness (Melo *et al.*, 2009), our higher threshold does not necessarily mean that feeding guilds rapidly declined in species numbers once forest cover drops below ~75%. In fact, increases in forest cover above 75% were associated with greater increases in species richness than below this level. Since a number of forest specialist species across several feeding guilds are known to exhibit strong preferences for forest interior (Laurance, 2012), we suspect that the added contribution of these species, which are absent in degraded or semi-open habitat (Peh *et al.*, 2005), drive this pattern. Inspecting the responses of forest specialist and edge tolerant forest species within particular feedings guilds demonstrated this was the case. For example, Crested Jay (*Platylophus galericulatus*), is defined as a forest specialist and Red-throated Barbet (*Psilopogon mystacophanos*) as an edge-tolerant forest species (Styring *et al.*, 2007), but both are included within the Arboreal foliage-gleaning insectivore/frugivore guild. Crested Jay occupancy increased slowly below 75% forest cover to 20% occupancy, but after this threshold, increased more rapidly to 55% occupancy with 100% forest cover. Similarly, Red-throated Barbet increased from 20% occupancy with 77% forest cover to 50% occupancy with 100% forest cover (Fig. 5). Similar patterns were found for each feeding guild where richness increased above a threshold of 70 – 80%.

The uncertainty around occupancy responses of individual species means that thresholds generated from such interpolated data ought to be regarded with a degree of caution. However, when species are accumulated together, such as in trait groups, occupancy responses are supported by a greater number of both model samples and species, such that inferences regarding abrupt changes in species' occupancy probability (which haven't been nullified by variation of member species responses), are more robust.

Idiosyncratic species responses

Trait groups are useful in generalising species responses to environmental variables. However, relying solely upon trait groups may obscure patterns of individual species responses (Laurance, 2012). Similarly, we found trait groups provide a useful way of understanding the general patterns of community break-points, but member species within groups should not necessarily be assumed to have similar thresholds to one another. We found that in species trait groups, both the overall effects and thresholds in responses for individual species were sometimes lost. For example, arboreal frugivores showed no increase in richness until a canopy height of ~18 metres. However, our capacity to break down this pattern to the individual species level revealed that two species (Little Green Pigeon, *Treron olax*; Green Broadbill, *Calyptomena viridis*), were unlikely to be present until the forest canopy was tall, exceeding 30 m (Fig. 3.4). The utility of our approach, therefore, is that not only is it possible to identify the thresholds associated with the loss or decline of particular guilds or functional groups, but also which species responses are most responsible for driving these changes.

Detecting species responses in narrow ranges of environmental change

A number of species demonstrated what would be significant relationships with skew over part of the gradient captured, but did not exhibit significant responses overall. For example, Blue-headed Pitta (*Hydrornis baudii*) responded strongly to changes in skew between values of 0.6 and 2.5, but show no relationship overall (Fig. S3.4). This demonstrates that, where species respond through only part of the overall environmental range, it is possible for type II errors to occur, due to the non-significance of an effect overall. Abrupt increases in response magnitude in our study were often associated with entirely flat response curves where the confidence bounds for occupancy crossed zero (which includes the possibility a species is absent), followed by an increase once certain levels of an environmental metric was reached. It seems likely that in these cases, species are often absent in particular habitats until niche requirements are met (e.g. Michael *et al.*, 2015; Pica-Roca *et al.*, 2018). Once a habitat meets a species minimum requirements and the area is colonised, further improvements in suitability are likely to result in an increase of abundance (Fuller, 2012), reflected by increased occupancy probability in our model. Based on visual inspection of occupancy plots, this was the case for 34 species in relation to canopy height and 57 species for forest cover.

Implications for biodiversity assessment, forest management and conservation planning

Our approach offers an increased capacity for understanding the underlying mechanisms of thresholds in community responses to environmental change. We show that, while particular trait groups may respond in broadly similar ways overall, individual species exhibit idiosyncratic thresholds. For conservation this is of value since the most fundamental unit of interest in planning and monitoring has tended to be species (Riddle & Hafner, 1999). Indicator species are widely used as proxies of overall community health or ecosystem integrity, as they are believed or demonstrated to have similar responses to the overall ecological community (Siddig *et al*., 2016). The best indicators should allow continuous assessment by responding to a wide range of intensity to stressors (O'Connell *et al*., 1998), and not bottom out or plateau once certain thresholds are reached (Gibbs *et al*., 1999; Carginan & Villard, 2002). However, if selected indicator species have markedly different thresholds compared to the overall community, then inappropriate management practices could be implemented.

Understanding how species responses vary within environmental ranges offers a significant advantage for management. Identifying where species, trait groups, or communities respond at the greatest magnitude within different ranges of the same environmental gradient, allows the prioritisation of both conservation and ecological restoration efforts based on specific management aims. Response thresholds provide a definite management target, as well as the potential to predict the economic efficiency of interventions at different points on an environmental gradient. One clear example of where this approach has already been successfully applied to provide management guidance is in Brazil’s Atlantic forest, where Banks-Leite *et al.* (2014), used a threshold in phylogenetic integrity to spatially prioritise cost-effective restoration scenarios via a payment for ecosystem service framework.

Identifying thresholds for particular trait groups is also highly relevant to ecological management, since certain species guilds are linked to particular ecosystem functions (Hevia *et al.*, 2017). A threshold approach allows the exploration of non-linear changes in ecosystem functions (e.g. pollination, insectivorey, seed dispersal) to be understood in the context of the species groups which provide them. The identification of thresholds for trait groups could facilitate the identification of crucial points for management intervention to avoid abrupt ecosystem change or restore ecosystems most effectively. Our framework allows ecosystem function to be characterised, not only in comparison to the thresholds of particular associated trait groups, but with reference to particular member species. Not all species within trait groups contribute equally to linked ecosystem functions (Maas *et al.*, 2015), meaning thresholds of some species may be of more interest to an environmental manager than others.

Utilising a combination of occupancy modelling and LiDAR data to undertake threshold assessments for almost all members of an ecological community offers numerous advantages for statistical rigour, ecosystem management, biodiversity conservation and species protection. Whilst there may still be room to improve the methodological approaches for collecting and assessing these data, the utility of such an overall framework is clear. Further application of this modelling approach could help reduce type II statistical errors, predict the efficiency of conservation investment, identify better suited indicator species, and offer specific insights about otherwise overlooked habitat associations, particularly for specialist species.

Supplementary information

Table S 3.1. Vegetation strata associations, feeding guilds and habitat associations of the birds of lowland Sabah. Strata associations follow Chapman *et al.*, (2018) del Hoyo *et al.*, (2018). Feeding guilds and habitat assocations follow Lambert (1992), Styring (2004) and Sheldon (2010). Feeding guild and habitat association codes are detailed in Table S3.2.

English name	Latin name	Strata	Guild	Habitat
Arctic Warbler	*Phylloscopus borealis*	Understorey	AFGI	ETF
Ashy Tailorbird	*Orthotomus ruficeps*	Understorey	AFGI	ES
Asian Brown Flycatcher	*Muscicapa dauurica*	Understorey	SI	ES
Asian Fairy Bluebird	*Irena puella*	Canopy	AF	ES
Asian Glossy Starling	*Aplonis panayensis*	Canopy	AFGI	G
Asian Paradise Flycatcher	*Terpsiphone paradisi*	Canopy	SI	ETF
Red-eyed Bulbul	*Pycnonotus brunneus*	Understorey	AFGIF	ETF
Banded Bay Cuckoo	*Cacomantis sonneratii*	Understorey	AFGI	ETF
Banded Broadbill	*Eurylaimus javanicus*	Canopy	NA	ETF
Banded Pitta	*Pitta guajana*	Ground	TI	FS
Banded Woodpecker	*Picus mineaceus*	Canopy	AFGI	FS
Barred Eagle Owl	*Bubo sumatranus*	Canopy	NA	ETF
Bar-winged Flycatcher-shrike	*Hemipus picatus*	Canopy	SI	ETF
Black Eagle	*Ictinaetus malayensis*	Ground	R	OS
Black Hornbill	*Anthracoceros malayanus*	Canopy	NA	ETF
Black Magpie	*Platysmurus leucopterus*	Understorey	SI	FS
Black-and-red Broadbill	*Cymbirhynchus macrorhynchos*	Canopy	NA	OS
Black-and-yellow Broadbill	*Eurylaimus ochromalus*	Canopy	NA	ETF
Black-bellied Malkoha	*Phaenicophaeus diardi*	Understorey	AFGI	ETF
Black-capped Babbler	*Pellorneum capistratum*	Ground	TI	ETF
Black-headed Bulbul	*Pycnonotus atriceps*	Understorey	AFGIF	ES
Black-headed Pitta	*Pitta ussheri*	Ground	TI	ETF
Black-naped Monarch	*Hypothymis azurea*	Canopy	AFGI	ETF
Black-throated Babbler	*Stachyris nigricollis*	Understorey	SI	ETF
Black-throated Wren-babbler	*Turdinus atrigularis*	Ground	TI	FS
Black-winged Flycatcher-shrike	*Hemipus hirundinaceus*	Canopy	SI	ETF
Banded Kingfisher	*Lacedo pulchella*	Ground	MIP	FS
Blue-banded Kingfisher	*Alcedo euryzona*	Understorey	MIP	FS
Blue-banded Pitta	*Pitta arcuata*	Ground	TI	FS
Blue-crowned Hanging Parrot	*Loriculus galgulus*	Canopy	NIF	ETF
Blue-eared Barbet	*Megalaima australis*	Canopy	AF	G
Blue-eared Kingfisher	*Alcedo meninting*	Understorey	MIP	ETF

Blue-headed Pitta	*Pitta baudii*	Ground	TI	FS
Blue-rumped Parrot	*Psittinus cyanurus*	Canopy	AF	FS
Blue-tailed Bee-eater	*Merops philippinus*	Canopy	SI	OS
Bold-striped Tit-Babbler	*Macronous bornensis*	Understorey	AFGI	ES
Bornean Blue Flycatcher	*Cyornis superbus*	Understorey	SI	FS
Bornean Bristlehead	*Pityriasis gymnocephala*	Canopy	AFGI	FS
Bornean Ground-cuckoo	*Carpococcyx radiatus*	Ground	TI	FS
Bornean Wren-Babbler	*Ptilocichla leucogrammica*	Ground	TI	FS
Brahminy Kite	*Haliastur indus*	Ground	R	OS
Bronzed Drongo	*Dicrurus aeneus*	Canopy	NA	ETF
Brown Barbet	*Calorhamphus fuliginosus*	Canopy	AFGIF	ETF
Brown Fulvetta	*Alcippe brunneicauda*	Canopy	AFGIF	FS
Brown-throated Sunbird	*Anthreptes malacensis*	Understorey	NIF	OS
Buff-necked Woodpecker	*Meiglyptes tukki*	Canopy	NIF	OS
Buff-rumped Woodpecker	*Meiglyptes tristis*	Canopy	NIF	OS
Buff-vented Bulbul	*Iole olivacea*	Understorey	NIF	OS
Bushy-crested Hornbill	*Anorrhinus galeritus*	Canopy	NA	FS
Cattle Egret	*Bubulcus ibis*	Ground	TI	OS
Changeable Hawk-eagle	*Nisaetus cirrhatus*	Canopy	R	G
Checker-throated Woodpecker	*Picus mentalis*	Canopy	AFGI	FS
Chestnut Munia	*Lonchura atricapilla*	Ground	NA	OS
Chestnut-backed Scimitar Babbler	*Pomatorhinus montanus*	Canopy	NA	FS
Chestnut-breasted Malkoha	*Phaenicophaeus curvirostris*	Canopy	AFGI	ETF
Chestnut-capped Thrush	*Zoothera interpres*	Ground	TI	FS
Chestnut-naped Forktail	*Enicurus ruficapillus*	Ground	MIP	FS
Chestnut-necklaced Partridge	*Arborophila charltonii*	Ground	TIF	FS
Chestnut-rumped Babbler	*Stachyris maculata*	Canopy	AFGI	ETF
Chestnut-winged Babbler	*Stachyris erythroptera*	Understorey	AFGI	ETF
Cinammon-rumped Trogon	*Harpactes orrhophaeus*	Understorey	NA	FS
Collared Kingfisher	*Todiramphus chloris*	Ground	MIP	OS
Hill Myna	*Gracula religiosa*	Understorey	AF	G
Cream-vented Bulbul	*Pycnonotus simplex*	Understorey	AFGIF	ES
Crested Fireback	*Lophura ignita*	Ground	TIF	FS
Crested Goshawk	*Accipiter trivirgatus*	Canopy	R	ETF
Crested Jay	*Platylophus galericulatus*	Understorey	AFGIF	FS
Crested Partridge	*Rollulus rouloul*	Ground	TIF	FS
Crested Serpent-eagle	*Spilornis cheela*	Canopy	R	G
Crimson Sunbird	*Aethopyga siparaja*	Understorey	NIF	G
Crimson-winged Woodpecker	*Picus puniceus*	Canopy	NA	ETF
Dark-necked Tailorbird	*Orthotomus atrogularis*	Understorey	AFGI	ES
Dark-sided Flycatcher	*Muscicapa sibirica*	Understorey	SI	ES
Dark-throated Oriole	*Oriolus xanthonotus*	Understorey	AFGI	ETF
Diards Trogon	*Harpactes diardii*	Understorey	NA	FS
Dusky Broadbill	*Corydon sumatranus*	Canopy	SI	ETF
Dusky Munia	*Lonchura fuscans*	Ground	SI	ETF

Emerald Dove	*Chalcophaps indica*	Ground	NA	ETF
Ferruginous Babbler	*Trichastoma bicolor*	Understorey	AFGI	FS
Fiery Minivet	*Pericrocotus igneus*	Canopy	AFGI	ETF
Finschs Bulbul	*Alophoixus finschii*	Understorey	AFGIF	ES
Fluffy-backed Tit-babbler	*Macronous ptilosus*	Understorey	AFGI	ETF
Giant Pitta	*Pitta caerulea*	Ground	TI	FS
Golden-whiskered Barbet	*Megalaima chrysopogon*	Canopy	NA	ETF
Great Argus	*Argusianus argus*	Ground	TIF	FS
Great Slaty Woodpecker	*Mulleripicus pulverulentus*	Canopy	AFGI	FS
Greater Coucal	*Centropus sinensis*	Ground	TI	OS
Greater Green Leafbird	*Chloropsis sonnerati*	Canopy	NIF	ETF
Greater Racquet-tailed Drongo	*Dicrurus paradiseus*	Canopy	NA	ETF
Green Broadbill	*Calyptomena viridis*	Canopy	AF	FS
Green Imperial Pigeon	*Ducula aenea*	Canopy	AF	FS
Green Iora	*Aegithina viridissima*	Canopy	AFGI	ETF
Grey-and-buff Woodpecker	*Hemicircus concretus*	Canopy	AFGI	ETF
Grey-bellied Bulbul	*Pycnonotus cyaniventris*	Understorey	AFGIF	ETF
Grey-capped Pygmy Woodpecker	*Dendrocopos canicapillus*	Canopy	AFGI	ETF
Grey-cheeked Bulbul	*Alophoixus bres*	Understorey	AFGIF	FS
Grey-chested Jungle-Flycatcher	*Rhinomyias umbratilis*	Understorey	NA	FS
Grey-headed Babbler	*Stachyris poliocephala*	Understorey	AFGI	FS
Grey-headed Canary-flycatcher	*Culicicapa ceylonensis*	Canopy	SI	ES
Grey-rumped Treeswift	*Hemiprocne longipennis*	Canopy	NA	OS
Hairy-backed Bulbul	*Tricholestes criniger*	Understorey	AFGIF	FS
Helmeted Hornbill	*Rhinoplax vigil*	Understorey	NA	ETF
Hooded Pitta	*Pitta sordida*	Ground	TI	ETF
Horsfields Babbler	*Malacocincla sepiaria*	Ground	TI	ETF
Indian Cuckoo	*Cuculus micropterus*	Canopy	NA	OS
Jerdon's Baza	*Aviceda jerdoni*	Understorey	R	ES
Large Frogmouth	*Batrachostomus auritus*	Canopy	AFGI	FS
Large Green Pigeon	*Treron capellei*	Canopy	AF	ETF
Large Woodshrike	*Tephrodornis gularis*	Canopy	AFGI	ETF
Large-billed Blue Flycatcher	*Cyornis caerulatus*	Understorey	SI	FS
Lesser Coucal	*Centropus bengalensis*	Ground	TI	OS
Lesser Cuckooshrike	*Coracina fimbriata*	Canopy	AFGI	ETF
Lesser Fish-Eagle	*Ichthyophaga humilis*	Ground	R	OS
Lesser Green Leafbird	*Chloropsis cyanopogon*	Canopy	NIF	ETF
Little Bronze Cuckoo	*Chrysococcyx minutillus*	Canopy	AFGI	ETF
Little Egret	*Egretta garzetta*	Ground	NA	OS
Little Green Pigeon	*Treron olax*	Canopy	AF	ETF
Little Spiderhunter	*Arachnothera longirostra*	Understorey	NIF	G
Long-billed Spiderhunter	*Arachnothera robusta*	Canopy	NA	ETF
Long-tailed Parakeet	*Psittacula longicauda*	Canopy	AF	ETF
Malayian Eared-nightjar	*Eurostopodus temminckii*	Understorey	SI	ES
Malaysian Blue Flycatcher	*Cyornis turcosus*	Understorey	SI	ETF

Malaysian Hawk-cuckoo	*Hierococcyx fugax*	Understorey	AFGI	ETF
Mangrove Blue Flycatcher	*Cyornis rufigastra*	Understorey	SI	ETF
Maroon Woodpecker	*Blythipicus rubiginosus*	Canopy	NA	ETF
Maroon-breasted Philentoma	*Philentoma pyrhoptera*	Understorey	SI	FS
Moustached Babbler	*Malacopteron magnirostre*	Understorey	AFGI	ETF
Moustached Hawk-cuckoo	*Hierococcyx vagans*	Understorey	AFGI	FS
Narcissus Flycatcher	*Ficedula narcissina*	Understorey	SI	ETF
Olive-backed Pipit	*Anthus hodgsoni*	Ground	TI	ES
Olive-backed Sunbird	*Nectarinia jugularis*	Understorey	NIF	OS
Olive-backed Woodpecker	*Dinopium rafflesii*	Canopy	NA	FS
Olive-winged Bulbul	*Pycnonotus plumosus*	Understorey	AFGIF	ES
Orange-backed Woodpecker	*Reinwardtipicus validus*	Canopy	NA	FS
Orange-bellied Flowerpecker	*Dicaeum trigonostigma*	Canopy	NIF	G
Orange-breasted Trogon	*Harpactes oreskios*	Understorey	SI	FS
Oriental Dollarbird	*Eurystomus orientalis*	Canopy	SI	ES
Oriental Dwarf-kingfisher	*Ceyx erithaca*	Understorey	NA	FS
Oriental Honey Buzzard	*Pernis ptilorhyncus*	Canopy	R	ES
Oriental Magpie-Robin	*Copsychus saularis*	Ground	AFGI	OS
Oriental Pied Hornbill	*Anthracoceros albirostris*	Canopy	NA	OS
Pale Blue Flycatcher	*Cyornis unicolor*	Understorey	SI	FS
Pied Fantail	*Rhipidura javanica*	Understorey	SI	ES
Plain Sunbird	*Anthreptes simplex*	Understorey	NIF	ETF
Plaintive Cuckoo	*Cacomantis merulinus*	Understorey	AFGI	G
Puff-backed Bulbul	*Pycnonotus eutilotus*	Understorey	AFGIF	FS
Purple-naped Sunbird	*Hypogramma hypogrammicum*	Understorey	NIF	ETF
Purple-throated Sunbird	*Nectarinia sperata*	Understorey	NIF	ETF
Raffles's Malkoha	*Phaenicophaeus chlorophaeus*	Understorey	AFGI	ETF
Red-bearded Bee-eater	*Nyctyornis amictus*	Canopy	SI	FS
Red-naped Trogon	*Harpactes kasumba*	Understorey	NA	FS
Red-throated Barbet	*Megalaima mystacophanos*	Canopy	AFGIF	ETF
Red-throated Sunbird	*Anthreptes rhodolaemus*	Understorey	NIF	ES
Rhinoceros Hornbill	*Buceros rhinoceros*	Canopy	NA	ETF
Ruby-cheeked Sunbird	*Anthreptes singalensis*	Understorey	NIF	ES
Rufous Piculet	*Sasia abnormis*	Understorey	AFGI	ETF
Rufous Woodpecker	*Celeus brachyurus*	Canopy	AFGI	ETF
Rufous-bellied Hawk-Eagle	*Lophotriorchis kienerii*	Ground	R	ETF
Rufous-chested Flycatcher	*Ficedula dumetoria*	Understorey	SI	FS
Rufous-crowned Babbler	*Malacopteron magnum*	Understorey	AFGI	FS
Rufous-fronted Babbler	*Stachyris rufifrons*	Canopy	AFGI	ETF
Rufous-tailed Shama	*Trichixos pyrropygus*	Ground	AFGI	FS
Rufous-tailed Tailorbird	*Orthotomus sericeus*	Understorey	AFGI	ES
Rufous-winged Philentoma	*Philentoma velata*	Understorey	SI	FS
Scaly-crowned Babbler	*Malacopteron cinereum*	Understorey	AFGI	FS
Scarlet Minivet	*Pericrocotus flammeus*	Canopy	AFGI	ETF
Scarlet rumped Trogon	*Harpactes duvaucelii*	Understorey	NA	FS

Scarlet-breasted Flowerpecker	*Prionochilus thoracicus*	Canopy	NIF	ETF
Short-tailed Babbler	*Malacocincla malaccensis*	Ground	TI	ETF
Short-toed Coucal	*Centropus rectunguis*	Ground	AFGI	FS
Siberian Blue Robin	*Luscinia cyane*	Ground	TI	FS
Slender-billed Crow	*Corvus enca*	Ground	AFGIF	OS
Sooty-capped Babbler	*Malacopteron affine*	Understorey	AFGI	ETF
Spectacled Bulbul	*Pycnonotus erythropthalmos*	Understorey	AFGIF	ETF
Spotted Dove	*Stigmatopelia chinensis*	Ground	NA	OS
Spotted Fantail	*Rhipidura perlata*	Understorey	SI	FS
Square-tailed Drongo-Cuckoo	*Surniculus lugubris*	Canopy	AFGIF	ETF
Storm's Stork	*Ciconia stormi*	Ground	NA	FS
Streaked Bulbul	*Ixos malaccensis*	Understorey	AFGIF	ETF
Streaky-breasted Spiderhunter	*Arachnothera affinis*	Understorey	NIF	FS
Striped Wren-babbler	*Kenopia striata*	Ground	TI	FS
Thick-billed Green Pigeon	*Treron curvirostra*	Canopy	AF	ETF
Thick-billed Spiderhunter	*Arachnothera crassirostris*	Canopy	NIF	ETF
Tree Sparrow	*Passer montanus*	Ground	NA	OS
Velvet-fronted Nuthatch	*Sitta frontalis*	Canopy	NA	FS
Verditer Flycatcher	*Eumyias thalassinus*	Canopy	SI	ETF
Violet Cuckoo	*Chrysococcyx xanthorhynchus*	Canopy	AFGI	ETF
Wallace's Hawk-Eagle	*Nisaetus nanus*	Canopy	R	ETF
Whiskered Treeswift	*Hemiprocne comata*	Canopy	SI	OS
White-bellied Erpornis	*Erpornis zantholeuca*	Understorey	AFGI	FS
White-bellied Munia	*Lonchura leucogastra*	Ground	TIF	OS
White-bellied Woodpecker	*Dryocopus javensis*	Canopy	AFGI	ETF
White-breasted Waterhen	*Amaurornis phoenicurus*	Ground	MIP	OS
White-chested Babbler	*Trichastoma rostratum*	Ground	TI	ES
White-crowned Forktail	*Enicurus leschenaulti*	Ground	TI	FS
White-crowned Hornbill	*Aceros comatus*	Canopy	NA	FS
White-crowned Shama	*Copsychus stricklandii*	Understorey	AFGI	ETF
Wreathed Hornbill	*Aceros undulatus*	Canopy	NA	ETF
Yellow-bellied Bulbul	*Alophoixus phaeocephalus*	Understorey	AFGIF	FS
Yellow-bellied Gerygone	*Gerygone sulphurea*	Canopy	SI	ETF
Yellow-bellied Prinia	*Prinia flaviventris*	Understorey	AFGI	OS
Yellow-breasted Flowerpecker	*Prionochilus maculatus*	Canopy	AFGIF	ETF
Yellow-crowned Barbet	*Megalaima henricii*	Canopy	AF	ETF
Yellow-eared Spiderhunter	*Arachnothera chrysogenys*	Canopy	NIF	FS
Yellow-rumped Flowerpecker	*Prionochilus xanthopygius*	Canopy	NIF	G
Yellow-vented Bulbul	*Pycnonotus goiavier*	Understorey	AFGIF	G

Table S 3.2. Details of feeding guild and habitat association codes used in the study.

