Amphibian and reptile diversity of Northern Guatemala.

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Abstract

Throughout the world an ever-burgeoning human population is putting increasing pressure on natural resources. One result of that pressure is an increasing loss of natural habitat through habitat destruction and change in land use. Currently the effects of change in land use are most strongly felt in tropical regions that also hold the highest levels of biodiversity. Significant gaps in our knowledge exist regarding how changes in land use affect faunal biodiversity and abundance, especially in the case of tropical amphibians and reptiles which can be particularly sensitive to environmental change and are often difficult to detect. Surveys were conducted in Laguna del Tigre National Park (LTNP) in Northern Guatemala with the aim of 1) comparing amphibian and reptile diversity in undisturbed forest and forest adjacent to land converted to agriculture; 2) determining predictors of diversity and finer scale effects of change in land use on assemblage structure; and 3) using the presence of common widespread species to predict hotspots of diversity on a wider regional level. Ninety-two species of amphibians and reptiles were detected from 2013 to 2016 representing 26 families and 5 orders. Eighteen percent of amphibian species and 50% of reptiles were found to be of regional conservation concern, considerably higher than when those species were considered at current national and global levels.

Diversity of amphibians and reptiles was significantly lower in forest adjacent to agriculture than in undisturbed habitat. Assemblage structure was significantly altered in disturbed habitat, with a few common species dominating other species that were present. Tolerance of dry environmental conditions and specialised diet were identified as traits that allowed for successful colonisation of disturbed forest. The presence of species with widespread distributions revealed more information about overall diversity of a location than did the presence of rare species. Moreover, the presence of species common to multiple locations in the Mayan Biosphere Reserve (MBR) could be used to predict levels of diversity at under-sampled locations. Change in land use and resulting disturbance of adjacent forest could have a more significant impact on amphibians and reptiles than realized. Conservation policy for amphibians and reptiles within the MBR should take their local conservation status into consideration in addition to national and global assessments.

KEY WORDS: Change in land use; Mayan Biosphere Reserve; Laguna del Tigre National Park; amphibians; reptiles

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Speckled racer – *Drymobius margaritiferus*

1.1 Habitat Loss and Change in Land Use

Throughout the world, an ever-burgeoning human population is putting increasing pressure on natural resources (Ceballos et al. 2015). That pressure is driven by a need for energy, food production, and land for human settlement in order to sustain the population (Balmford et al. 2012; Ceballos et al. 2015). One result of that pressure is an increasing loss of natural habitats, through habitat destruction and change in land use, as natural resources are converted to human use, which is often cited as the primary driver of biodiversity loss (Mantyka-Pringle et al. 2011). Many studies have sought to address the need to balance human needs with biodiversity conservation (Bengtsson et al. 2003; Fischer et al. 2008; Fischer et al. 2011; Phalan et al. 2011). This is particularly important in tropical regions where human population growth rates and conversion of natural habitat for agriculture and food production are at their highest (Green et al. 2005). Recent debate has led to the development of two paradigms regarding how a growing human population can produce enough food to sustain itself whilst also sustaining levels of biodiversity, termed “Land Sharing” and “Land Sparing” (Fischer et al. 2008; Phalan et al. 2011).

Land sharing describes the concept of integrating conservation aims with food production on the same land (Phalan et al. 2011). This is achieved by using a variety of environmentally friendly approaches that potentially benefit wildlife and the overall biodiversity of an area. Typically, areas dedicated to land sharing include patches of native vegetation spaced throughout the landscape and farmed areas that are structurally similar to natural areas with habitat heterogeneity achieved though diverse crop planting (Fischer et al. 2008). Conversely, land sparing comprises the separation of land for conservation from land selected for agriculture (Phalan et al. 2011). The land sparing approach can result in a trend toward high intensity industrial farming with high outputs and low crop diversity (Fischer et al. 2008). Whilst this increase in intensive production can lead to lower biodiversity in areas that employ industrial agriculture, it could, in theory, reduce the need for agricultural expansion and thus lessens the pressure on remaining natural habitats (Phalan et al. 2011). Studies have shown that while land sharing results in high biodiversity in agricultural areas (Fischer et al. 2008), it can also result in increased declines of forest specialists due to densities of forest specialists being higher within forested areas than outside forest (Phalan et al. 2011). Studies in Ghana and India showed that land sharing can result in higher loss of biodiversity over time compared to land sparing (Phalan et al. 2011).

By adopting a policy of land sparing it may be possible to save biodiversity more effectively than land sharing, but only if the resulting intensification of agriculture is achieved through contextual knowledge about appropriate agricultural methods for use in a given natural ecosystem and innovations through the use of the labour force rather than increasing yields through use of chemicals (Phalan et al. 2011). However, this approach may not always be feasible. For example, many countries may lack the resources necessary to protect large areas of land but have a long record of sharing land with biodiversity. Some countries may have high yields and high biodiversity, or biodiversity that depends on agriculture, for example European birds that are associated with farmland (Gregory et al. 2005). Additionally, some countries have regions with shallow soils [for example, south-east Asia [Ziegler et al. 2009]) and/or low rainfall (for example, livestock grazing in southern Australia [Dorrough et al. 2007]) that are only suitable for low intensity use, and so are not suitable for land-sparing approaches that implement intensive agriculture (Fischer et al. 2011). With demand for land for agriculture increasing fastest in developing tropical countries the effect of land use change on biodiversity is greatest in tropical regions where biodiversity levels are also at their highest (Green et al. 2005). In tropical regions conservation policies need to take into account local socioeconomic conditions and possibly adopt a combination of both approaches (Scariot 2013). The combination of these two theoretical approaches could create a habitat mosaic at a landscape level where biodiversity is capable of reaching spared land by moving through shared land, and therefore may help to create connections between existing protected areas and increase the adaptive capacity of natural habitats and species to environmental change (Fischer et al. 2008).

1.2 Land use change in Central America

The American region has been inhabited by humans since between 130,000 to 10,000 BC, though exact timings are still under debate and it is entirely possible that multiple ancient colonisations occurred from Asia via both land and sea (Foster 2007; Holen et al. 2017).