Trait groups follow Styring (2004) and Sheldon (2010).

AF	Arboreal frugivore
AFGI	Arboreal foliage-gleaning insectivore
AFGIF	Arboreal foliage-gleaning insectivore / frugivore
SI	Sallying Insectivore
TI	Terrestrial Insectivore
TIF	Terrestrial Insectivore / Frugivore
NIF	Nectivore / Insectivore / Frugivore
MIP	Miscellaneous Insectivore / Pecivore
R	Raptor
FS	Forest specialist
ETF	Edge-tolerant forest
OS	Open habitat species
G	Generalist
NA	Information Not Available / Not assessed

Table S 3.3. Median thresholds points with confidence intervals in relation to mean canopy height and canopy hereogeneity.Canopy heterogenity is stardard deviation of canopy height. Both metrics calculated from mean LiDAR values within a 50 m radius. Lower 95% confidence interval; Lw CI, Upper 95% confidence interval; Up CI. Model ΔAIC denotes the reduction in AIC between linear model and segmented model. Negative ΔAIC signifies that the linear model out performed the segmented one. G+ denotes whether thresholds were associated with a strengthing (increasing gradient G+ = True), or weakening (more negative G+ = False) response after the threshold point**.**

Species	Canopy Height					Canopy Heterogeneity				
	Med	**Lw CI**	**Up CI**	**ΔAIC**	**G +**	**Med**	**Lw CI**	**Up CI**	**ΔAIC**	**G +**
Arctic Warbler	28	22	34.3	40.7	F	3	3.6	2.2	69.1	F
Ashy Tailorbird	21.5	14.2	28.5	62.6	F	2.5	6.5	-1.2	-2	F
Asian Fairy Bluebird	33.9	14.4	43.3	101.9	T	3	5.2	1.1	48.6	T
Asian Glossy Starling	33.9	17.9	44.9	39.8	T	5.7	7.8	2.8	28.9	F
Asian Paradise Flycatcher	32.3	16	43.8	9.3	T	3.3	4.9	1.9	13.8	F
Banded Bay Cuckoo	28.9	20.7	37.9	132.1	F	3	4	1.9	52.9	F
Banded Broadbill	33.9	24.6	41.2	35.5	F	2.9	4.2	1.7	31.6	F
Banded Kingfisher	32.3	-40.5	106	78.4	T	3.5	14.7	-7.2	6.3	F
Banded Pitta	29.4	6.1	45.5	112.8	T	3.2	6.3	0.9	8	F
Banded Woodpecker	10	5.7	15.3	53.7	F	3.9	8.6	-0.4	6.4	F
Bar-winged Flycatcher-shrike	26.4	18.4	34	22.7	F	3	3.8	2.1	55.1	F
Black Hornbill	32.1	0.6	59.5	310.6	T	3.6	8.2	-0.2	0.1	F
Black Magpie	32.3	19.4	42.7	58.4	F	2.9	5.3	0.9	27.8	F
Black-and-yellow Broadbill	22.3	5.3	31.9	14.3	T	3.4	6.1	1.1	43.6	T
Black-bellied Malkoha	10.3	5.9	15.6	7.3	T	5.7	10.4	-0.1	-2	F
Black-capped Babbler	32.2	12.6	55.7	195.8	T	3.2	5	1.8	6	F
Black-headed Bulbul	29	12.4	44.2	39.6	T	3.4	6.8	0.6	52.5	T
Black-headed Pitta	26	12	40.3	352.9	F	3	3.9	2	62.2	F
Black-naped Monarch	33.9	10.8	60.8	373.7	T	4.3	6.3	2	0.6	F
Black-winged Flycatcher-shrike	31.2	-3.2	59.8	208.1	T	3.3	5.1	1.7	22	F
Blue-banded Kingfisher	28.8	9.6	41.4	39.6	F	3	5.5	1	44.4	F
Blue-banded Pitta	24.7	13.5	32.2	33.3	F	3	4.1	1.9	61.6	F
Blue-crowned Hanging-parrot	25.4	8.8	45.6	3.8	T	3	4.4	1.8	26.9	F
Blue-eared Barbet	33.8	20	44.1	20.7	T	2.9	4.1	1.7	20.9	F

Blue-eared Kingfisher	31.2	18.6	42.8	148.8	F	3.3	7.1	0	6.5	F
Blue-headed Pitta	25.2	7.4	39.4	13.8	F	3	6.2	0.4	-0.6	T
Blue-throated Bee-eater	9.3	5	14.6	14.5	F	4.3	6.1	3	14.9	F
Bold-striped Tit-babbler	34.9	14.3	67.9	723	T	4.4	5.9	2.5	3.1	F
Bornean Blue Flycatcher	22.5	8.7	31.5	62.6	F	3.4	6.1	1.3	29	F
Bornean Bristlehead	27.3	16.5	36.9	61	F	3.1	4.6	1.8	76.5	F
Bornean Ground-cuckoo	35	4.7	62	58	T	3.2	7.3	-0.3	50.5	T
Bornean Wren-babbler	15.3	3.2	35.4	157.6	T	3.4	6	0.9	343	T
Bronzed Drongo	23.4	16.3	30.7	88.5	F	3.4	5.6	1.3	173	F
Brown Barbet	29	8.8	41.5	67.8	T	3.1	6.7	0.5	19.1	T
Brown Flycatcher	34.6	18.7	57.8	38.7	T	3	5	1.3	5.5	F
Brown Fulvetta	11.4	4.6	31.2	109.7	F	3.2	5.6	1	106	F
Brown-throated Sunbird	31.9	5.4	51.4	205.2	T	3.2	5.6	1.5	5.2	F
Buff-rumped Woodpecker	35.2	21.4	53.5	78.1	T	3	4.2	1.9	10	F
Buff-vented Bulbul	22.9	6.7	32.3	58.4	F	3.2	5.2	1.4	176	F
Bushy-crested Hornbill	34	18.2	47.2	14	T	3	5.2	0.7	21.6	T
Checker-throated Woodpecker	22.7	11.4	31.9	17.4	T	3.1	4.5	1.7	77.3	T
Chestnut Munia	22.9	8.5	33.5	16.6	T	2.7	4.7	0.9	38	T
Chestnut-backed Scimitar-babbler	33.9	19	45.9	130.6	T	2.8	3.9	1.8	36.5	T
Chestnut-breasted Malkoha	27.9	6.3	42.2	32.8	F	3.3	6.6	0.5	81.1	F
Chestnut-naped Forktail	32.3	0.9	56.5	54.6	T	3.4	11.1	-3	14.3	T
Chestnut-necklaced Partridge	20.2	7.9	26	53.4	F	3.2	4.6	2.1	63.8	F
Chestnut-rumped Babbler	26.1	6.9	41.8	23.1	F	3.2	5.4	1.4	77.5	F
Chestnut-winged Babbler	35.2	8.2	70.9	346	T	4.4	6.7	1.7	3.5	F
Collared Kingfisher	31.7	16	45.7	55.9	T	3	4.4	1.7	10.3	F
Cream-vented Bulbul	24.6	4.8	41.6	154.6	T	3.8	6.3	1.4	244	T
Crested Fireback	29.1	17.2	40.4	48.1	T	3.2	5	1.6	111	T
Crested Goshawk	21.4	0.7	44.3	-3.3	T	3.3	7.1	0	131	F
Crested Jay	34	26	40	34.7	F	3	3.9	2	37.3	F
Crested Serpent-eagle	11.2	6.9	20.7	155.4	F	3.3	5	1.8	304	F
Crimson Sunbird	25.2	17.6	32	22.3	F	3	4	2.2	41.1	F
Crimson-winged Woodpecker	25.6	12	37.5	0.5	T	3	4.4	1.8	26.2	F
Dark-necked Tailorbird	33.9	18.6	42.9	41.7	F	3	5.4	0.9	16	F
Dark-sided Flycatcher	31.2	13.1	42.5	206.4	F	3.2	6.1	1.2	71.4	F
Dark-throated Oriole	33.9	21.6	42.7	4.7	F	3	4.1	1.8	30.2	F
Diards Trogon	31.5	19	42.9	14.3	F	2.9	4.2	1.6	33.9	F
Drongo Cuckoo	25.6	20.3	32.7	64.3	F	3	4.2	2	81	F
Dusky Broadbill	9.8	4.7	14.7	197.9	F	3.4	4.7	2.1	295	F
Dusky Munia	25.3	15.5	34.5	52.6	F	3	3.7	2.2	45.6	F
Emerald Dove	28.2	20.1	35.6	44.8	T	3.2	4.5	2	90	T
Ferruginous Babbler	25.5	15.1	33.8	58.2	F	3.1	4.3	1.9	122	F
Fiery Minivet	21.2	10.1	27.8	49.7	F	3.2	4.2	2.2	111	F
Finschs Bulbul	26.6	18.8	34.3	95.2	T	2.8	3.7	2	56.8	T
Fluffy-backed Tit-babbler	9.9	8.1	19.1	12.8	F	3.2	4.2	2.3	40.6	F
Golden-bellied Gerygone	26.5	8.5	40.6	34	T	3.1	4.4	2.1	24.9	F

Gold-whiskered Barbet	31.5	8.2	53.5	239.5	T	3.6	7.6	0.1	-2.5	F
Great Argus	27.3	5.3	50.8	95.3	T	3	7.6	-0.6	-1.6	F
Great Slaty Woodpecker	24.6	13.8	33.3	96.3	F	3.7	6.3	1.1	220	F
Greater Coucal	34	17.7	52.2	199.4	T	3	4.4	1.8	5.1	F
Greater Green Leafbird	25.3	7.4	36.6	61.9	F	3.2	6.6	0.9	12.3	F
Greater Racket-tailed Drongo	28.7	15.5	39.9	11.5	T	2.8	4.1	1.6	38.4	T
Green Broadbill	34	21.2	46.9	57.7	T	3	4.4	1.5	8.7	F
Green Imperial Pigeon	33.9	20	44.6	34.5	T	3	4.2	1.7	15.1	F
Green Iora	25.4	19	32.2	88.7	F	3.2	4.6	1.8	130	F
Grey Wagtail	25.6	18.3	37.2	12.2	F	3	4	2	29.7	F
Grey-and-buff Woodpecker	10.2	6.1	17.8	61.2	F	3.2	4.8	1.8	209	F
Grey-bellied Bulbul	25.3	14.5	35.2	67.7	T	3.2	4.2	2.2	143	T
Grey-cheeked Bulbul	25.3	7	36	11.3	T	3.1	5.9	1	-3.4	T
Grey-chested Jungle-flycatcher	34.7	23.8	50.6	35.6	T	3.1	4.3	2	7.6	F
Grey-headed Babbler	31.7	10.3	48.4	44.6	F	3	7.1	-0.7	19.1	F
Grey-headed Canary-flycatcher	25.6	12.2	34.4	29.8	F	3	3.8	1.9	77.8	F
Grey-rumped Treeswift	32.5	9.6	47.4	213.1	T	3.3	5.5	1.6	6.1	F
Hairy-backed Bulbul	25.4	7.3	41.4	26.9	T	3	4.1	2.1	16.1	F
Helmeted Hornbill	25	4.3	41.5	621.6	T	3	5.4	1.1	48	T
Hill Myna	25.3	10	35.2	11.9	F	3.1	5.4	1.2	35	F
Hooded Pitta	34.1	25.1	41.4	62.5	F	3	4.2	1.8	36.7	F
Horsfields Babbler	21.7	7.3	33.2	10.5	F	3.8	8.1	0.5	12	F
Large Green Pigeon	25.3	4.6	39.1	207.8	T	3.6	5.9	1.4	241	T
Large Woodshrike	35.5	19	66.2	232.1	T	4.4	6.8	1.9	-1.1	F
Lesser Coucal	21	6.4	30.8	44.6	F	3.4	5.5	1.9	179	F
Lesser Green Leafbird	34	15.5	44.3	18.7	F	5.4	7.2	2.8	71.2	F
Little Egret	28.8	21.2	36	81.5	F	3	3.9	2.1	79.5	F
Little Green Pigeon	35.6	16.6	68	332.3	T	4.4	6.2	1.9	2.5	F
Little Spiderhunter	26.5	14.5	37.7	129.1	F	3	4.1	1.9	56.1	F
Long-billed Spiderhunter	31.5	8.2	43.6	8.6	T	4.2	6.6	1.7	16.5	F
Long-tailed Parakeet	28	21.8	35	63.3	F	3	3.8	2.1	62.1	F
Malaysian Blue Flycatcher	34.4	25.8	41.7	14.4	F	3	3.8	2.1	35.6	F
Maroon Woodpecker	14	5.3	31.6	151.6	F	3.1	4.8	1.6	193	F
Maroon-breasted Philentoma	33.9	10	56.5	97.5	T	4.4	11.6	-1.3	-3.1	F
Moustached Babbler	25.3	15.4	35.4	18.8	F	3	4.1	2	62.1	F
Olive-backed Woodpecker	10.3	4.4	19.9	244.4	T	3.5	5.3	1.8	294	T
Olive-winged Bulbul	25.4	16.2	33	131.7	F	3.2	4.5	1.9	116	F
Orange-backed Woodpecker	25	9.2	34.3	2.2	F	3	4.3	1.8	56.1	F
Orange-bellied Flowerpecker	34.2	20.5	47.4	7.7	T	3	4.6	1.7	14.7	F
Oriental Dwarf Kingfisher	31.8	11.5	45.7	37.5	T	4.4	6.5	2.2	13.1	F
Oriental Honey Buzzard	29.3	-0.2	51.3	16.9	F	3.6	10.3	-1.5	4.2	T
Oriental Magpie Robin	28.5	13.2	42.3	1.9	F	3	4.7	1.6	34.4	F
Pied Fantail	31.1	10.9	45.4	311.4	F	3.2	5.6	1.8	13.7	T
Plain Sunbird	25.4	20.4	31.9	34.6	F	3	3.7	2.2	52.2	F
Plaintive Cuckoo	34.2	27.2	40.9	8.7	F	2.9	3.9	2	22.9	F

Puff-backed Bulbul	25.3	15.2	32.6	34.2	F	3.1	5.7	0.6	9.9	F
Purple-naped Sunbird	15.6	3.8	34.7	18.2	F	3	6.6	-0.4	2.2	T
Pygmy White-eye	33.1	-15.1	78.3	144.9	T	3.4	11.9	-5	49.5	T
Raffless Malkoha	33.2	12.9	46.7	30.3	F	3	4	2	40.2	F
Red-bearded Bee-eater	28.8	5.2	45	53.5	F	3	9.6	-1.5	13.3	F
Red-billed Malkoha	22.9	4.8	36.4	50.2	F	3.2	7.6	-0.8	3.7	F
Red-eyed Bulbul	24	12.4	30.5	24.2	F	3	4.1	1.8	57.8	F
Red-naped Trogon	34.1	20.5	43.7	3.3	F	3	4	1.9	33.7	F
Red-throated Barbet	34.1	26.5	41.1	4.5	F	3	3.9	2	28.9	F
Red-throated Sunbird	32.7	16.3	43.9	17.9	F	3.2	4.4	2	17.9	T
Rhinoceros Hornbill	26.6	20.6	35.6	20	F	3	3.8	2.2	51.8	F
Ruby-cheeked Sunbird	33.9	22.7	42.2	25.4	F	3	4.3	1.7	37.9	F
Rufous Piculet	9.4	6.4	13.7	18.4	F	3.2	4	2.3	99.1	F
Rufous Woodpecker	10.6	6	18.8	37.2	F	3.8	7	1.4	20.9	F
Rufous-chested Flycatcher	32	11.9	54.2	128.8	T	4.3	9.2	-0.7	-3.3	F
Rufous-crowned Babbler	33.9	19.2	43.6	4.5	T	3	4.1	2	18.1	F
Rufous-fronted Babbler	25.4	5.6	42.5	41.8	F	3.1	5.9	0.1	2.9	F
Rufous-tailed Shama	31.2	4.3	46.2	266.8	T	3	6.5	0.1	16.9	T
Rufous-tailed Tailorbird	34.3	20.7	44.3	22.1	F	3.8	5.6	2.1	19.8	T
Rufous-winged Philentoma	23.1	5.9	35.6	101.8	F	3.1	5.8	1.1	198	F
Scaly-crowned Babbler	22.7	16.8	30.3	57	F	3.2	4.7	1.8	66.8	F
Scarlet Minivet	20.9	-2.2	44.3	379.1	F	3	4.8	1.2	58.9	F
Scarlet-rumped Trogon	28.4	13.8	40.8	22.3	F	3	5.6	0.6	4.1	T
Short-tailed Babbler	31.8	16.4	45.1	14.9	T	3.8	5.6	2.1	12	F
Short-toed Coucal	25.2	9.5	33.4	17.7	F	4.3	8.5	1.3	2.3	F
Slender-billed Crow	29.1	3.6	48.5	32.1	F	3.1	7.9	-0.8	53.2	F
Sooty-capped Babbler	28	24	32.5	65.4	F	3	3.7	2.2	46.4	F
Spectacled Bulbul	22.8	5.5	34.8	96	F	3.2	5.7	1	292	F
Spectacled Spiderhunter	33.9	24.9	40.2	40.4	T	2.8	3.7	1.9	40.9	T
Spotted Dove	9.5	2.7	18.8	193	T	3	3.9	2.2	116	T
Spotted Fantail	28.8	18.7	41.2	38	F	2.8	3.9	1.8	30.6	F
Stork-billed Kingfisher	26.3	18.4	34.9	87.8	T	2.8	3.7	1.9	25.6	T
Streaked Bulbul	28.2	21	34.6	72.8	F	3	3.9	2.1	68.8	F
Streaky-breasted Spiderhunter	10	6.2	16.6	62.7	F	3.5	5.4	2	162	F
Striped Wren-babbler	34	22.3	44.9	10	T	3	4.5	1.5	8.9	F
Thick-billed Green-pigeon	29.4	16.8	43.1	63.8	F	3.2	5.9	1.3	-3.3	T
Tree Sparrow	29.3	6.8	46.6	240.5	T	3.2	7	0.5	69.4	T
Van Hassalts Sunbird	31.5	14	42.7	40	F	3	5	1.3	68.9	F
Velvet fronted Nuthatch	28.5	5.6	46.3	30.6	T	3	4.6	1.6	21.9	F
Verditer Flycatcher	26.4	19.4	33.2	21.1	F	3	3.7	2.3	65.6	F
Violet Cuckoo	25.4	17.9	33.5	78.4	F	3	4.5	1.6	72.5	F
Wallacess Hawk-Eagle	27.9	20.3	36.6	49.7	F	2.9	4	1.8	59.2	F
Whiskered Treeswift	25.4	17.6	33.3	66.2	F	3.1	5.5	0.7	27.9	F
White-bellied Erpornis	32.6	21.4	43.4	133	T	4.4	5.9	3	2.8	F
White-bellied Woodpecker	27.3	6.5	48.4	63.9	F	3.1	7.3	-0.3	35.9	F

White-chested Babbler	28.1	22	36.1	48.1	F	2.9	3.8	2	47.9	F
White-crowned Forktail	25.3	18.7	33.6	44.9	F	3	4.2	1.7	37.4	F
White-crowned Shama	21.9	8.1	31.8	38.5	F	3	4	2.1	105	F
Wreathed Hornbill	34	18.1	60.5	701.5	T	3.5	5.7	2.1	2.7	F
Yellow-bellied Bulbul	25.6	13	40	26.3	F	3	4.7	1.2	36.3	F
Yellow-bellied Prinia	31.5	10.4	45.7	53.6	F	2.9	4.3	1.5	13.2	F
Yellow-breasted Flowerpecker	33.9	13.3	46.7	145.6	T	3.3	4.8	1.9	117	T
Yellow-crowned Barbet	26	10.8	38.1	1.6	F	3.2	6.6	0.9	3.4	F
Yellow-eared Spiderhunter	15.9	6.6	28.7	89.5	F	3.3	5.1	1.7	252	F
Yellow-rumped Flowerpecker	32.3	21.2	39.8	36.9	F	3	5.5	0.7	13.3	F
Yellow-vented Bulbul	25.5	16	32.7	35.3	F	3	3.7	2.2	72.1	F
Yellow-vented Flowerpecker	34	21.6	41	53.7	F	3	3.8	2.1	50	F
Zebra Dove	31.6	14.1	47.4	10.8	T	3.2	4.7	2.2	14	F

Table S 3.4. Median thresholds points with confidence intervals in relation to density height and skew. Both metrics calculated from mean LiDAR values within a 50 m radius. Lower 95% confidence interval; Lw CI, Upper 95% confidence interval; Up CI. Model ΔAIC denotes the reduction in AIC between linear model and segmented model. Negative ΔAIC signifies that the linear model out performed the segmented one. G+ denotes whether thresholds were associated with a strengthing (increasing gradient G+ = True), or weakening (more negative G+ = False) response after the threshold point.