However, in the region now known as Central America it was not until around 10,000 to 2,000 BC that crops such as tubers (primarily sweet potato and yucca) and later maize began to be cultivated (Piperno 2006). This cultivation, especially of maize, permitted small settlements to form from Petén in northern Guatemala to the Pacific slope of Panama (Foster 2007). This led to the rise and fall of various pre-Columbian civilizations starting with the Ocós (1700 to 1500 BC) and Olmecs (1200 – 400 BC), and later the Mayans (800 BC to 1521 AD), Teotihuacans (600 to 200 BC) and Aztecs (1200-1521 AD). The latter three civilisations flourished and formed great city states that rivalled their European contemporaries. Archaeological evidence suggests that in order to sustain such huge populations cultivation of large areas of land were necessary and in some cases this dramatic change in land use caused catastrophic localized climate change that led to the downfall of many of these empires (Hanson 2012). As a result, the forests of Mexico and Northern Central America went through at least one millennium long pulse of deforestation subsequent recovery (Bray 2010).

Modern changes in land use undoubtedly started in earnest post-independence from European colonialization and there has been a major pulse in deforestation in Mexico and Central America in the 20th Century that has accelerated since World War II and coincides with the expansion of export agriculture into the lowlands of the region (Bray 2010). From 1950 to 1986 deforestation was rapid and linear at a rate of 400,000 ha lost annually, this had slowed to around 300,000 ha by 1990 (Bray 2010). The most important driver in change in land use during this time was primarily due to expansion of small-scale agriculture (Geist and Lambin 2001; Rudel 2005). Since 2000 Central America has lost 0.61% of its forest annually with deforestation rates highest in Nicaragua, Honduras, Belize, and Guatemala, and between 2000 and 2016 nearly 10% of forest cover was lost (Foster 2007). Consequentially, Nicaragua and Guatemala find themselves among the 20 countries undergoing the highest rates of deforestation (Foster 2010). For example, in Guatemala, which has suffered some the highest rates of deforestation in the region, the extent of forest cover was reduced from nearly seven million hectares in the 1950's to four million by the early 2000's, with approximately 65% of that occurring in the Petén region (Foster 2007; Tolisano and López 2010).

1.3 Biodiversity of Guatemala

Guatemala is a small country (108,889 km^2) in Northern Central America (Tolisano and López 2010). However, despite its small size it is a mega-diverse country (Sales et al. 2016). Current estimates indicate that Guatemala holds 10,364 species of plants, 1,033 fish, 735 birds, 244 mammals, 143 amphibians, and 246 reptiles (Köhler 2008; Acevedo et al. 2010; Tolisano and López 2010; Köhler 2011). Those numbers continue to rise with advances in molecular methods reveal cryptic species, and species are newly discovered, or recorded in country (for example, Griffin and Powell 2014).

To understand the current diversity of Guatemala, the geological history of the Central American region must be examined as this had major consequences for several biotic exchanges between what is now North and South America (Tolisana and López 2010). As of around 80 million years ago (Ma) Laurasia and Gondwanaland had separated and fragmented to such an extent that modern continental landmasses were recognizable, with what would become modern North and South America, and their distinctly evolving biota, still separated from each other (Wilson and Johnson 2010). From 75 Ma onwards the interaction between five tectonic plates influenced how the northern and southern biotas have interacted with each other through the presence, and absence, of various land bridges between the two major landmasses of the Western Hemisphere (Wilson and Johnson 2010). The movement of the North American, Caribbean, South American, Nazca, and Cocos plates caused transform faulting to occur, that led to the creation of four blocks of displaced regions, or terrenes, of the planet's lithosphere (Wilson and Johnson 2010). Two of these - the Mayan block and the Chortis block - play a major role in the story of Guatemala's biodiversity. The Mayan block is positioned from the Orizaba fault in southern Mexico to the Motagua and Polochic faults of eastern Guatemala, and the Chortis block sits from the Mayan block southwards to the Santa Alena fault in northern Costa Rica. (Rogers et al. 2007; Gaite et al. 2012). The other two blocks, the Chorotega and Chocó, sit between northern Costa Rica and central Panama and central Panama and western Colombia and Ecuador respectively (Montes et al. 2012).

In the late Cretaceous the movement of these blocks created a proto-Antillean isthmus that temporarily joined the north and south landmasses until continental drift of the Caribbean plate fragmented the land bridge into the modern Great Antillean islands (Wilson and Johnson 2010). From the end of the Paleocene epoch until the of the Pliocene, around 4.3 to 3.1 Ma, the north and south continental landmasses remained isolated until a second land bridge was formed between the Chortis block and South America which is present to the modern day, although there is evidence of an interchange between Atlantic and Pacific marine faunas that took place around 2.8 to 2.5 Ma suggesting a temporary break in the modern isthmus at that time (Savage 2002). During these periods of connection between the two continents there were exchanges of faunal diversity between north and south that contributed to the diversity of Central America (Campbell Jr. et al. 2010). Additionally, the highlands of Northern Central America, which includes modern Guatemala, were formed during the Miocene through to the Pliocene (Campbell 1999). Much of Guatemala's biodiversity and endemism is found in these mountainous regions that form much of the central and southern part of the country (Tolisano and López 2010). This is especially the case for amphibians and reptiles, where all but one of Guatemalan endemics are restricted to the highlands. Endemics account for 27% of amphibians and 9.8% of reptiles in Guatemala (Acevedo et al. 2010). Levels of endemism are considerably higher in amphibians and reptiles than other vertebrate fauna, for example 1.2% mammals and 1% birds (Wilson and Reeder 2005; Fagan and Komar 2016). Yet the latter two taxa have received far more conservation attention (Donaldson et al. 2016; Davis et al. 2018).

1.4 Laguna del Tigre National Park and the Mayan Biosphere Reserve

The system of protected areas in Guatemala was established in the late 1980's (Bestelmeyer and Alonso 2000). Part of that initiative gave rise to the Mayan Biosphere Reserve (MBR), a two million hectare reserve in the northern department of Petén (Hughell and Butterfield 2008). The MBR consists of several zones including a buffer zone (22%), multiple use zone (38%), and several core protected areas in the form of National Parks and Biotopes (40%) (Hughell and Butterfield 2008). Together with adjoining protected areas in Mexico and Belize, the MBR forms the largest continuous protected area in the Neotropics outside of the

Amazon Basin (Hearne and Santos 2005). Laguna del Tigre National Park (LTNP) is the largest core protected area within the MBR, it covers 289,912 hectares and includes the Laguna del Tigre Biotope (Bestelmeyer 2000). The wetland areas of LTNP are an important resource for migrating birds, and as such are a designated RAMSAR site (Bestelmeyer and Alonso 2000). The habitat of LTNP is defined as tropical humid forest (Bestelmeyer and Alonso 2000). Tropical humid forests have received relatively little attention from ecologists, are exploited heavily by humans, and are endangered throughout the world (Bestelmeyer and Alonso 2000; Gentry et al. 1995).