Species	Density					Skew				
	Med	Lw CI	Up CI	-Δ AIC	G+	Med	Lw CI	Up CI	- Δ AIC	G+
Arctic Warbler	-0.1	0	-0.2	20.6	T	4	5.8	2	10.8	F
Ashy Tailorbird	0	0.2	-0.2	67.4	F	6	8.2	4	11.5	F
Asian Fairy Bluebird	0	0.3	-0.3	68.3	F	2	5	0.5	12.6	T
Asian Glossy Starling	0	0.4	-0.3	4.7	F	3.6	8	-0.3	-1.3	T
Asian Paradise Flycatcher	0	0.2	-0.2	28.4	T	4	6.5	1	9.1	F
Banded Bay Cuckoo	-0.1	0.2	-0.4	50	T	1.8	2.9	0.7	26.6	F
Banded Broadbill	0	0.4	-0.4	65.9	T	5.2	9.1	0.8	11	F
Banded Kingfisher	0	1.5	-1.4	12	T	4.5	18.2	-8.6	0.5	F
Banded Pitta	0	0.4	-0.4	35	T	4.4	8.4	0.2	7.1	F
Banded Woodpecker	0	0.5	-0.5	67.9	F	6.7	9.8	3.7	13.2	F
Bar-winged Flycatcher-shrike	-0.1	0.3	-0.3	14.7	T	1.8	2.8	0.8	7.2	F
Black Hornbill	0	0.4	-0.4	34.5	T	4.9	8.4	-0.2	3.9	F
Black Magpie	0	0.5	-0.4	49.3	T	4.8	9.6	-0.6	12.5	F
Black-and-yellow Broadbill	0	0.3	-0.4	2.8	T	3.6	7.8	0.2	6.8	F
Black-bellied Malkoha	0	0.2	-0.3	47.7	F	2.1	5	-0.3	6.8	T
Black-capped Babbler	0	0.3	-0.3	93.7	T	4.6	7.1	2.3	6.6	F
Black-headed Bulbul	0.1	0.5	-0.3	-2.6	T	3.3	7.1	-0.5	2.3	T
Black-headed Pitta	-0.1	0.1	-0.2	41.8	T	1.8	2.5	1.1	39.4	F
Black-naped Monarch	0	0.3	-0.3	151.8	T	5.1	7.7	2.1	2.3	F
Black-winged Flycatcher-shrike	0	0.3	-0.3	71.3	T	4.5	8.1	1.1	4.2	F
Blue-banded Kingfisher	0	0.5	-0.4	6.3	T	4	7.6	-0.1	9.8	F
Blue-banded Pitta	0.2	0.6	-0.3	-1.7	F	6	9.3	0.6	-0.1	F
Blue-crowned Hanging-parrot	-0.1	0.2	-0.5	30.6	T	1.8	3.7	0.5	5.2	F
Blue-eared Barbet	0	0.3	-0.4	66.2	T	4.5	7	1.5	16.5	F
Blue-eared Kingfisher	0	0.4	-0.3	35.8	F	5	9	-0.1	-3.6	F

Blue-headed Pitta	0	0.3	-0.3	61.5	F	5.6	8.9	1	19.9	T
Blue-throated Bee-eater	0	0.4	-0.3	18.1	F	6.7	10.4	2.4	169.1	T
Bold-striped Tit-babbler	0	0.2	-0.2	50.9	T	4.5	6.8	2.4	-0.1	F
Bornean Blue Flycatcher	0	0.3	-0.3	32.2	F	5.5	9.1	0.7	2.3	F
Bornean Bristlehead	-0.1	0.3	-0.3	8.5	T	2.1	5.9	0.4	7.8	F
Bornean Ground-cuckoo	0.1	0.6	-0.5	2.9	F	2.3	6.9	-1.4	0.2	T
Bornean Wren-babbler	0.1	0.4	-0.3	-0.8	F	1.8	4.5	-0.5	75.8	T
Bronzed Drongo	-0.1	0.2	-0.3	11.6	F	7.2	11.2	2.9	114	F
Brown Barbet	0	0.4	-0.4	78.2	F	3.6	8.5	-0.1	6.4	T
Brown Flycatcher	-0.1	0.3	-0.5	4.4	T	4.3	9.7	1.1	-1.9	F
Brown Fulvetta	0	0.3	-0.2	2.6	T	1.9	3.5	0.5	54.5	F
Brown-throated Sunbird	0	0.4	-0.3	91.2	T	4.6	7.6	1	7.1	F
Buff-rumped Woodpecker	-0.1	0.2	-0.4	28.2	T	4.1	6.6	1.5	1.4	F
Buff-vented Bulbul	0	0.3	-0.3	-1.9	T	1.9	3.5	0.2	50	F
Bushy-crested Hornbill	0	0.6	-0.6	68.1	F	4.5	10.5	-1.1	4	T
Checker-throated Woodpecker	0.4	0.6	0.2	-1.4	F	3.4	7.4	-0.6	4.9	T
Chestnut Munia	0	0.4	-0.3	1.4	F	2.6	6.4	-0.8	1.7	T
Chestnut-backed Scimitar-babbler	0	0.2	-0.2	60.4	F	5.4	8	1.6	28.4	T
Chestnut-breasted Malkoha	0	0.4	-0.4	43.1	F	2.2	5.9	0	32.6	F
Chestnut-naped Forktail	0	0.7	-0.6	31	F	3.9	11.1	-2.8	5.2	T
Chestnut-necklaced Partridge	-0.1	0	-0.3	13	F	7.1	9.8	3.8	22.9	F
Chestnut-rumped Babbler	0	0.3	-0.4	12.6	T	2.1	4.8	0.2	19.1	F
Chestnut-winged Babbler	0	0.4	-0.3	31.3	T	4.4	8.1	1.1	-1.3	F
Collared Kingfisher	0	0.3	-0.3	63.5	T	4.4	6.9	1.1	12.5	F
Cream-vented Bulbul	0.1	0.4	-0.3	-0.3	F	1.6	3.5	-0.3	75.7	T
Crested Fireback	0.1	0.5	-0.2	-0.5	F	3.4	5.7	0.2	18.2	T
Crested Goshawk	0.2	0.7	-0.4	25.3	T	3.4	8.9	-1.6	2.2	F
Crested Jay	-0.1	0.3	-0.5	40.6	T	3.9	6.7	1.1	7.8	F
Crested Serpent-eagle	0.1	0.3	-0.2	-0.9	T	6.5	8.5	0.9	92.8	F
Crimson Sunbird	0.2	0.5	-0.2	-2.7	F	6.3	8.9	2.7	-0.2	T
Crimson-winged Woodpecker	-0.1	0.3	-0.4	18.4	T	3.6	6.5	0.4	2.4	F
Dark-necked Tailorbird	0	0.3	-0.3	373.7	T	6.2	9.9	0.9	-2.2	F
Dark-sided Flycatcher	0	0.4	-0.3	21	T	2.1	5.1	0.5	24.2	F
Dark-throated Oriole	-0.1	0.3	-0.5	26.4	T	4	8	0.7	5.7	F
Diards Trogon	0	0.3	-0.3	69.4	T	4.6	7.6	0.9	26.1	F
Drongo Cuckoo	-0.1	0	-0.2	0.8	F	6.1	9.1	1	6.1	F
Dusky Broadbill	0.1	0.3	-0.1	NA	F	1.7	2.7	0.5	71.2	F
Dusky Munia	-0.2	0.1	-0.4	58.8	T	4	6	1.6	15.9	F
Emerald Dove	-0.1	0.1	-0.2	-2.4	F	3.2	5.7	0.4	5.7	T
Ferruginous Babbler	0	0.4	-0.3	2.7	T	1.9	3.6	0.4	20	F
Fiery Minivet	-0.1	0	-0.3	-0.9	F	1.2	2.8	0.4	19.5	F
Finschs Bulbul	-0.1	0	-0.2	58.2	F	4	6	1.2	24.6	T
Fluffy-backed Tit-babbler	-0.1	0.3	-0.3	3.2	F	6.6	9.6	2.8	4	T
Golden-bellied Gerygone	-0.1	0.2	-0.4	23.9	T	3.8	6.6	0.6	-0.7	F
Gold-whiskered Barbet	0	0.3	-0.3	86.6	T	5.3	8.7	0.9	3.5	F

Great Argus	0	0.3	-0.4	54.1	T	5.5	8.5	0.8	-1	F
Great Slaty Woodpecker	-0.1	0.2	-0.3	0.6	F	6.8	12.5	0.1	142	F
Greater Coucal	0	0.2	-0.3	52.6	T	4.4	6.7	2	5.2	F
Greater Green Leafbird	0	0.4	-0.4	46.1	F	3.8	7.7	0.1	-1.9	T
Greater Racket-tailed Drongo	0	0.3	-0.3	53.6	F	4.5	7.5	0.7	23.7	T
Green Broadbill	-0.1	0.3	-0.4	18.5	T	4.2	7.3	1.2	3.3	F
Green Imperial Pigeon	-0.1	0.2	-0.4	38.7	T	4.2	6.8	1.4	6.5	F
Green Iora	-0.1	0.1	-0.3	NA	F	3.8	7.1	0.3	25	F
Grey Wagtail	-0.1	0.2	-0.5	0.6	T	7.3	10.2	3.1	-2.8	F
Grey-and-buff Woodpecker	0.1	0.3	-0.3	-1.2	T	1.7	3.2	0.3	57.8	F
Grey-bellied Bulbul	-0.1	0	-0.2	3.9	F	1.1	2.1	0.4	25.1	T
Grey-cheeked Bulbul	-0.1	0.2	-0.3	51.8	F	2.1	5.5	0.5	5.2	T
Grey-chested Jungle-flycatcher	-0.1	0.2	-0.4	18.1	T	4	6.6	1	0	F
Grey-headed Babbler	0	0.7	-0.7	28.1	T	4.3	11.2	-1.3	14.6	F
Grey-headed Canary-flycatcher	-0.1	0.2	-0.3	8.3	T	1.7	2.7	0.7	14	F
Grey-rumped Treeswift	0	0.2	-0.2	62.2	T	4.4	7.4	1	10.9	F
Hairy-backed Bulbul	-0.1	0.2	-0.3	42.4	T	4	6.3	1	10.4	F
Helmeted Hornbill	0	0.2	-0.3	32.1	F	2	3.5	0.7	36.9	T
Hill Myna	0	0.3	-0.3	1.2	F	5.8	9	0.6	-0.5	T
Hooded Pitta	-0.1	0.2	-0.5	62.1	T	1.9	3.6	0.7	6.8	F
Horsfields Babbler	0	0.3	-0.4	17.8	F	6.4	10.2	0.2	12	F
Large Green Pigeon	0.1	0.4	-0.3	-0.5	F	1.8	3.8	0.1	33.5	T
Large Woodshrike	0	0.3	-0.3	16.6	T	4.4	7.9	0.9	-2.5	F
Lesser Coucal	0.1	0.5	-0.3	-1.2	F	3.6	7.1	0	93.5	F
Lesser Green Leafbird	0	0.3	-0.3	9.3	F	1.4	3.1	0.1	24.8	F
Little Egret	-0.1	0	-0.3	24.3	T	1.7	2.5	0.5	18.8	F
Little Green Pigeon	0	0.2	-0.3	21.4	T	4.4	7.2	1.5	-1.7	F
Little Spiderhunter	-0.1	0.2	-0.3	46.3	T	1.9	2.8	0.9	26.5	F
Long-billed Spiderhunter	0	0.5	-0.4	4.4	F	4.2	9.1	0.1	46.7	T
Long-tailed Parakeet	-0.1	0	-0.3	43	T	1.8	2.8	0.7	18.4	F
Malaysian Blue Flycatcher	-0.1	0.2	-0.5	29.9	T	3.8	7.4	1	4	F
Maroon Woodpecker	0	0.3	-0.2	2.6	T	1.9	3.1	0.4	61	F
Maroon-breasted Philentoma	0	0.4	-0.3	31.9	T	3.2	8.4	-0.7	-1.9	F
Moustached Babbler	-0.1	0.2	-0.4	10.4	T	1.8	3.3	0.7	2.1	F
Olive-backed Woodpecker	0.1	0.3	-0.2	0	F	1.7	3.3	0.1	33.3	T
Olive-winged Bulbul	-0.1	0	-0.2	0.9	T	5.7	9.2	0.7	22.5	F
Orange-backed Woodpecker	0.2	0.6	-0.3	-0.1	T	3.8	7	0.3	-0.6	F
Orange-bellied Flowerpecker	-0.1	0.2	-0.4	11.8	T	4.4	8.5	1.9	0.4	F
Oriental Dwarf Kingfisher	0	0.3	-0.4	0.3	T	4.3	7.4	0.6	1.5	T
Oriental Honey Buzzard	0	0.6	-0.5	23.9	F	3.3	9.2	-2.8	1.1	T
Oriental Magpie Robin	-0.1	0.3	-0.4	24.2	T	3.6	6.7	0.5	4.4	F
Pied Fantail	0	0.2	-0.2	60.9	F	5.2	7.5	1.9	12.8	T
Plain Sunbird	-0.1	0.2	-0.5	33.1	T	1.8	4.1	0.6	7.4	F
Plaintive Cuckoo	-0.1	0.2	-0.4	29.3	T	4	6.9	1.6	7.2	F
Puff-backed Bulbul	0	0.3	-0.3	8.4	T	4.8	9.2	0.1	10.2	T

Purple-naped Sunbird	0	0.2	-0.3	73	F	1.9	4	0.5	4.1	T
Pygmy White-eye	0	1	-0.9	9.9	F	2.2	10.3	-5.5	6.1	T
Raffless Malkoha	-0.2	0.1	-0.4	72.8	T	4	6	1	14.8	F
Red-bearded Bee-eater	0	0.8	-0.7	8.8	T	4.5	11.2	-3.3	8.6	F
Red-billed Malkoha	0	0.6	-0.5	38.6	F	6.2	11.2	-1.6	18.5	T
Red-eyed Bulbul	0	0.4	-0.2	-2.6	T	3.9	7.2	0.5	1.7	F
Red-naped Trogon	-0.1	0.3	-0.5	20.9	T	4	7.4	0.5	2.3	F
Red-throated Barbet	-0.1	0.3	-0.5	61.4	T	4	6.2	1.9	12.2	F
Red-throated Sunbird	0	0.2	-0.2	37.8	F	4.4	7	1.7	8.5	T
Rhinoceros Hornbill	-0.1	0.2	-0.5	24.4	T	3.9	6.2	1	3.2	F
Ruby-cheeked Sunbird	-0.1	0.3	-0.5	51.9	T	4	8.1	0.6	11.5	F
Rufous Piculet	-0.1	0.1	-0.3	0.4	T	1.1	2.1	0.2	12.5	F
Rufous Woodpecker	0	0.4	-0.4	37.3	F	6.6	9.9	3.2	21	F
Rufous-chested Flycatcher	0	0.4	-0.3	64.3	T	5.5	9.8	-0.3	-2	F
Rufous-crowned Babbler	-0.1	0.2	-0.4	17.5	T	4.2	7.4	1.9	0.3	F
Rufous-fronted Babbler	0	0.4	-0.4	38.2	F	3.1	8.2	-0.1	33.8	T
Rufous-tailed Shama	0	0.2	-0.3	41.9	F	2	3.4	0.7	28.2	T
Rufous-tailed Tailorbird	0	0.2	-0.2	22.6	F	5.1	7.5	1.4	7.4	T
Rufous-winged Philentoma	0	0.3	-0.3	-1.8	T	3	7.6	0.3	48	F
Scaly-crowned Babbler	-0.1	0.1	-0.3	16.8	F	6.7	10.1	3.1	12.1	F
Scarlet Minivet	0	0.2	-0.2	30.9	T	1.9	3	0.7	37.3	F
Scarlet-rumped Trogon	0	0.2	-0.2	40.8	F	5.4	7.9	1.3	18.3	T
Short-tailed Babbler	-0.1	0.2	-0.4	0.5	T	4.1	7.8	1.1	-3.5	T
Short-toed Coucal	0	0.4	-0.3	54.1	F	4	8.5	0.2	2.6	T
Slender-billed Crow	0	0.7	-0.6	23.6	T	4.4	12.2	-2.2	14.3	F
Sooty-capped Babbler	-0.1	0	-0.3	56.5	T	3.8	5.6	1.2	16.1	F
Spectacled Bulbul	0.1	0.4	-0.3	-1.4	T	2.2	6.3	-0.5	93.4	F
Spectacled Spiderhunter	-0.1	0.2	-0.3	67.3	F	4.5	6.5	2.2	24.8	T
Spotted Dove	-0.1	0.2	-0.2	17.9	F	1.7	2.6	0.9	36.5	T
Spotted Fantail	0	0.2	-0.2	58.1	T	4.6	7.1	2.1	23.9	F
Stork-billed Kingfisher	-0.2	0.1	-0.4	66.7	F	4.5	6.4	3.1	22.7	T
Streaked Bulbul	-0.1	0	-0.3	16.5	T	1.7	2.8	0.6	15.6	F
Streaky-breasted Spiderhunter	0.1	0.4	-0.3	-0.1	F	1.7	3.7	0.1	67.6	F
Striped Wren-babbler	-0.1	0.2	-0.5	13.6	T	4	6.8	1.2	3.4	F
Thick-billed Green-pigeon	0	0.2	-0.2	67.7	F	5.8	8.6	1.7	10.1	T
Tree Sparrow	0	0.4	-0.4	52	F	2.5	8.4	-0.4	22.4	T
Van Hassalts Sunbird	0	0.4	-0.4	14.9	T	4.7	9.3	0.3	7	F
Velvet fronted Nuthatch	-0.1	0.2	-0.4	43.4	T	1.9	3.8	0.8	9.4	F
Verditer Flycatcher	-0.1	0.2	-0.3	9.3	T	3.4	5.6	0.6	1.5	F
Violet Cuckoo	-0.1	0.2	-0.3	-1.2	F	6.7	11.3	2	7.3	F
Wallacess Hawk-Eagle	0	0.6	-0.4	21	T	3.7	6.1	0.1	10.6	F
Whiskered Treeswift	-0.1	0.4	-0.6	10.9	F	6.7	10	3.5	4.9	F
White-bellied Erpornis	0	0.1	-0.2	22.9	T	4.4	6.7	1.7	-3.3	T
White-bellied Woodpecker	0	0.5	-0.5	22.9	T	4.5	10	-0.8	2	F
White-chested Babbler	-0.1	0.3	-0.4	45	T	1.8	3.3	0.7	17.8	F

White-crowned Forktail	0	0.3	-0.3	39.5	T	6.3	9.8	2.5	-0.7	F
White-crowned Shama	-0.1	0.1	-0.3	2.8	T	1.1	2.2	0.3	20.6	F
Wreathed Hornbill	0	0.2	-0.2	58.5	T	4.5	6.7	2.4	1.8	F
Yellow-bellied Bulbul	0.2	0.7	-0.5	2.7	T	6.5	12.1	-0.2	0.1	F
Yellow-bellied Prinia	0	0.1	-0.2	54.7	T	5.4	7.7	2.4	22.3	F
Yellow-breasted Flowerpecker	-0.1	0	-0.3	12.9	F	1.2	2.5	0.5	13.9	T
Yellow-crowned Barbet	0	0.4	-0.3	72.3	F	5.1	8.9	0.4	8	F
Yellow-eared Spiderhunter	0.1	0.3	-0.3	-0.8	T	3.1	6	0.4	99.8	F
Yellow-rumped Flowerpecker	0	0.3	-0.3	414.9	T	6.4	10.2	2.1	-1.7	F
Yellow-vented Bulbul	-0.1	0.1	-0.3	17.1	T	1.2	2.6	0.7	11.3	F
Yellow-vented Flowerpecker	-0.1	0.1	-0.4	76.3	T	3.8	5.9	1	17.5	F
Zebra Dove	-0.1	0.2	-0.4	1.1	T	4	7.4	0.9	-3	F

Table S 3.5. Median thresholds points with confidence intervals in relation to density height and skew. Forest calculated from mean values of Gaveau *et al*, (2014)., forest cover layer within a 50 m radius. Lower 95% confidence interval; Lw CI, Upper 95% confidence interval; Up CI. Model ΔAIC denotes the reduction in AIC between linear model and segmented model. Negative ΔAIC signifies that the linear model out performed the segmented one. G+ denotes whether thresholds were associated with a strengthing (increasing gradient G+ = True), or weakening (more negative G+ = False) response after the threshold point.

Species	Forest Cover				
	Med	Lw CI	Up CI	-Δ AIC	G+
Arctic Warbler	0.8	1.3	0.2	131.7	T
Ashy Tailorbird	0.8	1.1	0.4	3.6	F
Asian Fairy Bluebird	0.6	1.2	0	3	F
Asian Glossy Starling	0.1	0.5	-0.2	3.7	F
Asian Paradise Flycatcher	0.1	0.6	-0.2	6	T
Banded Bay Cuckoo	0.8	1.2	0.1	2.2	T
Banded Broadbill	0.6	1.4	-0.4	21.3	T
Banded Kingfisher	0.8	3	-1.4	12.8	T
Banded Pitta	0.2	1.1	-0.1	3.5	T
Banded Woodpecker	0.3	0.9	-0.2	10	F
Bar-winged Flycatcher-shrike	0.6	1.3	-0.1	143.3	T
Black Hornbill	0.1	1	-0.1	-1	F
Black Magpie	0.6	1.6	-0.4	28.4	T
Black-and-yellow Broadbill	0.1	1.1	-0.2	6.2	F
Black-bellied Malkoha	0.8	1.1	0.3	0	F
Black-capped Babbler	0.8	1.3	0.2	10.8	T
Black-headed Bulbul	0.1	0.5	-0.2	6.4	T
Black-headed Pitta	0.1	0.3	-0.1	0.3	F
Black-naped Monarch	0.2	1.1	-0.1	-1.3	T
Black-winged Flycatcher-shrike	0.8	1.6	-0.1	7.6	T
Blue-banded Kingfisher	0.6	1.3	-0.2	195	T
Blue-banded Pitta	0.6	1.5	-0.2	46.7	T
Blue-crowned Hanging-parrot	0.8	1.2	0.3	8.8	T
Blue-eared Barbet	0.8	1.3	0.1	25.3	T
Blue-eared Kingfisher	0.1	0.7	-0.2	NA	F

Blue-headed Pitta	0.5	1.2	-0.2	-0.9	F
Blue-throated Bee-eater	0.8	1.2	0.2	-1	T
Bold-striped Tit-babbler	0.8	1.2	0.4	5.9	T
Bornean Blue Flycatcher	0.6	1.2	-0.1	8.7	F
Bornean Bristlehead	0.5	1.1	-0.1	11.7	T
Bornean Ground-cuckoo	0.1	0.7	-0.3	12.2	T
Bornean Wren-babbler	0.1	0.4	-0.2	472.4	T
Bronzed Drongo	0.1	0.4	-0.2	138.9	F
Brown Barbet	0.4	1	-0.1	11.2	F
Brown Flycatcher	0.8	1.6	0	23.4	T
Brown Fulvetta	0.1	0.2	-0.1	103.7	F
Brown-throated Sunbird	0.6	1.2	-0.1	5.8	T
Buff-rumped Woodpecker	0.8	1.4	0.2	29.3	T
Buff-vented Bulbul	0.1	0.4	-0.2	175.8	F
Bushy-crested Hornbill	0.6	1.4	-0.2	12.9	F
Checker-throated Woodpecker	0.1	1	-0.2	18.5	F
Chestnut Munia	0.6	1.2	-0.2	10.6	F
Chestnut-backed Scimitar-babbler	0.8	1.3	0.4	3.5	F
Chestnut-breasted Malkoha	0.1	1	-0.2	106	F
Chestnut-naped Forktail	0.6	1.4	-0.5	8.7	F
Chestnut-necklaced Partridge	0.1	0.7	-0.3	7.1	F
Chestnut-rumped Babbler	0.2	1.1	-0.1	6.6	F
Chestnut-winged Babbler	0.8	1.4	0.2	11	T
Collared Kingfisher	0.8	1.3	0	18.8	T
Cream-vented Bulbul	0.1	0.5	-0.4	543.5	T
Crested Fireback	0.1	0.7	-0.3	398.5	T
Crested Goshawk	0.1	0.7	-0.3	24	T
Crested Jay	0.8	1.2	0.3	15.8	T
Crested Serpent-eagle	0.1	0.3	-0.1	373.2	F
Crimson Sunbird	0.8	1.2	0.2	51.3	T
Crimson-winged Woodpecker	0.7	1.4	-0.1	33	T
Dark-necked Tailorbird	0.5	1.2	-0.3	4.2	T
Dark-sided Flycatcher	0.1	0.8	-0.1	12.8	F
Dark-throated Oriole	0.7	1.5	-0.2	41	T
Diards Trogon	0.8	1.3	-0.1	11.9	T
Drongo Cuckoo	0.6	1.3	-0.2	-1.7	F
Dusky Broadbill	0.1	0.2	-0.1	362.4	F
Dusky Munia	0.8	1.2	0.4	24.4	T
Emerald Dove	0.5	1.1	-0.1	17.8	F
Ferruginous Babbler	0.1	1	-0.1	8.3	F
Fiery Minivet	0.1	0.4	-0.3	22.8	F
Finschs Bulbul	0.8	1.2	0.4	18	F
Fluffy-backed Tit-babbler	0.8	1.2	0.4	23.4	T
Golden-bellied Gerygone	0.8	1.3	0	28.8	T
Gold-whiskered Barbet	0.1	1	-0.1	1.5	F

Great Argus	0.8	1.1	0.3	0.3	T
Great Slaty Woodpecker	0.1	0.6	-0.3	209.2	F
Greater Coucal	0.8	1.3	0.3	17.5	T
Greater Green Leafbird	0.5	1.2	-0.2	6.7	F
Greater Racket-tailed Drongo	0.5	1.3	-0.2	24.3	F
Green Broadbill	0.8	1.4	0.2	16.1	T
Green Imperial Pigeon	0.8	1.3	0.1	20.9	T
Green Iora	0.1	1.2	-0.3	101.2	F
Grey Wagtail	0.8	1.4	0.2	58.2	T
Grey-and-buff Woodpecker	0.1	0.3	-0.1	310	F
Grey-bellied Bulbul	0.6	1.2	-0.2	78	T
Grey-cheeked Bulbul	0.6	1.1	-0.1	2.5	F
Grey-chested Jungle-flycatcher	0.8	1.4	0.2	39.6	T
Grey-headed Babbler	0.6	1.6	-0.5	11.1	T
Grey-headed Canary-flycatcher	0.1	1.1	-0.2	22.9	T
Grey-rumped Treeswift	0.1	0.4	-0.1	-0.7	T
Hairy-backed Bulbul	0.1	0.5	-0.1	9.1	T
Helmeted Hornbill	0.1	0.3	-0.1	17.3	T
Hill Myna	0.3	1.2	-0.2	0.9	T
Hooded Pitta	0.8	1.1	0.4	4.9	T
Horsfields Babbler	0.8	1.2	0.4	10.9	F
Large Green Pigeon	0.1	0.6	-0.3	528.9	T
Large Woodshrike	0.8	1.3	0.2	8.4	T
Lesser Coucal	0.1	0.6	-0.2	161.3	F
Lesser Green Leafbird	0.1	0.3	-0.1	36	F
Little Egret	0.6	1.3	-0.1	20.8	T
Little Green Pigeon	0.8	1.3	0.2	9.1	T
Little Spiderhunter	0.5	1.1	-0.1	2.8	T
Long-billed Spiderhunter	0.6	1.3	-0.2	12.2	T
Long-tailed Parakeet	0.8	1.3	0.1	31.3	T
Malaysian Blue Flycatcher	0.6	1.3	0	29.5	T
Maroon Woodpecker	0	0.2	-0.1	175.8	F
Maroon-breasted Philentoma	0	0.2	-0.1	13.1	F
Moustached Babbler	0.8	1.2	0.2	20.4	T
Olive-backed Woodpecker	0.1	0.3	-0.2	606.6	T
Olive-winged Bulbul	0.1	0.6	-0.1	23.5	F
Orange-backed Woodpecker	0.1	1.3	-0.4	102.1	T
Orange-bellied Flowerpecker	0.8	1.4	-0.1	29.5	T
Oriental Dwarf Kingfisher	0.6	1.3	-0.1	20.9	T
Oriental Honey Buzzard	0.6	1.3	-0.3	1.5	F
Oriental Magpie Robin	0.7	1.2	-0.1	22	T
Pied Fantail	0.2	0.9	0	-0.3	F
Plain Sunbird	0.8	1.2	0.4	28.5	T
Plaintive Cuckoo	0.8	1.3	0.2	30	T
Puff-backed Bulbul	0.3	1.2	-0.2	2.7	T

Purple-naped Sunbird	0.8	1.2	0.4	2.7	F
Pygmy White-eye	0.1	1.8	-0.8	-0.1	T
Raffless Malkoha	0.8	1.2	0.4	5.1	T
Red-bearded Bee-eater	0.1	1.8	-0.9	6.5	T
Red-billed Malkoha	0.3	1.3	-0.4	-0.6	F
Red-eyed Bulbul	0.6	1.2	-0.3	153.5	T
Red-naped Trogon	0.8	1.3	0.2	42.7	T
Red-throated Barbet	0.8	1.2	0.3	19.6	T
Red-throated Sunbird	0.1	1.1	-0.1	9.5	F
Rhinoceros Hornbill	0.6	1.3	0.1	44.6	T
Ruby-cheeked Sunbird	0.8	1.3	0.1	19.4	T
Rufous Piculet	0.1	0.5	-0.3	1.1	F
Rufous Woodpecker	0.6	1.1	0.1	8	F
Rufous-chested Flycatcher	0.1	0.6	-0.1	9	F
Rufous-crowned Babbler	0.8	1.3	0.1	27.7	T
Rufous-fronted Babbler	0.1	1.1	-0.3	-2.6	F
Rufous-tailed Shama	0.6	1.1	0	4.3	T
Rufous-tailed Tailorbird	0.1	0.3	-0.1	-2.3	F
Rufous-winged Philentoma	0.1	1.1	-0.1	220.9	F
Scaly-crowned Babbler	0.3	1.2	-0.3	5.4	F
Scarlet Minivet	0	0.2	-0.1	18.2	F
Scarlet-rumped Trogon	0.1	0.6	0	NA	F
Short-tailed Babbler	0.8	1.3	0	34.7	T
Short-toed Coucal	0.6	1.1	0.1	4.9	F
Slender-billed Crow	0.1	1.4	-0.5	67.4	T
Sooty-capped Babbler	0.8	1.2	0.4	16.3	T
Spectacled Bulbul	0.1	0.4	-0.2	373.5	F
Spectacled Spiderhunter	0.8	1.5	0	40.5	F
Spotted Dove	0	0.2	-0.1	25.2	T
Spotted Fantail	0.6	1.2	-0.1	19.5	T
Stork-billed Kingfisher	0.8	1.2	0.5	16.8	F
Streaked Bulbul	0.7	1.3	0	18.1	T
Streaky-breasted Spiderhunter	0.1	0.3	-0.1	112.2	F
Striped Wren-babbler	0.8	1.4	0.3	27	T
Thick-billed Green-pigeon	0.1	0.5	0	5	T
Tree Sparrow	0.1	1.1	-0.2	NA	F
Van Hassalts Sunbird	0.5	1.4	-0.3	47.1	T
Velvet fronted Nuthatch	0.8	1.2	0.3	5.2	T
Verditer Flycatcher	0.6	1.4	-0.1	93.6	T
Violet Cuckoo	0.1	1.2	-0.4	-2.6	F
Wallacess Hawk-Eagle	0.6	1.6	-0.5	73.3	T
Whiskered Treeswift	0.1	0.5	-0.3	5	F
White-bellied Erpornis	0.8	1.2	0	10.2	T
White-bellied Woodpecker	0.4	1.3	-0.3	7.1	T
White-chested Babbler	0.8	1.4	0.2	41.3	T

White-crowned Forktail	0.5	1.3	-0.3	24	T
White-crowned Shama	0.1	0.5	-0.3	11.4	F
Wreathed Hornbill	0.8	1.1	0.4	5.5	T
Yellow-bellied Bulbul	0.8	2.3	-1.2	102.7	T
Yellow-bellied Prinia	0.1	0.7	0	-1	T
Yellow-breasted Flowerpecker	0.6	1.3	-0.1	13.4	T
Yellow-crowned Barbet	0.1	0.6	-0.1	47.7	F
Yellow-eared Spiderhunter	0.1	0.5	-0.1	327.7	F
Yellow-rumped Flowerpecker	0.1	1	-0.6	3.9	T
Yellow-vented Bulbul	0.6	1.2	-0.1	58.3	T
Yellow-vented Flowerpecker	0.8	1.2	0.4	11.7	T
Zebra Dove	0.8	1.3	0.3	26.9	T

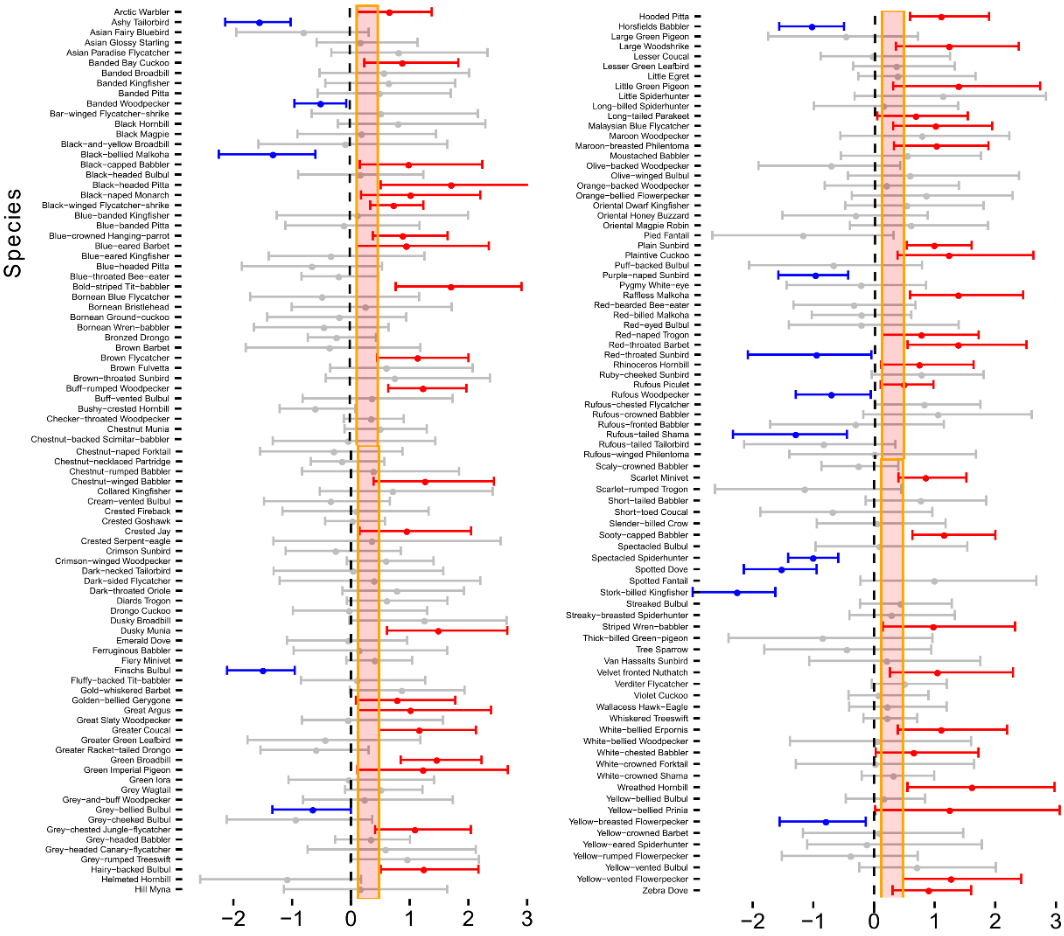

Figure S 3.1. Occupancy-modelled species-level effects of mean canopy height within 50 m radius. Median values with 95% Bayesian credible intervals are displayed for each species. Significant positive associations are denoted in red, significant negative assocations in blue. 95% Bayesian credible intervals for whole community-average effect (model effect hyperparameters) denoted by pink band.

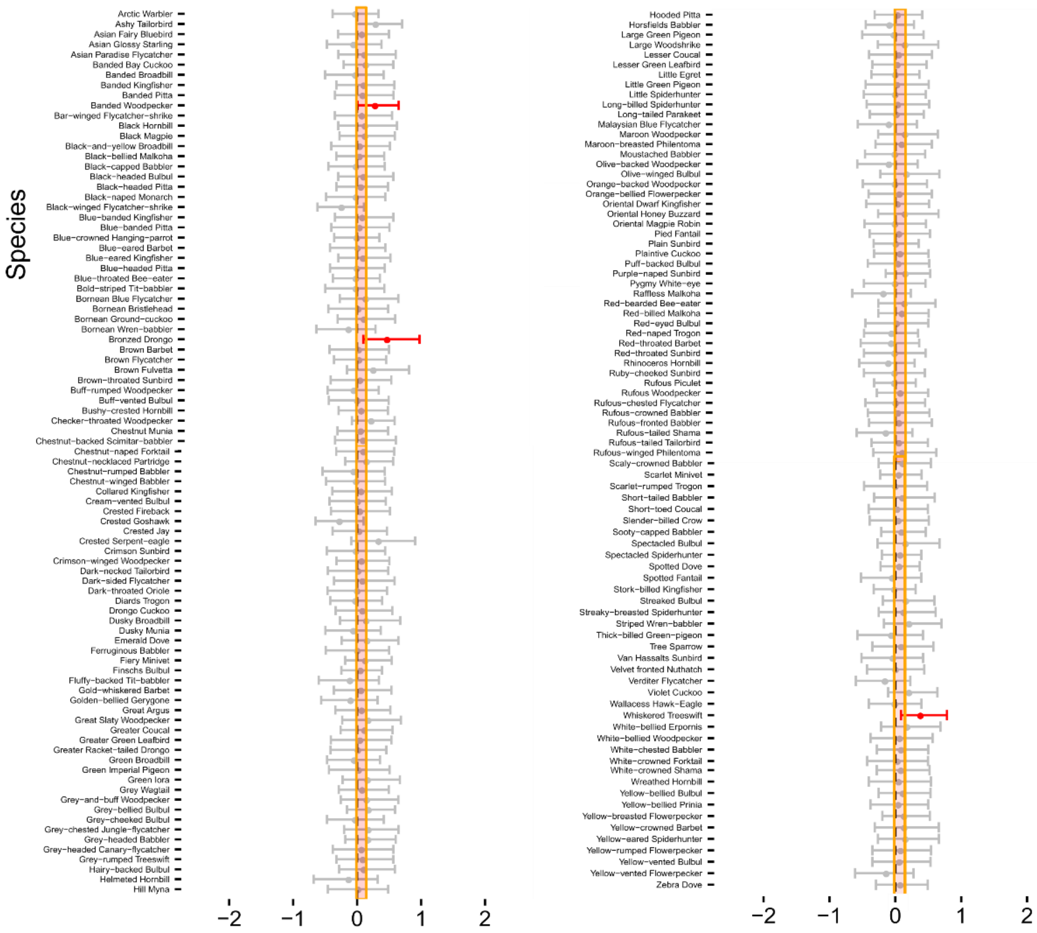

Figure S 3.2. Occupancy-modelled species-level effects of canopy heterogeneity with 50 m radius. Median values with 95% Bayesian credible intervals are displayed for each species. Significant positive associations are denoted in red. 95% Bayesian credible intervals for whole community average effect (model effect hyperparameters) denoted by pink band.

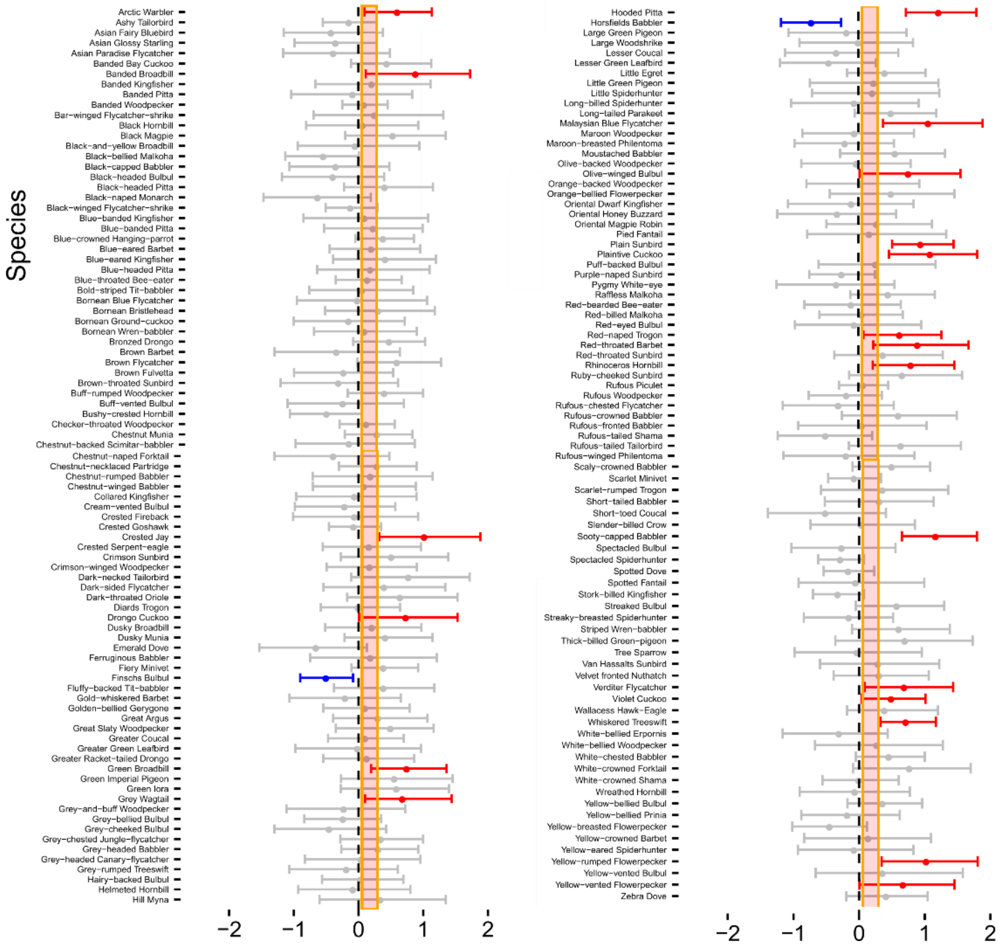

Figure S 3.3. Occupancy-modelled species-level effects of mean vegetation density within 50 m radius. Median values with 95% Bayesian credible intervals are displayed for each species. Significantly positive associations are denoted in red, significant negative assocations in blue. 95% Bayesian credible intervals for whole community average effect (model effect hyperparameters) denoted by pink band.