In 1999 Conservation International undertook a rapid biological assessment (RAP) of the park (Bestelmeyer and Alonso 2000). The RAP took place over 22 days at four sites within the boundaries of LTNP. It identified a rare freshwater mollusc reef that was previously unknown (Bestelmeyer and Alonso 2000). Amongst others, the RAP recorded 173 species of birds, 40 mammals (including bats), 14 amphibians and 22 reptiles (Bestelmeyer and Alonso 2000). The current understanding of biodiversity in LTNP is that it is home to 365 species of birds (approximately 50% of all bird species recorded in Guatemala), 57 mammals (23%), 22 amphibians (16%), and 73 reptiles (30%) (Chable pers. comm.; Chapter 3 this volume). The majority of those records come from the forest surrounding the Estación Biológica Las Guacamayas (EBG). Prior to the formation of LTNP two communities of Quecchi Mayan origin had settled within the proposed boundaries. They were given concessionary rights within the national park and allowed to continue their practices of low-level agriculture, growing mostly traditional crops including maize, black beans, squash, and papaya. One of these communities, known as Paso Caballos, is located to the east of EBG, with its concessions directly bordering land stewarded by EBG. Paso Caballos consists of approximately 200 families living on the banks of the San Pedro River, one of the main waterways in LTNP.

1.5 Conservation in Laguna del Tigre National Park

Conservation in Guatemala faces considerable challenges. For example, 39% of annual deforestation in Guatemala occurs within protected areas (Tolisano and López 2010). In Guatemala, growing population and agricultural expansion are responsible for drastic changes in land-use and habitat loss (Tolisano and López 2010). Since the 1950's

Guatemala's forests have been reduced by 39.6% (Tolisano and López, 2010). Current estimates of forest loss in Guatemala (0.92% per yr) are the highest in Central America (Sesnie et al. 2017). Deforestation in the Department of Petén accounts for 65% of total annual deforestation in Guatemala (Tolisano and López, 2010). Within Petén, the highest rates of deforestation occur within Laguna del Tigre National Park, where between 2012 and 2016, 22,927 ha of forest were lost (WCS 2016).

As a result of these high rates of deforestation within LTNP, only a small fraction of forest remains intact (WCS 2016). The majority of intact forest, ca. 5050 ha located in the south east of LTNP, is within the stewardship of EBG, and consists of several habitat types including both primary and secondary forest, saw-grass swamp and thorn scrub. Current conservation efforts within LTNP include securing the future of the remaining forest, education of Mayan communities within the park, and tackling human-induced forest fires (WCS 2016). Investigation of the amphibian and reptile assembalges of Laguna del Tigre National Park represents a unique opportunity to investigate how land-sparing (nationally protected land of a national park in biosphere reserve) and land-sharing (concessional community agriculture) interact with wildlife in the same protected area.

Due to the fact that most amphibian and reptile species that are known to occur in northern Guatemala are not considered of conservation concern there is a paucity of data about their distribution or how their population statuses are being affected by high rates of deforestation in the region (Lee 1996; Campbell 1998; Tolisano and López 2010). Given the well documented sensitivity of amphibians and reptiles to environmental change (Gibbons et al 2000; Mendelson et al. 2006), there is an urgent need to understand how change in land use is affecting amphibian and reptile assemblages in northern Guatemala.

1.6 Thesis Aims and Structure

This thesis aims to elucidate levels and patterns of amphibian and reptile diversity in Laguna del Tigre National Park and to investigate how change in land-use in northern Guatemala affects the amphibian and reptile assemblages that occur there. The data chapters presented herein follow the structure of a paper-based thesis, as such each chapter contains its own methodology section.

This thesis presents data on the amphibian and reptile assemblage of LTNP that was collected between 2013 and 2016. Prior to this study the herpetofauna of LTNP was poorly understood. A full description of the conservation status of the amphibian and reptile assemblage of LTNP is presented in Chapter 2 and includes a thorough description of the national park and a full species list as currently understood. Change in land use is a major cause of biodiversity loss. Chapter 3 employs generalized linear mixed models to examine the effects of agriculture within LTNP on the diversity and abundance of amphibians and reptiles. In Chapter 4 these concepts are explored further by investigating how agriculture affects the structures of the amphibian and reptile assemblages. The life history traits of a given species can influence how that species might react to changes in land-use. Chapter 5 uses latent variable trait modelling to investigate how the natural histories of species occurring in LTNP predict the occurrence of species within the national park. A growing body of work suggests that commonly encountered species divulge more information about the diversity of a given biological assemblage over wide geographical scales than does the presence of rare species that are difficult to detect. Chapter 6 investigates whether this is true for amphibians and reptiles in LTNP, many of which are highly cryptic, and then it extrapolates this information and attempts to predict patterns of diversity across the wider geographic region of the Mayan Biosphere Reserve.

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Chapter 2 - The Herpetofauna of Estación Biológica Las Guacamayas, Laguna del Tigre National Park.

Mexican climbing salamander – *Bolitoglossa mexicanus*

2.1 Abstract

Biodiversity is increasingly under threat, with species becoming endangered or going extinct at unprecedented rates globally. The conservation strategies of many countries and NGOs are made using international and national threat statuses (e.g. IUCN Redlist) to guide policy making. While there is clear justification to this approach it can lead to species, assemblages and habitats not receiving the attention they need in terms of regional conservation strategies. The herpetofauna of Laguna del Tigre National Park includes 93 native species, plus two non-native gekkonid lizards. The native species of LTNP represent 23.9% of Guatemala's total amphibian and reptile diversity and yet received little conservation attention for its herpetofaunal assemblage. Environmental Vulnerability Score (EVS) assessment was used to assess the regional conservation status of the LTNPs amphibian and reptile assemblage. Overall, 18% of amphibians and 49.3% of reptiles were found to be of conservation concern. These deviate from both IUCN (4.5% of amphibians and 9.5% of reptiles) and Guatemalan protected species list statuses (4.5% of amphibians and 23.9% of reptiles). EVS has been used extensively at national and regional levels in Central America, this chapter shows that the same approach is also effective at assessing species conservation status at a local level.

2.2 Introduction

Guatemala is known as a mega-diverse country and is currently understood to contain around 388 species of amphibians (143 species) and reptiles (245 species) (Acevedo et al. 2010; Griffin and Powell 2014; Ariano-Sanchez and Campbell 2018). Like many countries in the tropics the herpetofauna of Guatemala is highly endemic with 27% of amphibian and 10% of reptiles only occurring in the country (Acevedo et al. 2010). As a consequence, much of the amphibian and reptile conservation focus has been centred on regions with high levels of endemism, including the Western and Central Highlands and the Motagua Valley (Duellman and Campbell 1992; Campbell and Frost 1993; Coti and Ariano-Sánchez 2008; Campbell et al. 2010). Although the northern region of Petén, the northernmost department of Guatemala, has been devoted to protected land in the form of the Mayan Biosphere Reserve (MBR) most conservation research has been focussed on large enigmatic vertebrates such as jaguar (*Panthera onca*) (Wultsch et al. 2016), Central American tapir (*Tapirus bairdi*) (Lepe-López et al. 2018), scarlet macaw (*Ara macao*) (Schmidt et al. 2020), Morelet's crocodile (*Crocodylus moreletii*) (Corado García et al. 2020), and Central American river turtle (*Dermatemys mawii*) (García-Anleu et al. 2007).

Laguna del Tigre National Park (LTNP) is located in north western Petén in Northern Guatemala and borders Mexico to the north and west. It is the largest of the core zones within the MBR, and covers approximately 289,000 hectares, and contains the largest protected wetland in Central America (Wallace 1997; Bestelmeyer 2000; Monzón-Alvarado et al. 2012). Northern Petén forms the southern limits of the Yucatán Platform and is characterized by a karst landscape, that is dominated by thin, fragile limestone soils (Monzón-Alvarado et al. 2012). The limestone that forms the platform was laid down during the Miocene and is typified by limestone cliffs along the few river courses that exist (Bestelmeyer 2000). The terrain of LTNP is mostly flat with undulations reaching a maximum of 300 m altitude (Bestelmeyer 2000; Monzón-Alvarado et al. 2012). LTNP is subject to distinct wet and dry seasons and receives, on average, 1600 mm of rain annually. The dry season lasts from January to April where temperatures may exceed 40º C (Bestelmeyer 2000). This high degree of seasonality may present significant challenges for the ecological communities of LTNP. The vegetation of LTNP is dominated by corozo palm (*Attalea cahune*), ceiba (*Ceiba pentandra*), guarumo (*Cecropia* spp.) and ramón (*Brosimum alicastrum*) and is classed as Tropical Moist Forest under the classification system of Holdridge (1967) or Subtropical Moist Forest (warm) by Acevedo et al. (2010). The undulating limestone leads to variation of soil drainage and consequentially two main forests types have developed (Bestelmeyer 2000). Over 50% of the forest cover in LTNP is classed as high forest (known locally as Bosque Altos) which is situated on the higher undulations (Monzón-Alvarado et al. 2012). High forest is characterized by well drained soils, a 30 m canopy with abundant leaf litter and little undergrowth (Bestelmeyer 2000; Monzón-Alvarado et al. 2012). A further 20% of LTNP is covered by seasonally flooded low forest (known locally as Bosque Bajo), which possess a lower canopy that is between 15 to 20 m, along with a dense understory (Bestelmeyer 2000; Monzón-Alvarado et al. 2012). The remaining area of LTNP is made up of wetlands (16%), seasonally flooded savannas (5%), and agriculture and pasture (9%) (Monzón-Alvarado et al. 2012).

A large body of recent work has focused on the conservation status of amphibians and reptiles at country level for Central America and at state level for Mexico (Wilson et al. 2010; Johnson et al. 2015; Mata Silva et al. 2015; González-Sánchez et al. 2018; Ramirez Bautista et al. 2020). This series of work has employed a scoring system known as Environmental Vulnerability Scores (EVS) to assess the conservation status of amphibians and reptiles at wide regional scales. The EVS takes into account the distribution of a given species at both global and regional scales, whilst accounting for sensitivities in breeding ecology (frequently the case for amphibians) and vulnerability to human persecution (frequently a risk for reptiles) (Johnson et al. 2015). As a consequence, the EVS system of assessment is effective at revealing species in need of conservation attention at the regional scale in which it is used. A disparity between EVS assessments and the widely known IUCN Red List assessments is often reported, where there are far fewer species of conservation concern at the IUCN level in a given region (Acevedo et al. 2010; González-Sánchez et al. 2018). The reason for this disparity is due in part to the fact that the IUCN Red List only considers distribution at the global scale. While the IUCN listings are undoubtably of key value, such lack of resolution at the regional scale can lead to misassigned conservation priorities when they are used to assess local conservation planning. Additionally, a national endangered species list (Lista de Especies Amenzadas or LEA) is compiled annually in Guatemala which places threatened species in one of three categories: 1) Critical Danger (PC) for species that are close to extinction; 2) Endangered (EP) for species that are nationally endemic and with restricted ranges that are threatened by habitat loss and often illegal trade; and 3) Vulnerable (VU) for species that are threatened by habitat loss or trade but where populations are such that regulated use of the species is possible (CONAP 2009). This study is the first attempt to use EVS to assess the conservation status of amphibians and reptiles in at a National Park level. EVS scores will then be compared to existing global and national endangered species lists to assess the usefulness of EVS for conservation planning at a regional scale.

The objectives of this chapter were to: a) provide a comprehensive assessment of the amphibian and reptile diversity of LTNP as currently understood and assess levels of amphibian and reptile diversity and endemism in LTNP; b) assess the conservation status of amphibian and reptile species in LTNP; and c) compare IUCN Red List and national LEA species with EVS assessments of amphibians and reptiles in LTNP.