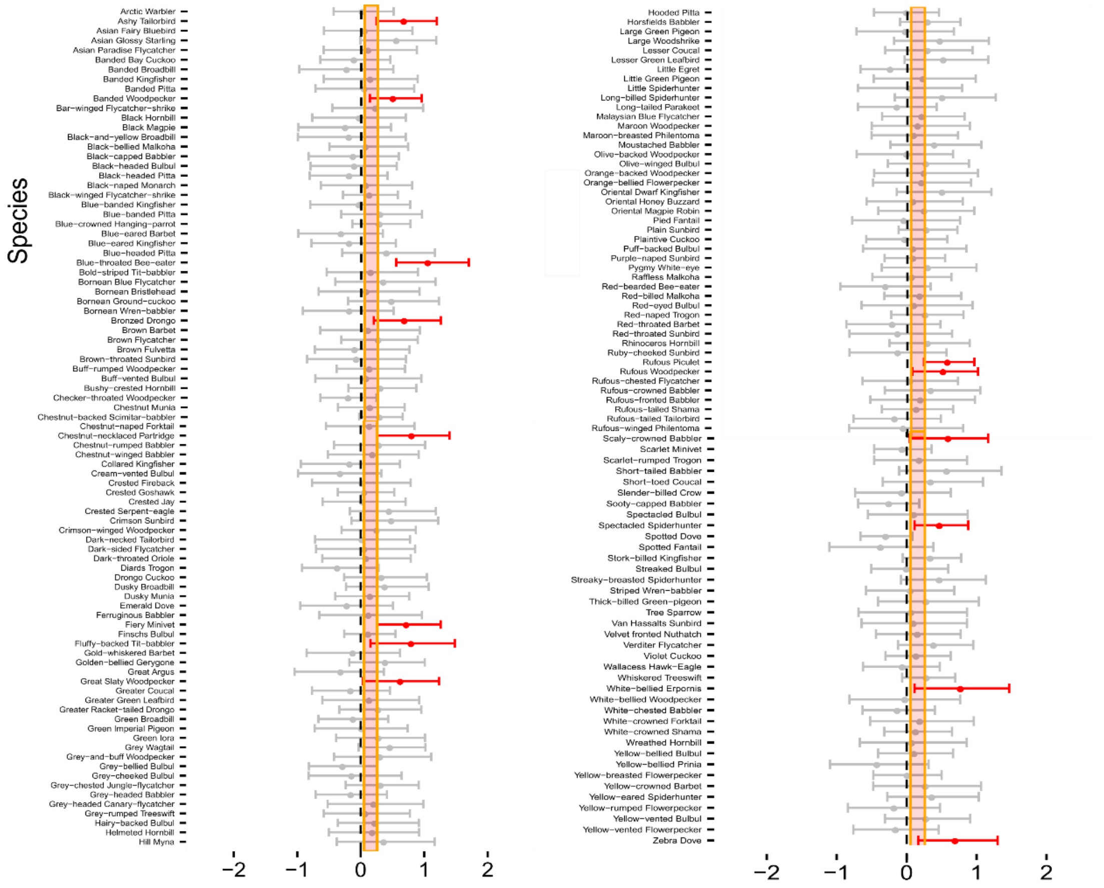

Figure S 3.4. Occupancy-modelled species-level effects of mean vegetation skew within 50 m radius. Median values with 95% Bayesian credible intervals are displayed for each species. Significantly positive associations are denoted in red. 95% Bayesian credible intervals for whole community average effect (model effect hyperparameters) denoted by pink band.

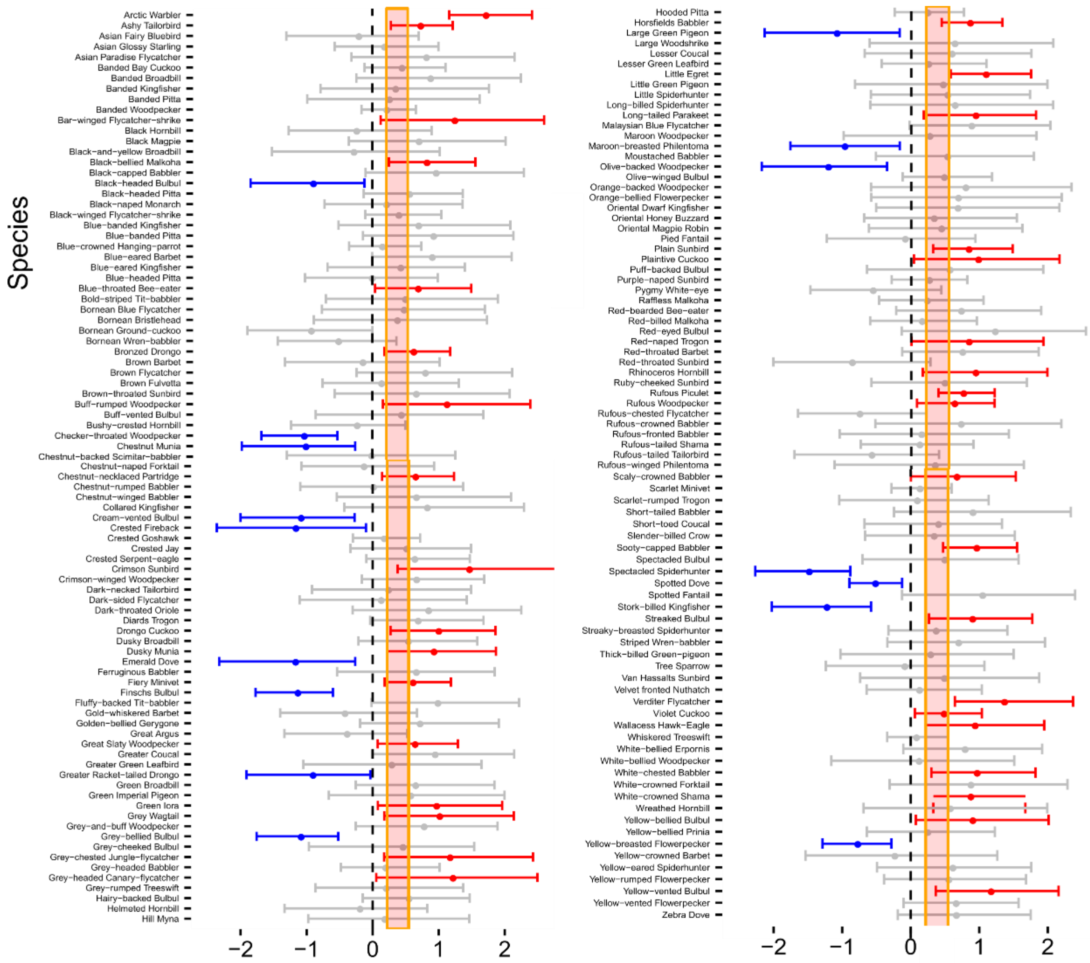

Figure S 3.5. Occupancy-modelled species-level effects of forest cover within 100 m radius. Median values with 95% Bayesian credible intervals are displayed for each species. Significantly positive associations are denoted in red, significant negative assocations in blue. 95% Bayesian credible intervals for whole community average effect (model effect hyperparameters) denoted by pink band.

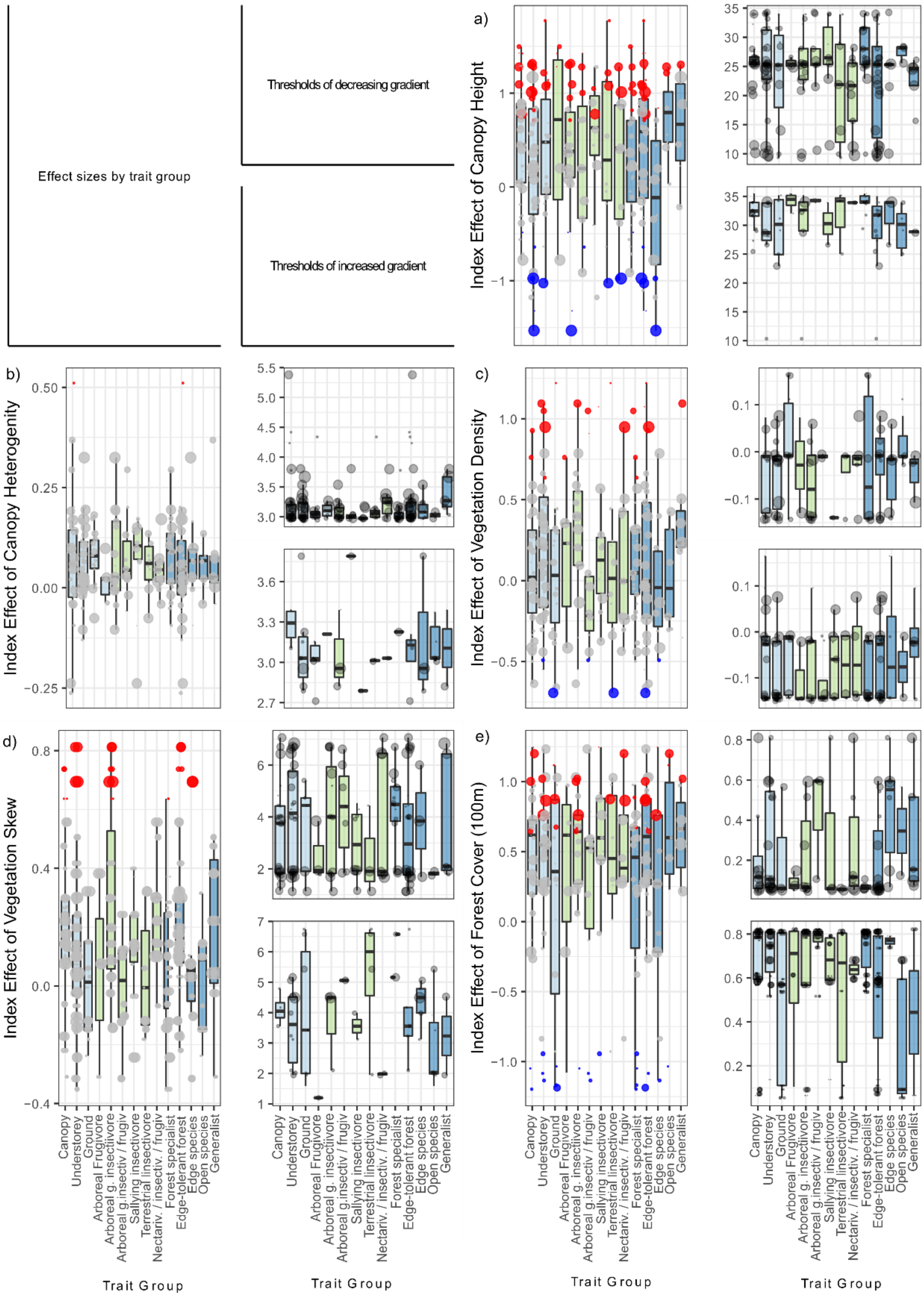

Figure S 3.6. Boxplots showing the distribution of threshold levels for different strata associatons, feeding guilds and habitat assocations (pale blue, pale green and dark blue respectively) listed for each environmental metric: a) mean canopy height in 50 m radius; b) canopy heterogeneity in 50 m radius; c) mean vegetation density in 50 m radius; d) mean skew in 50 m radius; e) mean forest cover in 50 m radius. Red dots indicate species with significant positive effects. Blue dots are species with significant negative effects. Grey dots indicate no significant effect. The size of dots correspond to the abundance of each species across the global dataset. Larger sub-panels for each metric (left side) denote all species for which segmented models had reduction in ΔAIC >4. Upper right panels denote the subset of species where thresholds were associated with decreasing gradient of reponse. Lower right panels denote the subset of species where thresholds were associated with increasing gradient of reponse.

Table S 3.6. Results of Kruskal Wallis tests for differences in group average effects and threshold levels between trait groups (Fig. S6). Results are given for each environmental metric included in the overall occupancy model.

Environmental metric / group	statistic	parameter	p value
Canopy height effects strata	1.5	2	0.472
Canopy height effects guilds	1.47	5	0.916
Canopy height effects habitat groups	9.54	4	0.049
Canopy height +g thresholds strata groups	0.49	2	0.784
Canopy height +g thresholds guilds	4.84	5	0.435
Canopy height +g thresholds habitat groups	6.66	4	0.155
Canopy height -g thresholds strata groups	1.84	2	0.399
Canopy height -g thresholds guilds	3.52	5	0.62
Canopy height -g thresholds habitat groups	5.93	4	0.205
Canopy heterogen. effects strata	2.39	3	0.495
Canopy heterogen. effects guilds	1.54	4	0.819
Canopy heterogen. effects habitat groups	2.56	4	0.634
Canopy heterogen. +g thresholds strata groups	5.45	3	0.142
Canopy heterogen. +g thresholds guilds	2.33	4	0.675
Canopy heterogen. +g thresholds habitat groups	0.96	4	0.916
Canopy heterogen. -g thresholds strata groups	2.02	3	0.568
Canopy heterogen. -g thresholds guilds	1.62	4	0.805
Canopy heterogen. -g thresholds habitat groups	3.24	4	0.518
Vegetation density effects strata	2.04	2	0.36
Vegetation density effects guilds	3.85	5	0.571
Vegetation density effects habitat groups	2.88	4	0.578
Vegetation density +g thresholds strata groups	1.45	2	0.485
Vegetation density +g thresholds guilds	3.43	5	0.634
Vegetation density +g thresholds habitat groups	2.11	4	0.716
Vegetation density -g thresholds strata groups	3.97	2	0.138
Vegetation density -g thresholds guilds	4.26	5	0.513
Vegetation density -g thresholds habitat groups	6.37	4	0.173
Vegetation skew effects strata	5.38	2	0.068
Vegetation skew effects guilds	8.53	6	0.202
Vegetation skew effects habitat groups	5.53	4	0.237
Vegetation skew +g thresholds strata groups	2.87	2	0.238
Vegetation skew +g thresholds guilds	3.45	5	0.631
Vegetation skew +g thresholds habitat groups	1.11	4	0.893
Vegetation skew -g thresholds strata groups	2.21	2	0.331
Vegetation skew -g thresholds guilds	5.89	5	0.317
Vegetation skew -g thresholds habitat groups	5.2	4	0.268
Forest cover (100m r) effects strata	0.44	2	0.804
Forest cover (100m r) effects guilds	1.52	5	0.911

Forest cover (100m r) effects habitat groups	4.34	4	0.362
Forest cover (100m r) +g thresholds strata groups	0.81	2	0.669
Forest cover (100m r) +g thresholds guilds	4.73	5	0.45
Forest cover (100m r) +g thresholds habitat groups	2.95	4	0.567
Forest cover (100m r) -g thresholds strata groups	0.31	2	0.855
Forest cover (100m r) -g thresholds guilds	4.7	5	0.453
Forest cover (100m r) -g thresholds habitat groups	3.63	4	0.458

Ackowledgements

This study was funded by the UK Natural Environment Research Council (NERC) (NE/K016407/1; http://lombok.hmtf.info/ and http://bali.hmtf.info; NE/K016377/1), and a Newton-Ungku Omar Fund grant from the British Council and Malaysia Industry-Group for High Technology (MIGHT) (216433953). SLM was supported by a PhD scholarship jointly funded by University of Kent and NERC. We thank the Sabah Biodiversity Council, Sabah Forest Department, Yayasan Sabah, Sime Darby, Benta Wawasan, Sabah Softwoods and Innoprise Foundation for permitting site access. We are grateful to Unding Jami and the LOMBOK research assistant team for their field assistance, and Suzan Benedic and Ryan Gray for facilitating fieldwork.

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Chapter 4. Sound methods for monitoring tropical biodiversity: Optimising acoustic indices to reflect species richness in forest habitats

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Abstract

Approaches to characterise and monitor biodiversity based on the sound signals of ecosystems appear to offer great potential, with acoustic indices reflecting avian species richness in a variety of environments. However, to date validation studies of how well acoustic indices reflect observed patterns of biodiversity have tended to use relatively low levels of spatial replication and have focussed on habitats with similar underlying anthropological and geophysical sound characteristics. For acoustic indices to be broadly applicable to biodiversity surveys and monitoring, their capacity to measure the ecological facets of soundscapes must be robust to these potential sources of bias. We examined the efficacy of five commonly used acoustic indices to reflect patterns of observed and estimated avian species richness across a land-cover gradient in Northeast Borneo. The gradient comprised intact forests to oil palm plantations, thus providing a highly variable anthrophonic and geophonic soundscape. We found that *Acoustic Complexity* had the strongest relationship with observed bird richness in old growth forest and logged forest, but that *Acoustic Evenness* had the strongest (negative) association with observed richness in riparian areas. No acoustic indices were associated with observed richness in oil palm riparian areas. We attempted to improve the associations between acoustic indices and species richness by digitally reducing background noise outside of the vocal frequency range for birds, controlling for time-of-day, and removing a habitat with high anthropogenic influence. Our *Adjusted Bioacoustic Index* was better than unaggregated point counts at capturing changes in species richness associated with changing canopy height, and the association between the *Adjusted Bioacoustic Index* and canopy height was comparable to that when species richness was estimated via occupancy-modelling.

Our findings underscore the potential utility of soundscape approaches to characterise biodiversity patterns in human-modified tropical landscapes, but demonstrate that for acoustic indices to be more effective the bias introduced by time-of-day, geophonic noise, cicada choruses and human voices needs to be better accounted for.

Introduction

In the midst of the current environmental crisis (Rockstrom *et al.*, 2009; Ripple *et al.*, 2017) conservation practitioners are seeking more efficient and cost-effective ways of monitoring biodiversity (Bustamante *et al.*, 2015). Recent advances have included the application of new remote sensing technologies (Pettorelli *et al.*, 2014), such as the use of Light Detection And Ranging (LiDAR; Guo *et al.*, 2017) and Synthetic Aperture Radar (Villard *et al.*, 2016) to identify species habitat associations (Taft *et al.*, 2003). Additional developments include, new statistical approaches to derive robust estimates of species occupancy from sparse data for rare species (Royle & Kery, 2007), novel methods environmental DNA procedure facilitating rapid impact assessments (Valentini *et al.*, 2006), and the use of autonomous wildlife surveillance methods, such as camera traps and sound-recorders (Harrison *et al.*, 2012).

The increased availability and reduced cost of sound-recorders has opened up an entirely new field of conservation research and practice. Soundscape ecology is concerned with the same basic principles and questions as landscape ecology, including a focus on how acoustic signals in a particular location change with time, habitat-disturbance, and patterns of biological and human activity (Gasc *et al.*, 2016). One of the main focuses of soundscape assessments is to discern patterns of biodiversity (Pijanowski *et al*., 2006). This differs from the field of bioacoustics, which tends to focus on the physics and variation of biological sound production among organisms.

Birds are excellent surrogates for wider patterns of biodiversity (Lewandowski *et al*., 2008; Gardner *et al*., 2008) and are also one of the most dominant terrestrial taxonomic groups in terms of abundance, biomass and contribution to soundscapes (Gasc *et al*., 2016). Due to these characteristics, they have been a focus of efforts to characterise or estimate species richness and community structure from soundscape recordings. A large number of indices have been developed to statistically describe the distribution of acoustic information in a given recording. Some of these acoustic indices seek to determine variation in anthropogenic disturbance (i.e. 'anthrophony'; Kasten *et al*., 2012), or acoustic dissimilarity between recordings (Sueur *et al*., 2008), whilst the majority are designed to reflect the richness and complexity of ecological communities, such as total acoustic complexity, entropy or bioacoustic activity (e.g Pieretti *et al*., 2011; Sueur *et al*., 2008; Depraetere *et al*., 2012). Acoustic indices have been applied across a wide variety of habitats and environmental contexts, including investigating patterns of species richness in temperate reefs (Harris *et al*., 2016), detecting the response of tropical wildlife to haze caused by forest fires (Lee *et al*, 2016), assessing avian richness in tropical open woodland savannah (Alequzar & Machado 2015), monitoring freshwater lakes for invasive *Tilapia* (Kottege *et al*., 2015), and quantifying patterns of species diversity in tropical forest (Mammides *et al*., 2017).

A central assumption behind the application of acoustic indices is that greater acoustic diversity reflects more vocal species in a given community (Gage *et al*., 2001). It is also assumed that acoustic diversity is positively correlated with measures of biodiversity and ecosystem functioning (Pijanowski *et al* 2011). For birds, validation studies have compared acoustic indices directly with two established methods for assessing species richness: point count data and expert identification of birds from recordings (Darras *et al*., 2018). Acoustic indices correlate with avian richness in temperate (Depraetere *et al*., 2012; Eldridge *et al*., 2018), sub-tropical (Fuller *et al*., 2015) and tropical (Mammides *et al*., 2017) environments. Proponents of soundscape ecology tend to advocate the use of sound-recorders as a more efficient way of measuring bird diversity than expert ornithologists collecting survey data (Eldrige *et al*., 2018). However, to date, acoustic validation attempts have used fairly small datasets in terms of their spatial replication. For instance, Mammides *et al*. (2017) used 97 sampling points for the deployment of autonomous recorders, across seven landuse categories, Eldridge *et al*. (2018) used 90 sampling points, and Izaguirre *et al*. (2018) used 60 sampling points. Other studies have concentrated on comparing two different habitat types, which are often highly distinct from one another, such as gallery forest compared to cerrado vegetation in Brazil (Machado *et al*., 2017). Thus, while validations have provided useful insights into which metrics best correlate with observed avian richness, it remains unclear whether such patterns remain consistent over large spatial scales and complex environmental gradients. Similarly, the extent to which such indices perform as reliable proxies for actual richness across habitats containing varying levels of other acoustic signals, such as those from anthropogenic and geo-physical sources, is uncertain. For example, recent work from urban areas in the UK suggests that many acoustic indices do not perform well in landscapes with a high contribution of anthrophonic signal (Fairbrass *et al*., 2017). Therefore, determining which indices are consistently robust remains a research priority, as does finding ways to optimise existing indices to avoid the biases introduced by potentially confounding acoustic signals.

Here, we assess the performance of five commonly used acoustic indices in reflecting variation in avian diversity across a land-cover gradient in Sabah, Malaysian Borneo – a region characterised by exceptional levels of biodiversity, and intense forest degradation and deforestation. Our species data were generated from point counts conducted simultaneous with sound recordings, as well as highly precise estimates of richness derived from a Bayesian occupancy model that accounts for differences in species detection. Accounting for variation in detection probability is currently another hurdle in improving the effectiveness of acoustic methods, since detection probabilities vary between species and are not accounted for within indices. We test a number of approaches to improve the potential association between acoustic indices and diversity data, and compare the ability of each of these indices to capture patterns of species richness across the landscape gradient. We also compare the performance of acoustic indices in capturing changes in species richness associated with canopy height across tropical forests, as derived from high-resolution LiDAR data, to determine whether soundscape indices reflect habitat structure.

Methods

Bird sampling

Birds were sampled via 15-minute 50 m radius point counts at 373 localities in five habitat types in Sabah, with three or four visits to each site between 2014 and 2017 (1,259 point counts in total; Chapter 3). These were carried out by a single experienced observer (SLM) between 05:50am and 11:00am on days without rain. Temporal independence between repeated point counts at a given site was ensured as repeat counts at sites were always undertaken on different days. Spatial independence was ensured by all sites being located at least 180 m from one another. Sound recordings were taken simultaneously alongside each point count, using a single field recorder (Olympus LS-11/LS-12) comprising dual cardioid microphones positioned perpendicular to one another. In riparian areas, where background geophonic sound from running water was sometimes significantly higher, the recorder was placed at least 10 m from the fastest flowing sections of watercourses and oriented away from areas producing the most noise.