2.3 Methods

2.3.1 Biological Records

Field data was collected in Laguna del Tigre National Park from 2013 to 2016 using adhoc and transect based surveys (Figure 2.1). Estación Biológica Las Guacamayas (EBG) is located in the south east of Laguna del Tigre National Park (LTNP) on the banks of the Rio San Pedro (Figure 2.2). The Tropical Moist Forest (Holdridge 1967) of EBG consists of several habitat types including both primary and secondary forest, saw-grass swamp and thorn scrub. It is bordered to the east by concessional agricultural lands that belong to the nearby Quecchi Maya community of Paso Caballos. Transect surveys were conducted in four forest habitats, Agricultural Edge, High Forest, Low Forest and Natural Edge within the ownership of EBG

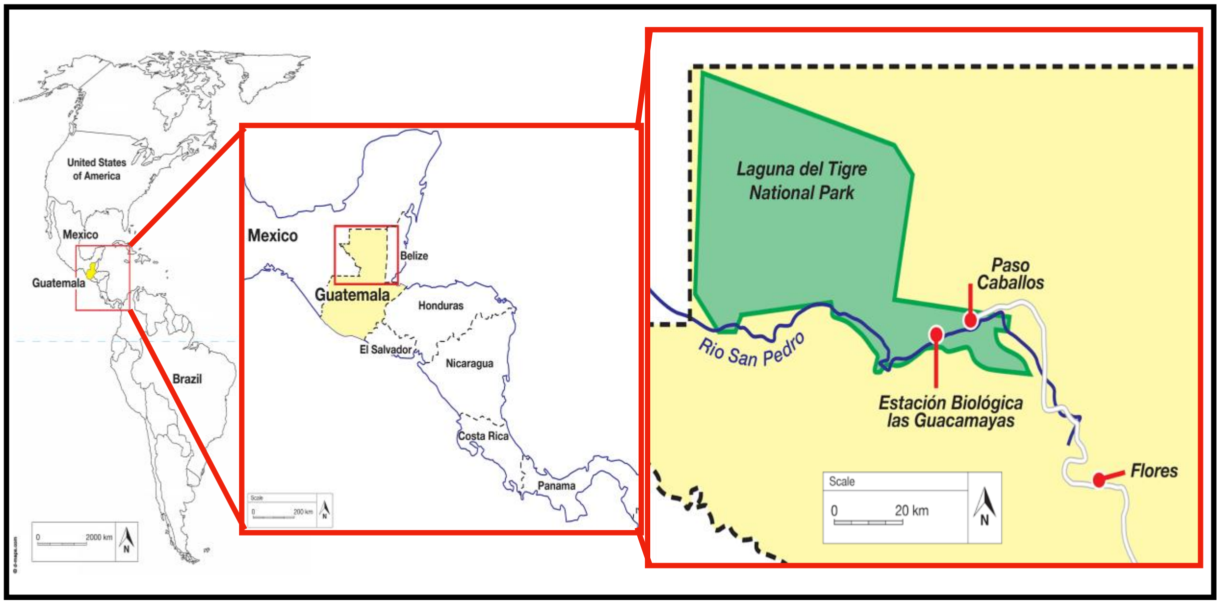

Figure 2.1: Map of the Americas, showing the location of Laguna del Tigre National Park within Guatemala. Red box indicates area shown in Figure 2. Due to the curvature of the map the scale shown is representative of the scale at the equator. Map adapted from D-Maps.com

(Figure 2.2). Additional adhoc visual encounter surveys were conducted around the buildings of EBG and the saw-grass swamp near the confluence of the San Pedro and Sacluc rivers (Figure 2.2). Field data was augmented with information garnered from a literature search and from photographically verified personal communications with other fieldworkers in LTNP.

2.3.2 Field Methods

In each of the four habitats, 100 m transects were conducted both along existing trail systems and on transects cut sensitively into the forest away from the trails. Transects were placed to allow a representative sample of each habitat and promote heterogeneous sampling across microhabitats for efficient detection of herpetofauna (Crump and Scott 1994; Doan

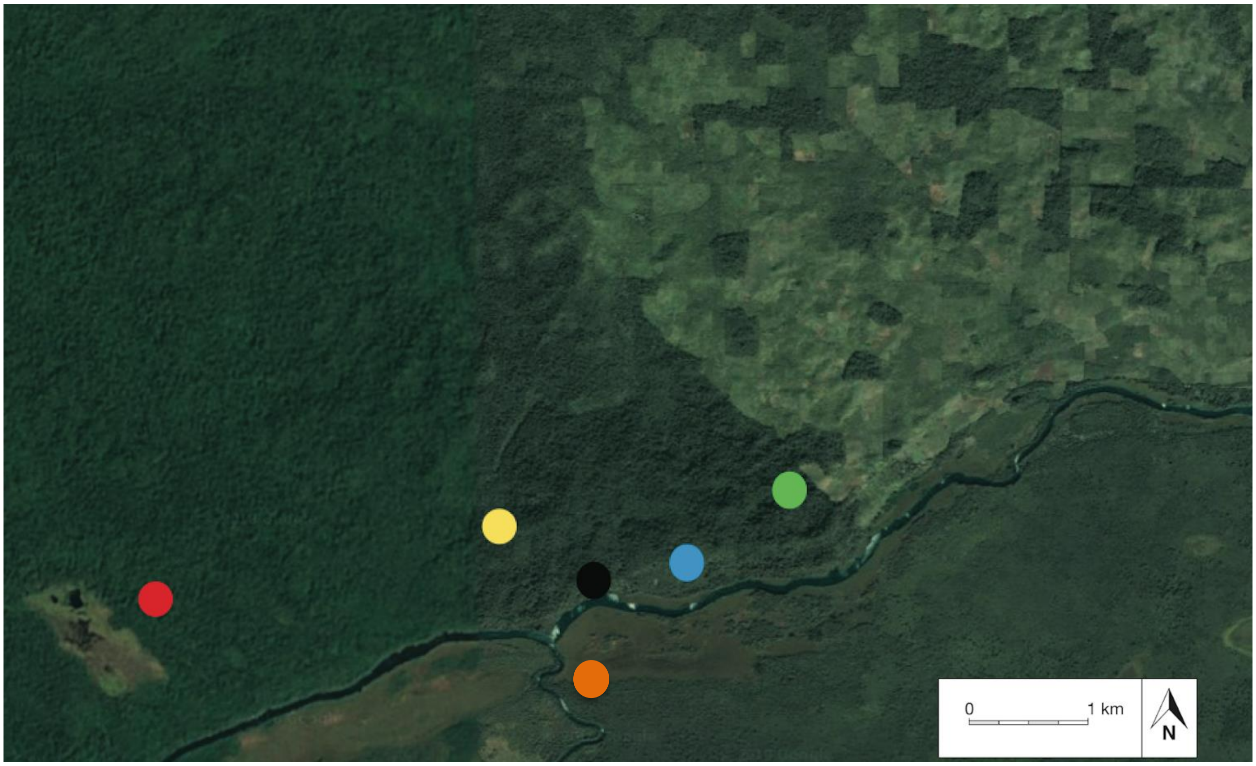

Figure 2.2: Satellite image of the southeast region of Laguna del Tigre National Park showing the location of survey sites indicated by coloured dots: Green = Agricultural Edge; Yellow = High Forest; Red = Low Forest; Blue = Natural Edge; Orange = Saw-grass swamp; Black = Estación Biológica las Guacamayas. The two rivers are the San Pedro River flowing east to west, and the Sacluc River flowing south to north. North of the San Pedro dark green areas indicate forest areas, lighter green indicates the concessional agricultural land of Paso Caballos. South of the San Pedro, green indicates a mixture of saw grass swamp (sabinal) and seasonally flooded thorn scrub. Image adapted from Google Maps.