Point count localities (total n=373) covered a gradient of habitat degradation and increasing human presence, from unlogged old-growth dipterocarp forest to oil palm plantations (Fig. 3.1, Chapter 3). Old-growth forests (n=50 point count locations) were sampled at Danum Valley Conservation Area (n=20), Sepilok Forest Reserve (n=20) and Maliau Basin Conservation Area (n=10). We surveyed riparian areas in continuous logged forest (riparian forest; n=80), isolated riparian reserves within oil palm plantations (riparian reserves, n=100), and riparian areas without natural vegetation in oil palm estates (oil palm riparian; n=20) in and around the Stability of Altered Forest Ecosystems (SAFE) landscape. Additionally, we sampled non-riparian areas within the continuous logged forests within the SAFE area and the adjacent Ulu-Segama Forest Reserve (logged forest; n=123).

Each habitat type supported not only a different ecological community (Chapters 2 and 3), but also a different acoustic context. Anthropogenic noise levels varied for each of these habitats, being associated with distant machinery from adjacent logging, or agricultural operations and road and trail maintenance, the latter being especially prominent within oil palm. Old-growth and selectively logged forests comprised terra-firma lowland dipterocarps with low geophonic sound, while riparian forests were situated on fast-flowing streams with variable levels of peak discharge and high levels of background geophonic noise. Riparian reserves (i.e. those in the oil palm estates) consisted of a few high-noise fast-flowing streams, but in general were slower-flowing alluvial areas with few riffles or cascades resulting in lower levels of geophonic noise than counterpart localities in the riparian forest. Although oil palm riparian sites were located along water courses, these were all very small slow-flowing streams with no significant sounds of running water (low geophonic influence). Riparian forest and old-growth sites were located along streams or trails in transects comprising 10 point counts, whilst point counts at logged forest sites followed the SAFE fractal design (Ewers *et al.*, 2015). This design uses constellations of points spaced at least 180 m apart in groups of 16, which were undertaken as intersecting transects of 8 points on separate days.

Acoustic Indices

The first minute of each sound recording included the observer stating the date, time and location, and then moving away from the recorder. This sequence was therefore cut from all recordings prior to analysis. We assessed five commonly used acoustic indices over the remaining 14-minute portion of each recording: *Acoustic complexity* (AC); *Bioacoustic Index* (BA); *Acoustic Diversity* (AD); *Acoustic Evenness* (AE) and the *Normalised Difference in Soundscape Index* (NDSI). The indices were quantified using the packages soundecology (Villanueva Rivera and Pijanowski, 2013) and seewave-R (Sueur *et al*., 2008) in R (R Core Team, 2014).

Acoustic complexity is designed to capture the intricacy of biophonic signals, while ignoring the influence of many anthrophonic and geophonic noises. It is based on the premise that biotic sounds intrinsically encompass a large variety of intensities, whereas sounds such as overflying airplanes or running water are associated with constant intensity values (Pieretti & Morri, 2011). The *Bioacoustic Index* (BA) describes mean spectral power between 2,000 kHz and 8,000 kHz, as this frequency range covers most infrasonic ecological sound, but excludes many anthropogenic noises which, in general, register below 2,000 kHz (Boelman *et al*., 2007). *Acoustic Diversity* calculates Shannon's diversity index for each recording based on the power of each 1 kHz frequency band. *Acoustic Evenness* measures evenness between ten equal frequency bands 0 – 22,050 kHz as the proportion of the signals in each band above a -50 dBFS threshold, where dBFS is decibels relative to the 'full scale' maximum amplitude within a given file (Villanueva-Rivera *et al*. 2011). We also computed the *Normalised Difference in Soundscape Index* (NDSI), which is simply the ratio of biotic to anthropogenic signal (Kasten *et al*., 2012).

Acoustic Diversity is based on the Shannon-Wiener index (Jost, 2006) whereas *Acoustic Evenness,* which is based on the Gini-Simpson index (Gini, 1997). These two indices therefore characterise inverse soundscape properties to one another (Eldridge 2018). Therefore, after confirming this was also the case in our results (Table 4.1), we opted to use only *Acoustic Evenness* since it showed stronger associations with point count richness than *Acoustic Diversity*.

A pre-processing procedure was run on each of 1,299 recordings, following the protocol used by Arnold (2013) to maximise the clarity of recordings for human hearing. Using the free audio editing software Audacity (1999-2013 Audacity Team; SourceForge.net), we first removed frequencies of >10,000kHz and <800kHz, using high- and low-pass filters to remove extreme unwanted anthrophonic sounds, such as traffic noise (e.g. Eldridge *et al.* 2018). We also added a small notch filter to remove a narrow range of frequencies that included the commonest cicada chorus (7,950 - 8,050 kHz). In order to remove background noise we selected a two-minute section of one of our riparian recordings in which only river sounds (and no biological signals) could be detected by human examination. Using Audacity's proprietary noise removal process, we set this as a background 'noise profile' and used the specific profile to determine where spectral power exceeded those of the background noise profile for each 100 kHz frequency band in a recording (i.e not background signals that were assumed as biologically relevant). Signals exceeding those in the noise profile were subsequently set to 0 dB gain (no change in volume). Where spectral power fell below those of the background noise profile this was assumed to be background noise and a -12 dB gain (volume reduction of 12 decibels) was applied to suppress it. Effectively, this procedure selects a single portion of one recording containing high background noise, but no apparent biological signal, and uses this to inform which signals are less relevant in the target recordings, eliminating noise above and below certain frequencies, as well as in a small envelope at around 8,000 kHz. Using the 'chain' function in Audacity, we applied this process in batch to 1,259 out of 1299 recordings (errors in processing occurring in 40 recordings).

Our results indicated that no relationships existed between any of our acoustic indices and species richness in oil palm (Fig. S4.2). We therefore removed this data from this habitat type from our analysis relating to estimate species richness.

Estimated species richness

To compare the acoustic indices with avian diversity, we used an occupancy modelling approach to estimate species richness at every point count location based on the occupancy probabilities of each species and controlling for differing detection probabilities between species. Occupancy was estimated using a Bayesian hierarchical community model, whereby each species could be affected by five structural vegetation metrics and overall community means, and detection probability was influenced by time-of-day and survey date (Chapter 3). Estimated richness was calculated from the model as the sum of the median probabilities of each species being present at a particular site. Thirty two species recorded during our survey were only encountered on three or less occasions and, therefore, were excluded from the model and assumed that they did not contribute to richness at any given site.

LiDAR forest metrics

To measure canopy height at each site we used data derived from LiDAR point clouds. These data were gathered in November 2014 with a Leica ALS50-II sensor aboard a light aircraft (Asner *et al.* 2018). Canopy height values were taken as the mean within a 50 m radius of each point count location, mirroring our survey radius (Chapter 3). We used canopy height as it has been shown previously to strongly influence tropical bird communities (Cleary *et al*., 2005), as well as reflecting other forest quality metrics such as biomass and carbon density (Jucker *et al*., 2018).

Statistical analyses

To test the relative performance of indices based on adjusted and unadjusted recordings in reflecting habitat, time-of-day and observed richness, we ran a series of GLMs using the appropriate link function for each index derived from the package 'fitdistrplus' (Delignette-Muller & Dutang, 2015). We fitted *Acoustic complexity* and *Bioacoustic Index* with Gamma family models, while *Acoustic Diversity*, *Acoustic Evenness*, *NDSI*, *Adjusted Acoustic Complexity*, *Adjusted Acoustic Diversity*, *Adjusted Acoustic Evenness* and *Adjusted NDSI* were fitted with Beta distribution models. Values acquired for the *Adjusted Bioacoustic Index* followed a Gaussian distribution. Beta distributions were not supported by base R and were standardised using the package 'reghelper' (Hughes & R. Core Team, 2017). The relative performance of models using indices derived from unadjusted versus adjusted recordings was compared via their relative AIC values.

To understand the relationship between acoustic metrics and observed species numbers from the point counts or species richness estimates from the occupancy modelling, we fitted a series of linear regressions. We then repeated this process for each index via models restricted to individual habitats. We also assessed the effects of time-of-day upon each index using linear regressions. In order to compare model improvements using indices based on adjusted versus unadjusted recordings we re-tested the acoustic indices from our adjusted recordings to examine whether this altered the relationships with point count richness, time-of-day and habitat. We used this process to identify the best performing indices to assess further. We used linear regressions to demonstrate associations since this provided information on the pattern of the relationships between observed species richness and each acoustic index, as well as the level of correlation. To confirm levels of correlation we also computed Pearson's coefficient for the associations between each index and both observed richness and time of day.

Both acoustic indices and richness of individual point counts are likely to be affected by time-of-day, following the diurnal variation in activity for many species. However, the effects of time on each measure are not necessarily equal since point counts rely on visual as well as audio detection. Therefore, we sought to uncouple the relationship between acoustic indices and species richness from the effects of time-of-day. We did this by performing linear regressions of point count richness and acoustic indices against time in order to obtain the residuals of these relationships. This was done for indices based on adjusted or unadjusted recordings depending on which best reflected species richness (i.e. the greatest value of R^2 in linear models across all habitats; Table 4.1). We then re-ran linear regressions between acoustic index residuals and point count richness residuals, to confirm this increased the associations between them.

Using additional linear regressions, we determined the performance of our best time-controlled indices in reflecting estimated richness. We compared the relationships of estimated richness and time-controlled acoustic indices with canopy height to examine the capability of soundscape analysis to capture real-world patterns of biodiversity associated with variation in the structure of forest. All statistical analyses were undertaken using R (R Core Team, 2014).

Results

Assocations between acoustic indices and point count richness

We found significant associations between observed species numbers at point counts and the acoustic indices derived from simultaneous sound recordings (Table 4.1). *Acoustic Complexity* was most strongly associated with richness, followed by *Acoustic Evenness*, *Bioacoustic Index* and *NDSI*. *Acoustic Diversity* exhibited a very weak but significant relationship with observed richness. *Acoustic Complexity* and *Bioacoustic Index* were also negatively associated with time-of-day (AC; R^2= 0.047, F= 56.97, p<0.001; BA R^2=0.013, F= 15.98, p<0.001) with higher values during recordings shortly after dawn and lower values for those later in the morning. *NDSI* showed a positive association with time-of-day (R^2=0.049, F=58.71, p<0.001), whilst *Acoustic Diversity* and *Acoustic Evenness* were not significantly associated. We also found a number of significant relationships between acoustic indices and time-of-day (Table 4.1)

Table 4.1. Linear regression model statistics of observed bird richness and time-of-day Results listed for each acoustic index (adjusted or non-adjusted), with intercept, F-statistic, p value, R^2, residual standard error, and degrees of freedom for each. Indices assessed as are follows: *Acoustic Complexity* (AC); *Adjusted Acoustic Complexity* (ACa); *Acoustic Diversity* (AD); *Adjusted Acoustic Diversity* (ADa); *Acoustic Evenness* (AC); *Adjusted Acoustic Evenness* (ACa); *Normalised Difference in Soundscape Index* (NDSI); *Adjusted Normalised Difference in Soundscape Index* (NDSIa).

Linear Model	Intercept	F	p value	R^2	Residual standard error	Degrees of Freedom	Pearson Coeff.
AC ~ Richness	23.76	54.79	<0.001	0.046	517.7	1132	0.214
ACa ~ Richness	16.067	6.5957	<0.001	0.006	1116	1145	0.068
AD ~ Richness	-0.009	7.374	<0.001	0.006	0.562	1132	-0.080
ADa ~ Richness	-0.011	60.8	<0.001	0.05	0.264	1145	-0.241
AE ~ Richness	0.007	25.74	<0.001	0.021	0.27	1145	-0.080
AEa ~ Richness	0.01	111.2	<0.001	0.088	111.2	1145	0.312
BA ~ Richness	0.04	6.537	0.05	0.005	2.69	1145	0.121
BAa ~ Richness	0.083	8.742	0.05	0.006	5.134	1145	0.103
NDSI ~ Richness	0.006	14.17	<0.001	0.012	0.295	1145	0.117
NDSIa ~ Richness	0.011	29.11	<0.001	0.024	0.388	1145	0.170
AC ~ Time-of-day	-1.515	56.97	<0.001	0.047	517.2	1132	-0.219
ACa ~ Time-of-day	-1.301	9.131	0.002	0.007	1115	1145	-0.085
AD ~ Time-of-day	0.0001	0.487	0.485	<0.001	0.563	1132	0.021
ADa ~ Time-of-day	0.0005	32.56	<0.001	0.027	0.268	1145	0.162
AE ~ Time-of-day	-0.0002	3.508	0.061	0.003	359.4	1132	-0.056
AEa ~ Time-of-day	-0.0004	42.41	<0.001	0.035	0.177	1145	-0.184
BA ~ Time-of-day	-0.004	15.98	<0.001	0.013	2.679	1145	-0.084
BAa ~ Time-of-day	-0.021	135.7	<0.001	0.106	4.872	1145	-0.325
NDSI ~ Time-of-day	0.0009	58.71	<0.001	0.049	0.289	1132	0.222
NDSIa ~ Time-of-day	0.0006	15.77	<0.001	0.013	0.39	1145	0.120

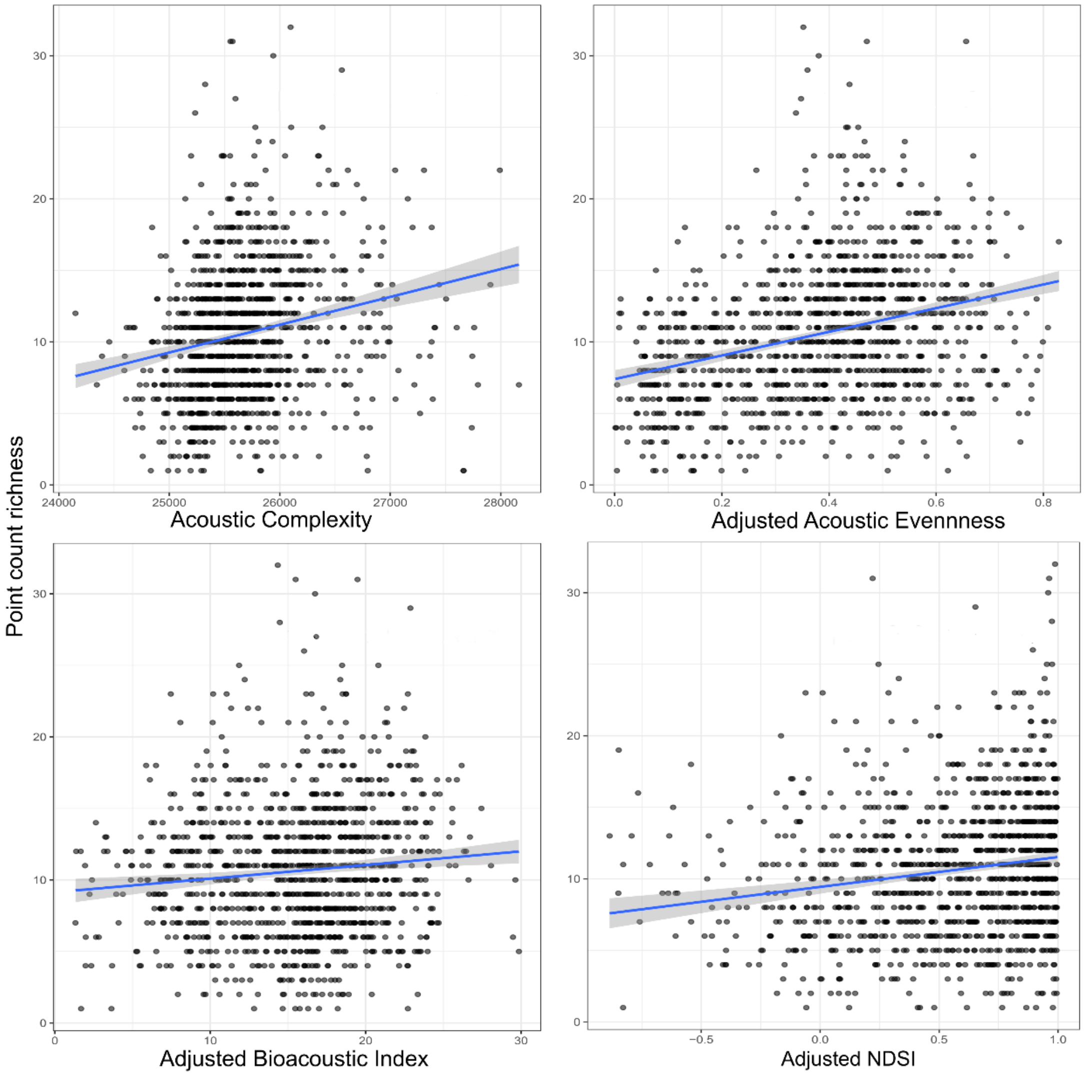

Figure 4.1. Relationships between acoustic indices and observed avian richness. Observed richness derived from point counts over a landuse gradient in Sabah, Borneo. Each plot is based on 1,259 recordings from multiple habitat types. The line-of-best-fit is derived

from a linear regression model. Shaded areas around the trend lines denote 95% confidence intervals.

Effects of habitat type

Linear models revealed that the associations between acoustic indices and bird richness was strongly mediated by habitat type (Table 4.2; Fig S4.1; Fig S4.2). Differences between habitat types were particularly strong for *Acoustic Complexity*, *Bioacoustic index* and *Acoustic Evenness*. The effect of habitat type was greater for adjusted indices than untransformed ones (Table 4.2; Fig. S4.1). We partitioned our data between the five habitat types in our study (Fig. S4.1) and found that bird diversity could be predicted by one or more acoustic indices in every habitat type except for oil palm riparian reserves, where no relationship was found.

Table 4.2. General linear models for each acoustic index in relation to richness, time-of-day, and habitat types covariates. Intercepts, standard errors and p values are listed for each parameter. Model AIC and degrees of freedom (DF) are present for each model. For negative intercepts < signifies values closer to zero. Indices assessed as are follows: *Acoustic Complexity* (AC); *Adjusted Acoustic Complexity* (ACa); *Acoustic Diversity* (AD); *Adjusted Acoustic Diversity* (ADa); *Acoustic Evenness* (AC); *Adjusted Acoustic Evenness* (ACa); *Normalised Difference in Soundscape Index* (NDSI); *Adjusted Normalised Difference in Soundscape Index* (NDSIa).

Model (family)	Parameter	Intercept	p value	DF	AIC
AC (Gamma)	observed richness	<-0.001	<0.001	1127	17258
	Time	<0.001	<0.001		
	logged forest	<-0.001	<0.001		
	riparian forest	<-0.001	<0.001		

	riparian oil palm	<-0.001	<0.001		
	riparian reserve	<-0.001	0.004		
AD (Beta)	observed richness	<-0.001	0.840	1127	1691
	Time	<-0.001	0.919		
	logged forest	7.58E-02	0.131		
	riparian forest	5.20E-01	<0.001		
	riparian oil palm	-0.445	<0.001		
	riparian reserve	0.251	<0.001		
AE (Beta)	observed richness	4.069	0.071	1127	16166
	Time	-0.053	0.667		
	logged forest	-67.043	0.024		
	riparian forest	-458.597	<0.001		
	riparian oil palm	216.904	<0.001		
	riparian reserve	-227.573	<0.001		
BA (Gamma)	observed richness	<-0.001	0.694	1118	4584
	Time	<0.001	0.052		
	logged forest	0.033	<0.001		
	riparian forest	0.139	<0.001		
	riparian oil palm	-0.016	0.030		
	riparian reserve	0.036	<0.001		
NDSI (Beta)	observed richness	0.007	<0.001	1127	304
	Time	0.001	<0.001		
	logged forest	-0.012	0.642		
	riparian forest	-0.153	<0.001		
	riparian oil palm	0.050	0.237		
	riparian reserve	-0.132	<0.001		
ACa (Beta)	observed richness	27.767	<0.001	1127	19000
	Time	-0.643	0.137		
	logged forest	1048.209	<0.001		
	riparian forest	1208.966	<0.001		
	riparian oil palm	739.726	<0.001		
	riparian reserve	1174.684	<0.001		
ADa (Beta)	observed richness	-0.004	<0.001	1127	-25
	Time	<-0.001	<0.001		
	logged forest	-0.167	<0.001		

	riparian forest	0.084	<0.001		
	riparian oil palm	-0.186	<0.001		
	riparian reserve	0.097	<0.001		
AEa (Beta)	observed richness	-0.004	<0.001	1127	1074
	Time	<-0.001	<0.001		
	logged forest	0.102	<0.001		
	riparian forest	-0.097	<0.001		
	riparian oil palm	0.117	<0.001		
	riparian reserve	-0.081	<0.001		
BAa (Gaussian)	observed richness	-0.128	<0.001	1118	6507
	Time	-0.025	<0.001		
	logged forest	-6.093	<0.001		
	riparian forest	-6.749	<0.001		
	riparian oil palm	-7.716	<0.001		
	riparian reserve	-7.061	<0.001		
NDSIa (Beta)	observed richness	0.012	<0.001	1127	969
	Time	<0.001	<0.001		
	logged forest	0.008	0.818		
	riparian forest	-0.149	<0.001		
	riparian oil palm	0.073	0.195		
	riparian reserve	-0.194	<0.001		

Effects of noise-reduction processing

Following our pre-processing adjustments, the strength of association with point count richness was weaker for *Adjusted Acoustic Complexity*, but increased for *Adjusted Acoustic Evenness*, *Adjusted Bioacoustic Index* and *Adjusted NDSI* all showed relationships of increasing strength (Table 4.1). After adjustment, the effect of time-of-day was weaker for *Adjusted Acoustic Complexity* and *Adjusted NDSI* but stronger for *Adjusted Acoustic Evenness* and *Adjusted Bioacoustic Index* (Table 4.1; Fig 4.1). We found no associations between indices based on either adjusted or unadjusted recordings with richness or time-of-day in oil palm riparian areas, and these data were therefore excluded from analysis with estimate richness and canopy height.

Assocations between time-controlled indices, estimated richness and canopy height

After adjustment for time and the exclusion of oil palm riparian data points, we found no association between estimated richness and *Acoustic Complexity time residuals* ($R^2<0.001$, F= 0.01632, p=0.898). *Adjusted Acoustic Evenness time residuals* showed a negative relationship with estimated richness, ($R^2=0.08259$, F=70.76, p<0.001), whereas *Adjusted Bioacoustic Index time residuals* showed a strong positive relationship ($R^2= 0.1581$, F=147.6, p<0.001). *Acoustic Complexity time residuals* were negatively associated with canopy height ($R^2=0.07872$, F=67.16, p<0.001), *Adjusted Acoustic Evenness time residuals* showed no association, while *Adjusted Bioacoustic Index time residuals* showed significant positive association ($R^2= 0.267$, F=286.3, p<0.001). Observed point count richness was associated with estimated richness ($R^2=0.08002$, F=68.37, p<0.001), but not with canopy height (Fig. 4.2, $R^2=0.000174$, F=0.1368, p=0.712). The strength of association between estimated richness and canopy height was stronger than for any indices metrics ($R^2=0.31$, F=367.8, p<0.001), although not markedly different from those revealed by *Adjusted Bioacoustic Index time residuals* (Fig. 4.2).