2003; Marsh and Haywood 2010). The start points for each transect (Figure 2.2) were positioned at least 50 m from the nearest forest edge to allow for any edge effects to be taken into account that may have risked biasing detection (Schlaepfer and Gavin 2001; Urbina-Cardona et al. 2006). Transects were marked every 25 m with flagging tape to indicate the path of the transect, and GPS waypoints were taken at the start and finish points using a handheld GPS device (Garmin™ GPSMap 62s) to facilitate accurate survey replication. After setup, transects were left for a minimum of two days before surveying commenced to allow for animals to resume normal activity prior to survey (Crump 1994). All transects had negligible changes in altitude and were positioned to avoid passing through broad habitat types in order to satisfy assignment of habitat categorisation (Babbitt et al. 2009). Surveys took approximately 45 minutes to one hour to complete and followed standardised protocols for Visual Encounter Surveys in tropical habitats (Rödel and Ernst 2004; Vonesh et al. 2009).

To maximise chances of detecting species with different autecology, each transect was surveyed three times, twice at night and once in the morning during each survey period (Heyer et al. 1994; McDiarmid et al. 2012). For the purposes of statistical analyses nocturnal and diurnal surveys were grouped. A minimum of two days was left between surveys of the same transect to maintain independence of sample survey periods. Surveys were conducted during seven fieldwork periods in May-June 2013, November-December 2013, June 2014, October 2014, June 2015, December 2015 and June-July 2016. A total of 86 transects were surveyed, comprising 17 in AE, 22 in HF, 23 in LF, and 24 in NE respectively. The order in which the four forest habitats were surveyed was randomized, as was the order of transects within each habitat. In some cases, fieldwork was hampered by inclement weather and surveys had to be abandoned, hence the non-equal survey effort.

2.3.3 Data Collection

The following environmental data were recorded at the start and finish of each transect: time (24 hr), air temperature (ºC), relative humidity (%), and cloud cover (%). When safe and practical to do so, each animal encountered was captured and the following data recorded: time encountered (24 hr), location (recorded using a Garmin GPSmap 62s), species, age (adult, juvenile, neonate), and sex (where possible).

Visual encounter surveys are a well-known method for surveying amphibians and reptiles (Crump and Scott 1994; Lovich et al. 2012). Surveys teams consisted of between two and eight people, and included one local guide, the author and two to six field assistants. At the start of each field session, all guides and field assistants were trained in survey techniques, data collection, and species identification by the author. All biometric and environmental data collection was overseen by the author to avoid observer bias. Transects were walked at a suitably slow pace to allow detection of reptiles and amphibians by thorough examination of vegetation and refugia, such as leaf litter, fallen limbs and rocks (Crump and Scott 1994; Lovich et al. 2012). The search area was defined as up to one metre each side of the transect and up to two metres high (Crump and Scott 1994; Lovich et al. 2012). Any individual found outside of this area was recorded as a casual observation but omitted from this study. Data collection followed the method outlined above.

2.3.4 Conservation Status Evaluations

Calculation of Environmental Vulnerability Scores (EVS) follows Acevedo et al. (2010) and included reassessments of seven species that have been revised taxonomically, and one species that was recorded in Guatemala for the first time since the 2010 assessment. EVS scores are a popular method for assessing the regional conservation status of species (Wilson et al. 2010; Johnson et al. 2015; Mata Silva et al. 2015). Scores are calculated based on a species' geographic distribution, specialisation of reproductive mode for amphibians, vulnerability to human persecution for reptiles, and ecological distribution based on the number 14 life-zones of Guatemala a given species occurs in as described by Acevedo et al. (2010) and summarized in Table 2.1. Scoring criteria are explained in more detail in Table 2.2. Each scoring criterion holds a value with the lowest scores being awarded for less specialized characteristics and higher scores awarded to those that are more highly specialized. After scores have been assessed for all characteristics of a given species, they are summed to give an overall EVS score. Following previous assessments of Guatemala herpetofauna (Acevedo et al. 2010), species with EVS scores between 3 to 9 were classed as of low vulnerability, those with scores between 10 to 13 of medium vulnerability, and those with scores between 14 to 19 of high vulnerability. Categorization of each species occurring

Table 2.1: Description of Guatemalan life-zones as described by Acevedo et al. (2010)

	Life-zone	Altitude (masl)	Annual Precipitation (mm)	Region in Guatemala
1	Tropical Wet Forest	0 - 1267	3600	Caribbean Coast
2	Tropical Dry Forest	440 - 600	1300	SE Guatemala around the area of Lago de Güila on the El Salvador border
3	Subtropical Rain Forest	460 - 1400	4410 - 6577	Sierra de las Minas in the E Guatemala and Sierra de Chamá
4	Subtropical Wet Forest (warm)	80 - 1600	1587 - 4327	Mainly in southern Petén and Izabal, Alta Verapaz, Quiché, and Huehuetenango. But also a small area in southwestern Guatemala near the Mexican border
5	Subtropical Wet Forest (cold)	1100 - 1800	2045 - 2514	Central highlands of Alta Verapaz
6	Subtropical Moist Forest (warm)	0 - 275	1160 - 2000	Northern Petén and extreme southern Guatemala
7	Subtropical Moist Forest (temperature)	650 -1700	1100 - 1349	A wide distribution acrosss moderate eleveations of central America
8	Subtropical Dry Forest	0 - 1200	500 - 1000	6 disjunct areas in central and south Guatemala
9	Subtropical Thorn Scrub Forest	180 - 400	400 - 600	Motagua Valley of eastern Guatemala
10	Subtropical Lower Montane Rain Forest	1500 - 1700	> 1400	Central highlands of Alta Verapaz
11	Subtropical Lower Montane Wet Forest	1800 - 3000	2065 - 3900	Western highlands of Guatemala
12	Subtropical Lower Montane Moist Forest	1500 - 2400	1057 - 1588	Southwestern Guatemala
13	Subtropical Montane Wet Forest	> 2800	2500	High elevations in Western Guatemala
14	Subtropical Montane Moist Forest	> 3500	1275	Limited to the very high elevations of the Sierra de Los Cuchumatanes in Western Guatemala

Table 2.2: Environmental Vulnerability Score (EVS) assessment criteria following Acevedo et al. (2010).

EVS Score	Geographic Distribution	Specialisation of Reproductive Mode (amphibians only)	Vulnerability to Human Persecution (reptiles only)	Ecological Distribution in Guatemala
1	Widespread in and outside Guatemala	Both eggs and tadpoles in large or small bodies of lentic or lotic water	Fossorial, typically escaping human notice	Occurs in 8 to 14 life-zones
2	Peripheral in Guatemala, widespread outside of Guatemala	Eggs in foam nests, tadpoles in small bodies of lentic or lotic water	Semifossorial, or nocturnal arboreal or aquatic, nonvenomous and usually nonmimicking, sometimes escaping human notice	Occurs in 7 life-zones
3	Restricted to Nuclear Central America	Tadpoles occur in small bodies of lentic or lotic water, eggs outside of water	Terrestrial and or arboreal or aquatic, generally ignored by humans	Occurs in 6 life-zones
4	Restricted to Guatemala	Eggs laid in moist situations on land or arboreally, direct development or viviparous	Terrestrial and or arboreal or aquatic, thought to be harmful (often mistakenly) and may be killed on sight	Occurs in 5 life-zones
5	Only known in the vicinity of the type locality in Guatemala	Eggs and/or tadpoles in water-retaining bromeliads or water-filled tree cavities	Venomous species or mimics thereof, usually killed on sight	Occurs in 4 life-zones
6			Species exploited by humans for their meat, eggs, or skin	Occurs in 3 life-zones
7				Occurs in 2 life-zones
8				Occurs in 1 life-zone

in LTNP by the IUCN were obtained from the IUCN list of threatened species website (IUCN 2021) and cross-referenced with Acevedo et al. (2010). Distributional statuses were assessed using distribution records in Köhler (2008) for reptiles and Köhler (2011) for amphibians and using online resources (AmphibiaWeb and ReptileDatabase accessed 17/07/2021). They were defined as those restricted to the Yucatán Peninsula classed as Regional Endemic (RE), those that occurred outside of Guatemala but that have restricted distributions with the country as Range Restricted (RR), and those that occurred widely outside of Guatemala as Non-Endemic (NE).

2.4 Results

2.4.1 Diversity and Endemism

During this study, fieldwork confirmed the presence of 92 species of amphibian and reptile in LTNP, including 20 species of amphibian (8 families / 17 genera), 27 species of lizard (10 families / 15 genera), 37 species of snake (4 families / 29 genera), seven species of turtle (3 families / 6 genera), and one species of crocodylian (1 family / 1 genus).

Three additional species have been recorded by other workers in LTNP but had not yet been recorded during this study: the hylid frog species *Dendropsophus ebracattus,* hourglass treefrog, (Bestelmeyer and Alonso 2000) and *Agalychnis moreletii,* black-eyed treefrog (Tut pers. comms. and photograph verified), and the colubrid snake *Senticolis triaspis,* green ratsnake (Tut pers. comms. and photograph verified). Therefore, when these records are included, LTNP is home to 95 species of which 22 are amphibian (8 families / 17 genera), 27 species of lizard (10 families / 15 genera), 38 species of snake (4 families / 30 genera), seven species of turtle (3 families / 6 genera), and one species of crocodylian (1 family / 1 genus).

No country endemics are found in LTNP, however 3 species of amphibian, 2 lizards, and 7 snakes are considered regionally endemic to the Yucatán Peninsula and are at the southernmost part of their range in northern Guatemala (Table 2.3). Several other species have highly restricted ranges, including the crocodylian *Crocodylus moreletii*, and 5 species of turtle, including *Dermatemys mawii* which is listed as Critically Endangered by IUCN, and 4 lizards (Table 2.3). No amphibian species were found to be range restricted in Guatemala, 9.1% were classified as regional endemics, with the remaining 90.9% being classified as non-endemic (Table 2.4). Whereas 15.1% of reptile species were classified as range restricted, 10.1% were classed as regional endemic, and the remaining 73.9% were classified as non-endemic (Table 2.5). Although the colubrid snake *Tropidopdipsas fasciatus* has a wide range in Mexico, LTNP is currently the only location in Guatemala where the species has been recorded and so is considered range restricted in the country in this study (Griffin and Powell 2014). Two species of gekkonid lizard are non-native, having been introduced through human activities and both belong to the African-Eurasian genus *Hemidactylus* (Table 2.3).

2.4.2 Conservation Status

Environmental Vulnerability Scores (EVS) were calculated for all 22 amphibian and 71 reptile species that are currently known to occur in LTNP, the two non-native geckos were excluded from this analysis as they were only detected around human constructs and were not considered a threat to native fauna. Five species of reptile (1 crocodylian and 4 turtles) were found to have High EVS scores (Table 2.3). Four species of amphibians, 3 turtles, 8 lizards, and 20 snakes were found to have Medium scores. The remaining 18 amphibian, 19 lizard, and 18 snake species were found to have low scores. The seven species that were reassessed did not change their EVS status compared to Acevedo et al. (2010). A review of the IUCN Red List website identified 1 Critically Endangered turtle, 1 Vulnerable amphibian and 1 Vulnerable crocodilian, 4 Near Threatened turtles and 1 Near Threatened lizards, and 7 Least Concern amphibians, 2 Least Concern turtles, 9 Least Concern lizards, and 37 Least Concern snakes, and 1 Data Deficient snake (Tables 2.4 and 2.5). There is a disparity between EVS and IUCN assessments of the conservation status of amphibians and reptiles in LTNP. In the case of amphibians 18% of species are of conservation concern using EVS scores (High and Medium vulnerabilities), whereas only 4.5% are of conservation concern using IUCN statuses (CR, EN, VU, NT). The disparity is more pronounced when reptiles are considered with 49.3% of species being of conservation concern using EVS scores, compared to only 9.5% using the same IUCN statuses.