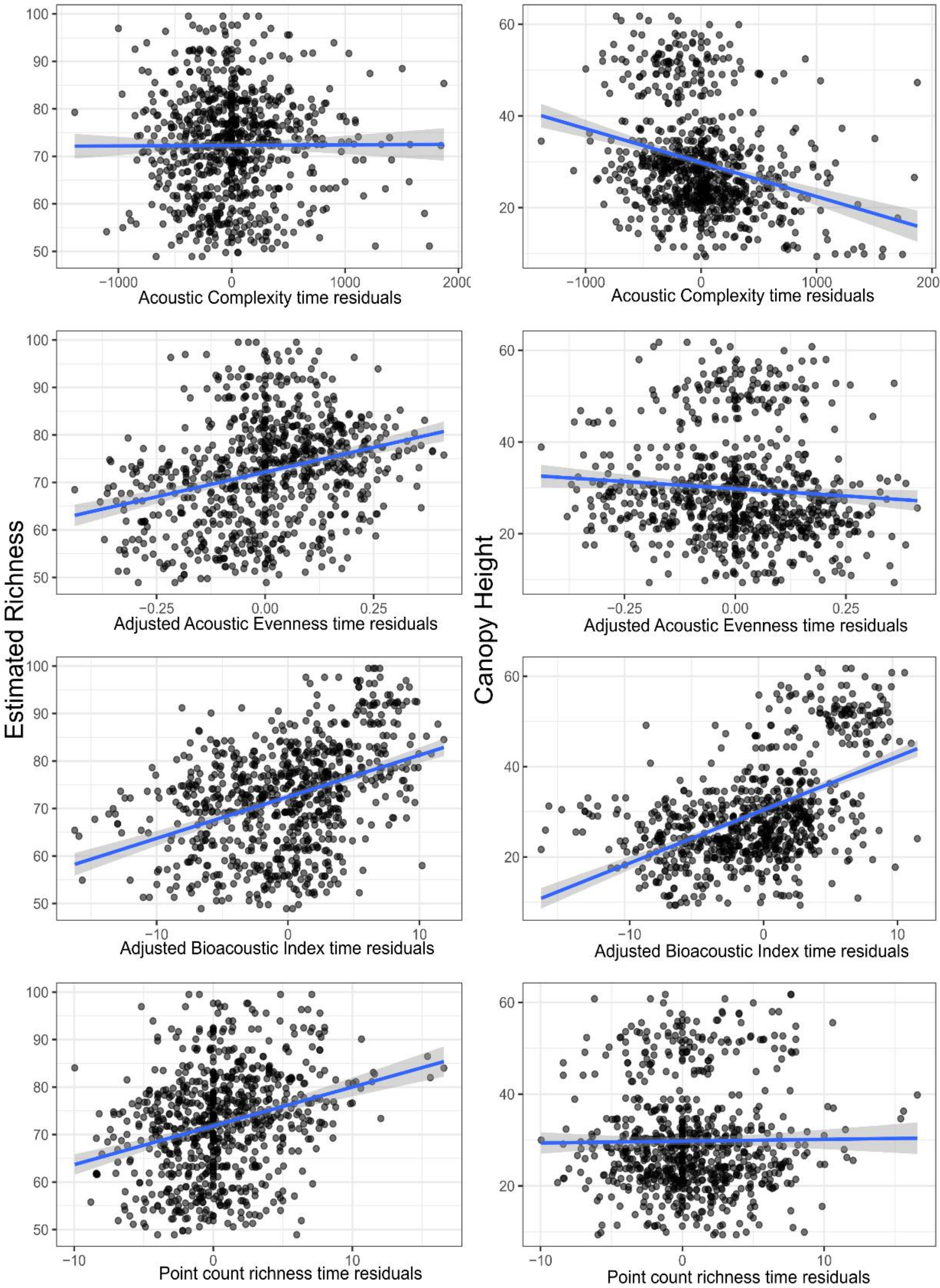

Figure 4.2. Time-controlled versions of the three best performing indices in predicting estimated richness of birds and canopy height. Blue lines denote trendlines, shaded areas mark

95% confidence intervals. Data points are different visits (n=1,229), with a maximum of four visits to any given site (n=356 sites with height and estimated richness data).

Discussion

Our findings demonstrate that acoustic indices, given an appropriate study design and analytical framework, reflect actual bird diversity patterns across a tropical forest landscapes, and so could be a viable method of characterising and monitoring avian biodiversity. However, we also find that in different habitat contexts, non-focal acoustic signals make highly significant contributions to the overall soundscape and potentially influence the indices. Although previous studies have sought to assess the validity of acoustic indices compared to a point count methodology, both in temperate and tropical regions (Depraetere *et al.*, 2012; Mammides *et al.*, 2017), our study includes fourfold more spatial replication than previous assessments and does so across a broad range of habitats and acoustic contexts. As a result, we are able to provide novel insights into some of the likely reasons for deviations between indices and point counts, and can make recommendations for how to mitigate factors which increase discrepancy between acoustic indices and patterns of biodiversity.

Acoustic indices across multiple tropical forest habitats in our study were associated with observed richness. However, these associations were rather weak and tended to be mediated by habitat type. Most significantly, none of the indices we tested showed any significant association with observed species richness in oil palm riparian areas. Additionally, oil palm riparian areas showed the highest mean levels of *Bioacoustic Index* and *Acoustic Complexity* of any habitat type despite the lowest levels of observed richness (Fig. S4.1; Fig S4.2). We believe a combination of factors caused a breakdown in any associations between the indices and richness in this habitat. First, we suspect the influence of human voices in oil palm estates may have obscured the differences in acoustic complexity driven by bird vocalisations. In urban environments of the UK, human speech is known to exert a significant bias upon the same indices quantified in our study (Fairbrass *et al*., 2017) and it appears likely that agricultural landscapes, which rely on large numbers of workers (Singana, 2013), have a similar acoustic profile in this regard. A second factor is that, as in urban areas, avian communities in oil palm landscapes are depauperate and comprise only a few avian generalists that occur at almost all sampling points (Chace & Walsh, 2006; Edwards *et al*., 2010). In practice, this means limited variation in both the observed number of species and any acoustic indices and therefore a lower statistically probability of finding significant associations between the two. This is supported by the fact that we observed only 3-16 (s.d 2.54) species per count in oil palm, compared to up to 29 (s.d 4.70) species in old-growth forest. For this reason, we removed oil palm riparian sites from our regression of landscape wide data before comparisons with estimate richness and canopy height.

Acoustic Complexity was associated with observed richness across the landscape-wide dataset, but this pattern was not apparent in riparian forests or oil palm riparian habitats (Fig. 4.1; Fig. S4.2). Riparian forest sites tended to be on steep fast-running streams where the background noise of running water was significantly louder than in all other habitats. We suspect this may have undermined the capacity of this index to detect differences in species richness. Since acoustic complexity is based upon absolute differences in signal power within each frequency band over time it should, in theory, account for constant background noise (Pieretti *et al*., 2011).

However, if such noise is sufficiently loud as to drown the signals of bird vocalisations, this would significantly dampen the variations in signal power over time and, therefore, reduce the capacity of the index to reflect overall acoustic complexity. Pre-processing our recordings to produce an adjusted index did not improve the association levels with observed richness globally, but did increase *Adjusted Acoustic Complexity* in riparian forest (with most background noise) relative to other habitat types (Fig. 4.1).

Across the landscape-wide dataset, we found a weak but significant association between bioacoustic index and observed richness. However, when broken down to different habitat types, this pattern was only significant in riparian forest (and not in old growth, logged forest, riparian reserves or oil palm riparian). A possible explanation for this pattern is the influence of cicada choruses. Cicadas are common throughout Bornean rainforests and make a major contribution to the overall soundscape (Gogala & Riede, 1995). However, cicadas tend to call at constant frequencies (e.g Gogala & Trilar 2004) and within the frequencies 2 KHz to 8 KHz. This frequency range is generally regarded as that within which most bird vocalisation fall (Goller & Riede, 2012) and therefore was used as the limiting bounds in the development of the bioacoustic index (Boelman *et al*., 2007). The index calculates the total spectral energy within this range and does not differentiate between constant-frequency signals (such as cicada calls) and complex signals (such as most bird songs). Therefore, a few generalist cicada species calling more frequently could potentially still result in high index values. Some endothermic species of tropical forest cicada have been found not to call until certain temperature is reached (Sanborn *et al*., 1994), and since old growth forest have been shown to have a greater thermal buffering capacity than logged forests (Frey *et al*., 2016), it is possible that the onset of certain species calls is delayed, therefore resulting in a differing level of contribution to the overall soundscape during the periods we analysed.

Acoustic Evenness decreased with observed bird richness, while previous studies have shown both positive (Eldrige *et al*., 2018) and negative (Mammides *et al*., 2017) associations. *Acoustic Evenness* is an entropic index based on overall evenness between 1 KHz frequency bands (Villanueva-Rivera *et al*. 2011). Its interpretation is complex since potentially high values can be reported for signals with opposing ecological characteristics. As noted by Eldridge *et al*. (2018), complex signals with many amplitude modulations have low temporal entropy, but sustained sounds of consistent frequency show very high temporal entropy. Therefore, we suspect that acoustic evenness may also have been influenced by the variation and regularity in cicada calls. This means that more cicada species calling at frequencies straddling multiple different bands would increase evenness. However, some species of cicada call at narrow, constant frequency bands (e.g Sanborn, 1997), if these were to fall within a particular 1 kHz bound assessed by the index, this would reduce evenness.

Although some studies have sought to control for cicada choruses by excluding them (Towsey *et al*., 2013), the uneven temporal distribution of such signals means excluding them would add new biases based the time of sampling. Previous studies have also found that temporal differences in cicada chorus introduced bias in entropic indices, which resulted in higher index values in degraded than intact tropical forest (Sueur *et al*., 2008). The loud insect chorus characteristic of Bornean rainforests has also been suspected of resulting in 'jamming avoidance', whereby some taxa sing less frequently during the loudest choruses of others (Reide, 1997). This could in theory also affect the acoustic evenness index, since complex signals such as birdsong may be inhibited by cicada calls. Therefore, understanding how changes in cicada choruses effect acoustic indices is therefore a major research priority for optimising their utility in tropical forests.

Our results showed a weak positive association between NDSI and observed richness across all habitats. However, the perceived influence of anthropogenic sound was highly heterogeneous when point counts were conducted. Whilst oil palm riparian areas undoubtedly had a greater proportion of anthropogenic sounds, many logged forest sites were still undergoing salvage logging nearby to where our counts were conducted. This resulted in distant chainsaw and vehicle sounds being relatively common within our recordings. A high proportion of old growth sites were influence by the sounds of vehicles, leaf-blowers and road construction nearby.

Bioacoustic index values were greater in old growth forest, followed by logged forests, then riparian reserves and riparian forest (Fig. 4.1). This pattern (excluding for oil palm) mirrored the aggregated habitat richness findings from our previous analysis of the landscape (Chapter 2; Mitchell *et al*., 2018), as well as a large literature showing that old growth forests support more bird species than logged forests (Edwards *et al*., 2014) or isolated fragments (Edwards *et al*., 2010). Associations between bioacoustic index values and observed richness from individual point counts may have been weak due to the observed richness being a poor reflection of actual avian richness patterns. This is because the majority of species in tropical forest are rather uncommon, with some not even calling every day (Robinson *et al.* 2018).

Incomplete sampling of some species due to a failure in detection contributes to the discrepancy between acoustic indices and richness patterns. This is supported by the negative relationships found between several indices and time-of-day (Table 4.1). This idea is supported by two patterns we observed. First, associations between bioacoustics index and estimate richness (controlled for detection probability), were far higher than those with observed richness (Fig. 4.3). Second the overall avian chorus (and hence the probability of a given species vocalising) decreased with time after dawn (Table 4.1). Similar patterns have been noted in several previous studies (Wimmer *et al*., 2013). Since observed richness from point counts can be based on upward of 95% aural encounters in tropical forests (Robinson *et al*., 2018), this metric also decreases with time after dawn. However, the effect of time upon acoustic indices and observed richness is not the same, since point counts do not rely solely upon vocalisations. This means that the differing effects of time upon the two metrics introduces a source of bias. We found that associations between indices and observed richness within our landscape-level dataset improved when we used time-controlled residuals for both. We therefore recommend this step for any sampling designs that base their acoustic indices upon samples from different times of day. However, for extended or constant autonomous recordings, there are alternatives to this approach, such as using sampling designs which validate recordings based on one minute samples, taken at random or via a stratified sampling approach depending on the results for particular indices (Wimmer *et al*., 2013).

Pre-processing our recordings to remove frequencies outside of our focal range of 800 - 10,000 kHz (the range within which tropical bird vocalisation fall), as well as removing 12 dB of background noise using a manually set noise profile, resulted in improved associations between indices and observed richness. We referred to these as adjusted indices for simplicity, although the actual process involved editing the recording themselves before re-running the same computations for calculating acoustic metrics. Adjusted indices, showed stronger associations with observed richness for evenness, *NDSI* and *Bioacoustics Index* (Table 4.1; Fig. 4.1; Fig. 4.2). Notably, *Adjusted Bioacoustic Index* values increased significantly in riparian habitats (riparian forest where the sounds of running water were strongest and riparian reserves where they were of variable intensity) relative to those without background noise. This supports our hypothesis that high level of geophonic background noise 'drown out' bird vocalisations in these habitats.

We also assessed the performance of the acoustic indices most associated with observed richness (*Acoustic Complexity time residuals*, *Adjusted Acoustic Evenness time residuals, Adjusted Bioacoustic Index time residuals)* against estimated richness (Fig. 4.2). Observed richness time residuals (Point count residuals; the total number of species encountered during each point count), does not account for imperfect detection (i.e. the majority of species are not heard or seen during the 15-minute period of a single point count). Whilst observed richness is appropriate for validating the link between the species heard by observer during points and resulting representation of this via a given acoustic index, it is not necessarily useful for measuring true patterns of avian richness across landscapes. In fact, we found no relationship between observed richness from individual point counts and canopy height; an environmental variable which has been found to strongly influence richness in Bornean tropical forests (Cleary *et al*., 2005). *Bioacoustic Index time residuals* were the most strongly associated metric with estimated richness (R^2 = 0.15), and was more closely linked than observed richness and estimated richness ($R^2 = 0.08$). This suggests that *Bioacoustic Index time residuals* could therefore be used as a viable proxy measure of biodiversity across tropical forest landscapes.

Although previous studies have demonstrated that acoustic indices are capable of measuring changes in species richness changes associated with changes in landscape configuration (Fuller *et al*., 2015), their ability to reflect patterns associated with environmental or structural gradients across multiple habitats remains uncertain (Farina & Pieretti, 2014). In fact, the latter study is the only one to date which has assessed the relationship between vegetation structure and acoustic indices and even in this case, indices were broken metrics down into smaller categorical variables, rather than using a continuous gradient approach. The way in which associations between vegetation metrics and acoustic indices is mediated by species richness is also still poorly understood and may be contingent upon a number of other factors such as bird community composition or vegetation structure (Boelman *et al*., 2007). For acoustic indices to be of similar utility to existing methodologies they must be able to reflect biological patterns at a comparable level to conventional methodologies. Comparisons between *Bioacoustic Index time residuals* and canopy height ($R^2 = 0.26$), showed a similar level of association to that of estimated richness and canopy height ($R^2 = 0.31$). This demonstrates that *Bioacoustic Index time residuals* t performs at a similar level to establish advanced modelling techniques reflected patterns of biodiversity associated with an environmental gradient. Since much biodiversity assessment and conservation research is concerned with identifying the effects of environmental and human-mediated changes to the landscape, the fact that acoustic indices are able to capture the effects of such environmental gradients supports their deployment more widely as a method of assessing biodiversity.

Soundscape indices can be used to reflect patterns of biodiversity across varied landscapes with significantly different community assemblages and different levels of species richness. By following these steps we were able to increase the associations between acoustic indices and richness from very weak (R^2 of 0.02 for *Acoustic Evenness* as the strongest initial association), to better than raw data from conventional point counts and comparable those of current best-available modelling approaches (R^2 of 0.26 for *Bioacoustic Index time residuals*).

With correct deployment and analysis, such indices are capable of capturing variation in ecological communities associated with environmental gradients such as differences in vegetation structure. The utility of acoustic indices provides efficient ways of quantifying biodiversity, without the need for expert validation, and means that such methods are an excellent tool for conservation and in particular rapid biodiversity assessments, especially in the context of limited resources and an ever-growing number of environmental crises. Future advances in acoustic approaches, particularly those based on deep-learning, have the potential accurately identifying individual species and show highly promising potential for assessing and monitoring tropical forests (Burivalova *et al.*, 2019). However, at present the main application of these indices rests with quantifying community-level acoustics, and misses vast information at the species level, which can inform which species are dominant and rare, and hence of a conservation priority.

Supplemental Materials

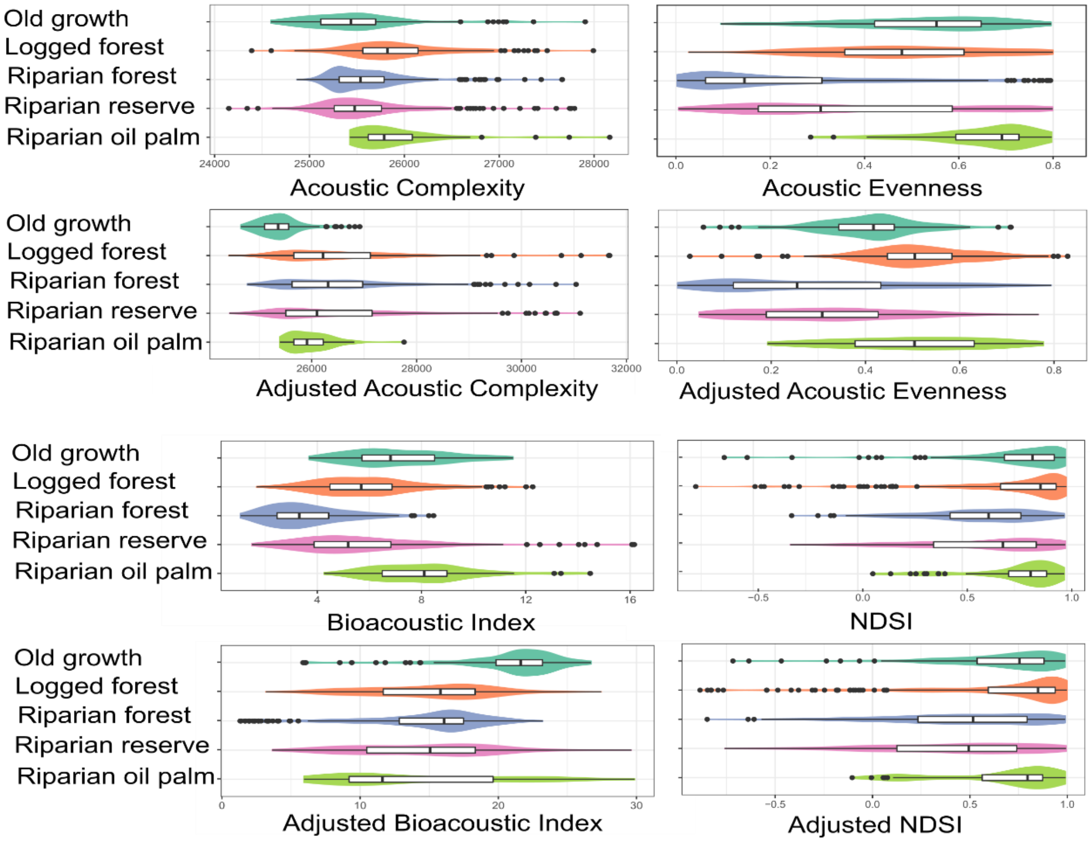

Figure S 4.1. Violin plots with embedded boxplots for adjusted indices. *Acoustic Acoustic Complexity*, *Adjusted Acoustic Complexity* and *Acoustic Evenness*, *Adjusted Acoustic Evenness*, *Bioacoustic Index*, *Adjusted Bioacoustic Index*, *NDSI* and *Adjusted NDSI* in each habitat: Old growth; Logged forest; Riparian forest; Riparian reserve and Riparian oil palm.

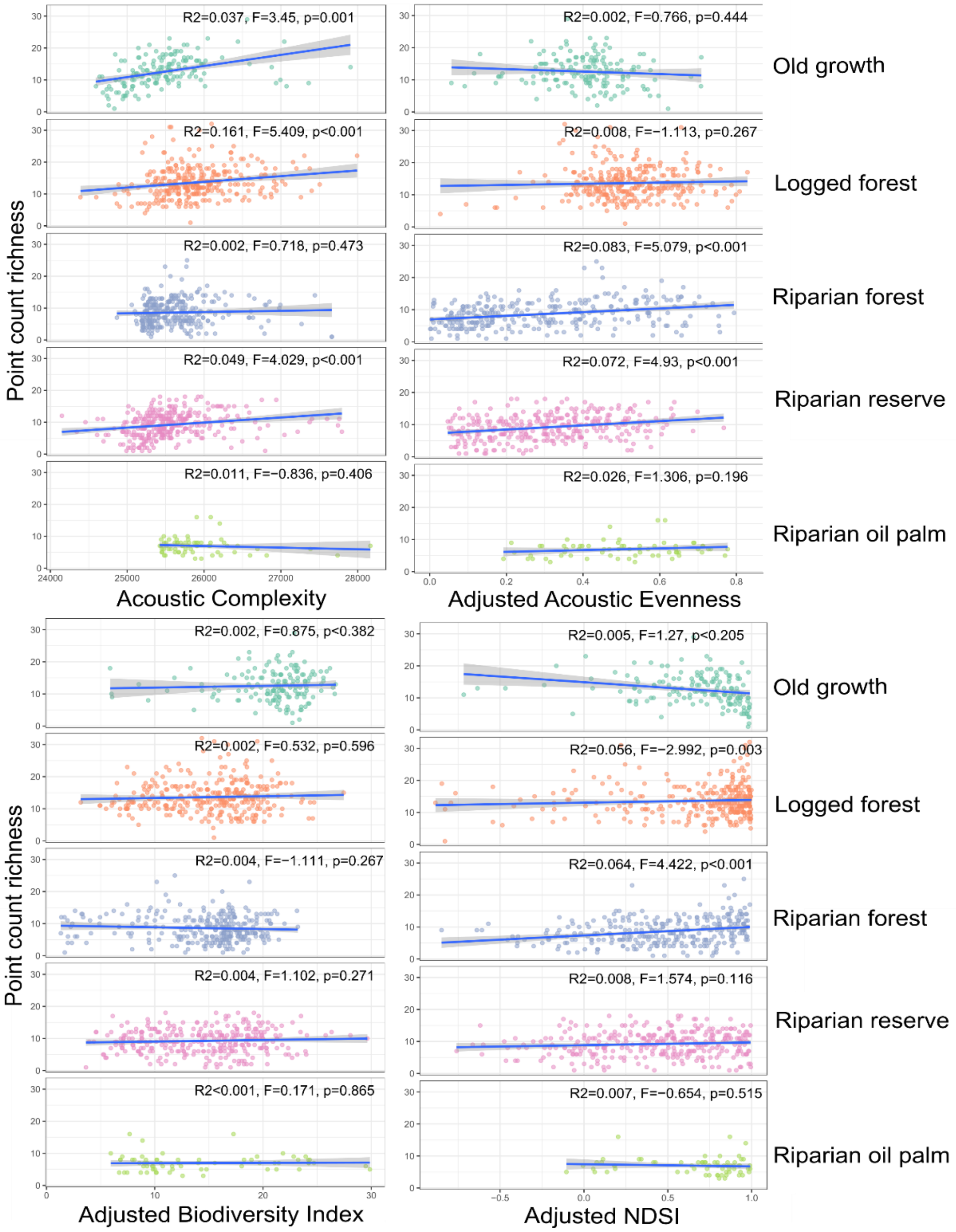

Figure S 4.2. Regressions of the best performing indices against observed species richness. *Acoustic Complexity*; *Adjusted Acoustic Evenness*; *Adjusted Bioacoustic Index* and *Adjusted NDSI* against Point count richness for each habitat: Old growth; Logged growth; Riparian forest; Riparian reserves and Riparian oil palm. R^2, F statistic and p values of each relationship are listed at the top right of each respective panel.

Acknowledgements

This study was funded by the UK Natural Environment Research Council (NERC) (NE/K016407/1; http://lombok.hmtf.info/ and http://bali.hmtf.info; NE/K016377/1), and a Newton-Ungku Omar Fund grant from the British Council and Malaysia Industry-Group for High Technology (MIGHT) (216433953). SLM was supported by a PhD scholarship jointly funded by University of Kent and NERC. We thank the Sabah Biodiversity Council, Sabah Forest Department, Yayasan Sabah, Sime Darby, Benta Wawasan, Sabah Softwoods and Innoprise Foundation for permitting site access. We are grateful to Unding Jami and the LOMBOK research assistant team for their field assistance, and Suzan Benedick, Joseph Tobias and Ryan Gray for facilitating fieldwork.

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Chapter 5. Discussion

Throughout this thesis I have explored the impacts of tropical forest degradation and loss on biodiversity across a landscape gradient from old growth forests, to agricultural plantations. The application of novel technological and statistical approaches has yielded two important insights. First, I have been able to address unanswered questions regarding biodiversity responses to landuse change including thresholds of response to habitat modification for many species. Second, I have been able to demonstrate the applicability of these novel approaches in the context of practical ecological questions, and give policy-relevant recommendations as a result.

The application of LiDAR technologies in biodiversity monitoring

In Chapter 1 I revealed the biodiversity value of riparian reserves in oil palm landscapes, using birds as surrogate taxa. To examining the relationship between riparian reserve width, carbon density and species richness, I utilised LiDAR derived data to gain insight that would not otherwise have been possible, and suggest practical recommendations. I recommended that reserves would become more optimal habitat for birds by increasing riparian vegetation from 30 to 40 m on each side of river, but that reserves still do not reach equivalent bird species richness until forest quality is improved (exceeding 60 tonnes of carbon per hectare in tree biomass). This appraisal was made possible by being able to use LiDAR data to measure both riparian width and carbon density. Although direct measures of river and riparian zone width could be undertaken in the field with measure tapes or rangefinders, my early attempts to do this proved futile given the terrain and difficulty in surveying a sufficiently representative cross-section of the river and reserve. Likewise, the implementation of on-the-ground vegetation plots in many areas of the landscape would have been prohibitively time consuming. In comparison, ground-truthing of LiDAR plots was only undertaken at a subset of sample points and as a collaborative effort out in by multiple members of the Stability of Altered Forest Ecosystem staff as well as members of the LOMBOK consortium (Jucker *et al*., 2018).

There has been a huge proliferation in remote sensing technologies in recent years. In 2001 LANDSAT imagery was virtually the only publically available earth-observation dataset (Pimm *et al*., 2015). However, by 2008 at least 19 different earth observation satellites were operating (Gillespie *et al*., 2008) and 268 additional missions were in the planning stage by 2012 (Selva & Krejci, 2012). Since 2000 the number of civilian missions has grown exponentially, with the spatial resolution of data also continuingly increasing (Belward & Skoien, 2015) As well as offering potentially new ways of mapping land cover (including in three dimensions), perhaps the most fundamental gain for biodiversity monitoring has been the increased efficiency and reduced cost of collecting data for large areas. As a result, the spatial scales on which biodiversity is assessed have expanded significantly, both in the context of single study landscapes, and meta-analytic global analyses. Remote sensing also allows the assessment of vegetation in areas which may be inaccessible due to terrain (e.g Avisse *et al*., 2017) or security issues.

LiDAR data were integral to the research presented in each data chapter. Chapter 3 in particular assessed species occupancy responses against the high resolution measures of forest structure derived from the LiDAR, including the overall density of vegetation and the vertical skew in the distribution of that density. These covariates would be difficult to derive from conventional reflectance-only remote sensing technologies, since they necessarily require hyperspectral signals that can penetrate through the top layers of canopy in order to map 3-dimensional vegetation structure. The application of LiDAR technologies to studies in other parts of the tropics could fundamentally change our understanding of how biodiversity is distributed from two dimensions to three.

Sabah now has near state-wide LiDAR coverage thanks to a recent aerial survey mission led by the Carnegie Airborne Observatory (Asner *et al*., 2018), which potentially allows for patterns of biodiversity to be modelled on a large scale in relation to the vegetation and landscape configuration data captured from these flights. The Sabah state government also has ambitions to increase its protected area network from 21% to 30% percent of the total land area. There is therefore an opportunity for modelling studies such as those I present in Chapter 3 to help inform state-wide conservation policy. The availability and applicability of LiDAR technology globally also looks set to expand. December 2018 marked the launch of the NASA Global Ecosystem Dynamics Investigation (GEDI) LiDAR mission - a global, satellite-based assessment of vegetation (Saarela *et al*., 2018). Deploying such assessments globally offers a genuine step change in the way conservation prioritisations can be done, and in particular could help discern the relative biodiversity value of different landuse intensities in human modified agricultural systems.

The ability to use LiDAR to define structural niches for highly specialised species is already proving useful in defining specific management plans. For example, LiDAR assessments have helped to define the habitat structure requirements of Red-cockaded Woodpecker in the Southern United States (Smart *et al*., 2012). In another study of the same species, researchers were able to identify lower and upper thresholds for densities of pines, basal area of pines, tree diameter at breast height, hardwood canopy cover and basal area of hardwoods using ground-based LiDAR assessments which have informed federal management plans in the United States (Garabedian *et al*., 2017). LiDAR has also been used to determine habitat association in studies on wood-mice (Jaime-Gonzalez *et al*., 2017), dormice (Goodwin *et al.*, 2018); bats (Froidevaux *et al*., 2016) and birds in tropical forests (Flaspohler *et al*., 2010), temperate woodland and agricultural landscapes (Bradbury *et al*., 2015). The trajectory of increase coverage and affordability of these technologies mean that including a third dimension in appraisals of habitat structure (particularly in contexts such as tropical forest where this is highly relevant), could eventually become the default approach to species-habitat studies.

Challenges in occupancy modelling to monitor rare species

Tropical forest bird communities often contain large numbers of species that are difficult to detect (Robinson *et al*., 2018). It has been noted previously that some tropical bird taxa are both visually cryptic and rarely vocalise. For example, radio-telemetry tracking of a Variegated Antpitta (*Grallaria varia*) documented instances of singing at just two of 68 locations within its home range (Jirinec*et al*. 2018; Robinson *et al*., 2018). We noted that this was also the case for several species with our study system. For example Giant Pitta (*Hydrornis caeruleus*) was only noted from point counts on three occasions during five field seasons, despite the observers being highly familiar with its distinctive vocalisation.

Additionally, a number of species in our study areas were mostly documented from distances of greater than 50 m. These encounters were removed from our occupancy modelling assessments, since we focussed on examining habitat associations within a 50 m radius of each point count station and points were separated by 180 m. These species tended to be quite vocal, but occurred at low-densities, and were not adequately assessed using a conventional point count methodology over limited-distances. Perhaps the most prominent example of this is that the far-carrying call of the Critically Endangered (IUCN, 2019) Helmeted Hornbill (*Rhinoplax vigil*), which was noted on 72 occasions, though only six of these were from within 50 m. Robinson *et al*. (2018) recommend the approach we adopted, of using unlimited distance surveys and then truncating data later. However, the advocated technique of using species-specific distance histograms to inform this approach is not possible when attempting to optimise sampling methods for an entire community and avoid including communities of adjacent habitats within the radius of point counts, particularly in the context of riparian reserves and fragments.

Southeast Asia, principally Indonesia, is also suffering a crisis in songbird trade. Analysis by Symes *et al*. (2018) suggests exploitation for wildlife trade has driven dramatic declines in many species within the region. This has occurred to such an extent that some species have already declined to a point where they are no longer easily available at songbird markets and new species are being exploited in a cascade of demand (Symes *et al*., 2018). Although cultural factors make wild bird trade a much more significant factor in Indonesia than Malaysia, several species have declined as a result of exploitation here too, most notably Helmeted Hornbill *Rhinoplax vigil* (Beastall *et al*., 2016), White-crowned Shama *Copsychus barbouri* and Straw-headed

Bulbul *Pycnonotus zeylanicus* (Bergin *et al*., 2018). Indeed the absence of the latter from areas much of our study areas has been attributed to illegal trapping (Sheldon *et al*., 2009.). Forest loss, increased infrastructure for agriculture and fragmentation has also further increased the problem of illegal bird trapping and hunt, since it results greater accessibility to ever higher proportions of remnant forests (Symes *et al*., 2018).

In order to apply a hierarchical modelling approach to these communities some standardisation of the data is required. For example, in Chapter 3, I excluded species that had been recorded on fewer than four occasions from the dataset completely, since trail runs of the modelling approach demonstrated these species to simply follow community-average trends in responses to environmental variation. The structure of Bayesian occupancy models mean that data are aggregated at the community level and this informs species-specific parameter estimates, therefore moving them toward the community mean (Broms *et al*., 2016). This remains a potential caveat for some of the rarer species remaining in the model. Defining specific thresholds for species trait groups required there be sufficient number of species in each group. On the other hand, including species based on too few observations would increase the representation of the community mean hyper-parameters from which they borrow power, and therefore potentially obscure the differing responses of different trait groups.

The models applied in Chapter 3 did not account for the influence of transects beyond differences in the five environmental variable we included. I explored the inclusion of a random factor variable for each of the 33 transects associated with detection probabilities. However, this increased the size of the model an order of magnitude, to the extent that even when running on the entire capacity of the supercluster server at the University of Kent, the analysis exceeded the active memory limits. This demonstrates that there are still some computational impediments for undertaking complex Bayesian models on very large ecological datasets such as the one I collected. However, increases in computer processing power are likely to continue, which should allow the introduction of more powerful models.

The application of bioacoustic approaches to biodiversity monitoring

The development of sophisticated and relatively inexpensive sound recorders in recent years has opened up new avenues of ecological research. Acoustic approaches to measure and monitor biodiversity have been undertaken in environments as diverse as freshwater lakes and coral reefs (Lindseth & Lobel, 2018) and tropical forests (Burivalova *et al*., 2018). In particular, algorithms which characterise the spectral energy or acoustic complexity of recordings and express them as single indexed values have been shown to be associated with to biodiversity patterns in many contexts (Buxton *et al*., 2018). However, the utility of theses methods for assessing biodiversity on larger scales relies on them being generalisable across multiple habitats, and in a number of scenarios these indices are not associated with biodiversity as measured by traditional means. Chapter 4 focussed on ways to optimise such acoustic approaches and improve their performance in landuse change studies applied across a broad environmental gradient. I found that the four indices applied typically became more congruent with species richness when processed for noise reduction and when I controlled for the effects of time in analyses. Based upon my findings, I offer a series of recommendations for future soundscape analyses that aim to characterise biodiversity patterns in tropical habitats:

1) Agriculturally intensive environments cannot be adequately compared using the indices I assessed at present, since these indices are currently unable to separate the influences of human sounds from signals generated by wildlife.
2) The ability of acoustic indices to act as proxies for biodiversity may be compromised in habitats with strong geophonic influences, such as fast flowing water. I demonstrate that the use of proprietary noise reduction functions software from the free software Audacity (1999-2013 Audacity Team; SourceForge.net), to transform recordings (Chapter 3) helps minimise this influence. Application of this transformation improves the performance of three out of four indices in all habitats, albeit to a small degree.
3) In tropical forests there is potentially a strong influence of cicada choruses upon acoustic indices. Further study into the specific effects of cicada and insect noise more generally upon the outcomes of acoustic indices is required. Assessment of how call diversity and regularity in insect taxa are associated with broader patterns of biodiversity will help in the appropriate deployment of existing acoustic indices as well as development of new metrics. Ideally, to control for potential discrepancies introduced by cicadas, future studies should attempt to quantify the regularity and diversity of these acoustic signals, and separate them from other sounds in downstream data processing.

   Time-of-day has an influence on virtually all the indices applied in this setting. In studies based on point count designs it is possible to improve the performance of acoustic indices by using time-controlled residuals. For studies based on long-recording times, random or stratified sampling of recordings may perform better (Wimmer *et al*., 2013)

By following these recommendations these simple acoustic indices could better reflect patterns of biodiversity across varied landscapes with significantly different animal community and different levels of species richness. By following these steps I was able to increase the correlations between acoustic indices and richness from very weak (R^2 of 0.02 for acoustic evenness as the strongest initial correlation), to coefficients that exceeded those achieved when using raw data from conventional point counts and comparable to those of current best-available modelling approaches (R^2 of 0.26 for Bioacoustic Index after controlling for noise-reduction and time).

Although acoustic indices have the advantage of being simple enough to compute easily for large datasets, they also have some potential limits. For instance they are limited in their ability to reflect patterns of beta-diversity (i.e. similarity/dissimilarity between sites) (Lellouch *et al*., 2015). They are also unable to discriminate between the effects of different species or even taxonomic groups. Approaches based on cluster analyses have been applied to ultrasonic sounds emitted by bats, with mixed success (Lemen *et al.,* 2015).

Emerging machine learning approaches could eventually be capable of identifying many bird vocalisations to the level of species with a high level of accuracy (Chakraborty *et al*o., 2016), whilst continuing advances in cellular technology offer the possibility that autonomous recordings captured anywhere in the world soon might be processed in real time (Sethi *et al*., 2018). Until very recently such technologies currently faced impediments in their affordability and durability (Aide *et al*., 2013).

Perhaps most significantly, the amount of data required to train automated identification processes in other areas is very high (Alwosheel *et al*., 2018) and this is currently prohibitive for the identification of most bird calls, simply because an insufficient number of reference recordings to train the algorithms are available. Currently, convolutional neural networks (a form of unsupervised machine learning) perform better in identifying the overall contributions of anthrophonic and biophonic signals in urban soundscapes (Fairbrass *et al*., 2018), and also separate bird song from other signals (Stowell *et al*., 2018). Some progress has been made in using these approaches to identify individual species (Aide *et al*., 2013), but these still require high levels of human supervision.

Synergies between novel approaches and technologies

Some of the key findings presented in this thesis involve combining the application of these different technologies and novel techniques. Chapter 1 utilised LiDAR data to assess the effects of width and carbon density in riparian reserves; a habitat which has previously received comparative little attention in terms of assessments of its biodiversity contribution in human-modified tropical oil palm landscapes. Chapter 2 focussed on using LiDAR data from across a whole forest gradient in order to offer novel insights into potential abrupt thresholds in species response to forest change. This required incorporating LiDAR data into a recently developed Bayesian occupancy modelling framework, and assessing the results using methods for statistically assessing change points change points, which have only been relatively recently applied to ecological data (Toms & Lesperance, 2003). Chapter 3 compared recently developed soundscape indices with species richness estimated from the occupancy models. This highlights the fact that many developments in both conservation and ecological research stem not necessarily from the advances in new technologies themselves, or in the deployment of single novel approach, but in applying combinations of these approaches in order to address questions that were previously difficult or impossible to answer.

This parallels the broader progress made in biodiversity monitoring through combining novel technologies and methodological or analytical advances. For example, recent advances in citizen science monitoring have been augmented by the capacity to use deep learning approaches in identifying photos of both species of birds, plants and insects (Waldchen & Mader *et al*., 2018). Even huge datasets and 'big data' approaches such as those which can be yielded through citizen science do not necessarily provide new insights into ecological patterns and mechanisms without the ability to adequately generalise the patterns within them (Najafabadi *et al*., 2015). The scale of these datasets is often too great for conventional human analysis and therefore necessitates deep learning approaches in order to unveil novel findings. Since advances on big data often require much larger collaborative scientific efforts, there have been increasing calls to improve the levels of collaboration in ecology, given that this field has sometimes lagged behind with the large-scale approaches that have been commonplace in the physical sciences for many years (Hampton *et al*., 2013).

Additional synergistic advances have occurred in remote sensing from the application of deep learning algorithms (Hethcoat *et al*., 2018). The combination of LiDAR technology with conventional remote sensing techniques as well as artificial intelligence makes it possible that in the near future we will develop the ability to identify individual tree to species level from space (Holmgren *et al*., 2008). Other new combinations of approaches have included the use of drones to capture both acoustic data (Wilson *et al*., 2017) and eDNA samples (Doi *et al*., 2017), thereby removing physical barriers which have previously prevented the collection of such data in certain areas. This thesis provides an example of how different technological and statistical advances can be used in conjunction to study pertinent questions in conservation science. By applying these advances to assessing biodiversity patterns in human-modified tropical landscapes I have been able to not only identify specific policy interventions in for riparian reserves, but also demonstrate potentially important tipping points in the responses of tropical bird communities to the structural vegetation changes associated with forest degradation and recommend improvements to deployment and analytical protocols to improve recently developed methods.

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Appendix: Co-authored publications:

Riparian buffers in tropical agriculture: Scientific support, effectiveness and directions for policy

Sarah H. Luke, Eleanor M. Slade, Claudia L. Gray, Kogila V. Annammala , Julia Drewer, Joseph Williamson, Agnes L. Agama, Miklin Ationg, Simon L. Mitchell, Charles S. Vairappan, Matthew J. Struebig

Published: *Journal of Applied Ecology* (2018)

Abstract

1. There is a weak evidence base supporting the effective management of riparian ecosystems within tropical agriculture. Policies to protect riparian buffers—strips of non-cultivated land alongside waterways—are vague and vary greatly between countries.
2. From a rapid evidence appraisal, we find that riparian buffers are beneficial to hydrology, water quality, biodiversity and some ecosystem functions in tropical landscapes. However, effects on connectivity, carbon storage and emissions reduction remain understudied. Riparian functions are mediated by buffer width and habitat quality, but explicit threshold recommendations are rare.
3. *Policy implications*. A one-size fits all width criterion, commonly applied, will be insufficient to provide all riparian functions in all circumstances. Context-specific guidelines for allocating, restoring and managing riparian buffers are necessary to minimise continued degradation of biodiversity and ecosystem functioning in tropical agriculture.

Co-producing knowledge for environmental sustainability: Defining the research agenda for palm oil

Rory Padfield, Sune Hansen, Zoe Georgina Davies, Albrecht Ehrensperger, Eleanor Slade, Stephanie Evers, Effie Papargyropoulou, Cécile Bessou, Norhayati Abdullah, Susan Page, Marc Ancrenaz, Paul Aplin, Dzulkafli Shahirah Balqis, Holly Barclay, Darshanaa Chellaiah, Sonal choudhary, Samantha Conway, Sarah Cook, Alison Copeland, Ahimsa Camposarceiz, Nicolas Deere, Simon Leo Mitchell, Simon Drew, David Gilvear, Ross Gray, Tobias Haller, Amelia St Clair Hood, Lee Kim Huat, Nhat Huynh, Nagulendran Kangayatkarasu, Lian Pin Koh, Sananth Kumaran, Robin Ah Hee Lim, Yeong Kok Loong, Jennifer Marie Lucey, Sarah Luke, Marvin Joseph Montefrio, Katherine Mullin, Anand Nainar, Anna Nekaris, Vincent Nijman, Matheus nunes, Siti Nurhidayu, Patrick O'Reilly, Chong Leong Puan, Nadine Ruppert, Hengky Salim, Greetje Schouten, Anne Tallontire, Thomas Smith, Hsiao-Hang Tao, Mun Hou Tham, Helena Varkkey, Jamie Wadey, Catherine Mary Yule, Badrul Azhar, Alexander Sayok, Charles Vairappan, Jake Bicknell, Matthew John Struebig

Accepted: *Frontiers In Forests And Global Change*

Abstract

The rise of palm oil as the world’s most consumed vegetable oil crop has coincided with an exponential growth in palm oil research activity. Bibliometric analysis of research outputs has shown a distinct imbalance in the type of research being undertaken, notably a disproportionate focus towards biofuel and engineering topics. Recognising the expansion of palm oil within frontier regions and the increasing awareness of the local and global environmental, social and economic impacts, this study aims to re-orient the existing research agenda towards one that addresses the most urgent questions and issues. Following consultation with 659 stakeholders from 38 countries the highest priority research questions were identified within 13 themes. Analysis of the priority questions and themes revealed a diversity of environmental and social research challenges ranging from the environmental impacts of production, to the livelihoods of plantation workers and smallholder communities. Stakeholders emphasised a need for research into policy, governance and certification topics in order to meet this challenge. Research addressing the consumption of palm oil also emerged as a priority as did studies to improve communication and cooperation between academic and non-academic stakeholders. Analysis of the ‘knowledge type’ of the questions revealed a need for fundamental science programmes and studies that involve the consultation of non-academic stakeholders to develop ‘transformative’ solutions. Key recommendations include improved regional academic leadership and coordination, greater engagement with private and public stakeholders in the frontier regions of Africa and Latin America, and enhanced collaborative efforts with researchers in the major consuming countries of India and China.