A review of the latest national LEA (CONAP 2021) revealed that 112 of the 143 amphibians (78% of all species) present in Guatemala are considered to be threatened (PC 42; EP 44; VU 26), although only one species present in LTNP is included at Vulnerable level. This represents 4.5% of the amphibians present in LTNP. 150 reptiles (61% of all species) are currently considered endangered at a national level (PC 19; EP 59: VU 72), of these 17 are present in LTNP (PC 1; EP 3; VU 13), representing 23.9% of the total reptile fauna of the park. Again, national assessments of endangered amphibians and reptiles are more conservative than those of the EVS assessments.

Table 2.3: Comparison of the conservation status of amphibian and reptile families in Laguna del Tigre National Park, Guatemala using Environmental Vulnerability Scores (EVS), IUCN Red List status, and distributional status. IUCN codes: CR = critically endangered; VU = Vulnerable; NT = Near threatened; LC = Least concerned; DD = Data deficient. Distributional status codes: RR = Range restricted; RE = Regional endemic; NE = Not endemic; NN = Non-native.

	EVS			**IUCN status**					**Distributional Status**			
	High	**Medium**	**Low**	**CR**	**VU**	**NT**	**LC**	**DD**	**RR**	**RE**	**NE**	**NN**
Amphibia												
Caudata												
Plethodontidae	0	1	0	0	0	0	1	0	0	0	1	0
Anura												
Rhinophryindae	0	0	1	0	0	0	1	0	0	0	1	0
Bufonidae	0	0	2	0	0	0	2	0	0	0	2	0
Leptodactylidae	0	0	3	0	0	0	2	0	0	0	3	0
Eleutherodactylidae	0	1	0	0	1	0	0	0	0	1	0	0
Hylidae	0	2	8	0	0	0	10	0	0	1	9	0
Microhylidae	0	0	2	0	0	0	3	0	0	1	1	0
Ranidae	0	0	2	0	0	0	2	0	0	0	2	0
Reptilia												
Testudines												
Dermatemidae	1	0	0	1	0	0	0	0	1	0	0	0
Kinosternonidae	2	2	0	0	0	3	1	0	3	0	1	0
Emydidae	1	1	0	0	0	1	1	0	1	0	1	0
Crocodylidae	1	0	0	0	1	0	0	0	1	0	0	0
Squamata												
Eublepharidae	0	1	0	0	0	0	1	0	0	0	1	0
Sphaerodactylidae	0	0	2	0	0	0	2	0	0	0	2	0
Gekkonidae	0	0	3	0	0	0	3	0	0	0	1	2
Corytophanidae	0	0	3	0	0	0	3	0	1	0	2	0
Iguanidae	0	1	0	0	0	0	1	0	0	0	1	0
Phrynosomatidae	0	2	0	0	0	0	2	0	1	1	0	0
Dactyloidae	0	2	6	0	0	0	8	0	0	1	7	0
Scincidae	0	1	3	0	0	0	4	0	1	0	3	0
Teiidae	0	0	2	0	0	0	2	0	0	0	2	0
Anguidae	0	1	0	0	0	1	0	0	1	0	0	0
Boidae	0	0	1	0	0	0	1	0	0	0	1	0
Colubridae	0	18	17	0	0	0	34	1	1	7	27	0
Elapidae	0	1	0	0	0	0	1	0	0	0	1	0
Viperidae	0	1	0	0	0	0	1	0	0	0	1	0

Table 2.4: Environmental Vulnerability Scores, IUCN statuses, and distributional statuses for amphibians occurring in Laguna del Tigre National Park. IUCN status categories are: CR = Critically endangered; VU = Vulnerable; NT = Near threatened; LC = Least concern; DD = Data deficient. Distributional Status categories are: RR = Range restricted; RE Regional endemic; NE = Non-endemic.

Species	**Geographic Distribution**	**Reproductive Specialisation**	**Ecological Distribution**	**EVS**	**IUCN Status**	**Distributional Status**
MEDIUM						
Bolitoglossa mexicana	1	4	5	10	LC	NE
Eleutherodactylus leprus	1	4	6	11	VU	NE
Dendropsophus ebreccata	1	3	7	11	LC	NE
Triprion petasatus	3	1	7	11	LC	RE
LOW						
Incilius valliceps	1	1	5	7	LC	NE
Rhinella horribilis *	1	1	1	3	LC	NE
Agalychnis callidryas	1	3	5	9	LC	NE
Agalychnis moreletii	3	3	3	9	LC	NE
Dendropsophus microcephala	1	3	5	9	LC	NE
Scinax staufferi	1	1	5	7	LC	NE
Smilisca baudinii	1	1	1	3	LC	NE
Tlalocohyla loquax	1	1	5	7	LC	NE
Tlalocohyla picta	1	3	5	9	LC	NE
Trachycephalus typhonius	1	1	4	6	LC	NE
Engystomops pustulosus	1	2	4	7	LC	NE
Leptodactylus fragilis	1	2	2	5	LC	NE
Leptodactylus melanolotus	1	2	2	5	LC	NE
Gastrophryne elegans	1	1	6	8	LC	RE
Hypopachus variolosus	1	1	5	7	LC	NE
Rana brownorum	1	1	3	5	LC	NE
Rana vaillanti	1	1	4	6	LC	NE
Rhinophrynus dorsalis	1	1	5	7	LC	NE

* reassessed from Acevedo et al. (2010) due changes in taxonomy.

Table 2.5: Environmental Vulnerability Scores, IUCN statuses, and distributional statuses for reptiles occurring in Laguna del Tigre National Park. IUCN status categories are: CR = Critically endangered; VU = Vulnerable; NT = Near threatened; LC = Least concern; DD = Data deficient. Distribution Status categories are: RR = Range restricted; RE Regional endemic; NE = Non-endemic.

Species	Geographic Distribution	Vulnerability to Human Persecution	Ecological Distribution	EVS	IUCN Status	Distribution Status
HIGH						
Crocodylus moreletii	1	6	7	14	VU	RR
Dermatemys mawii	3	6	7	14	CR	RR
Rhinoclemmys areolata	3	6	6	15	NT	RR
Claudius angustus	2	6	7	15	NT	RR
Kinosternon acutum	3	6	7	16	NT	RR
MEDIUM						
*Trachemys venusta **	1	6	4	11	NT	NE
Kinosternon leucostomum	1	6	5	12	LC	NE
Staurotypus triporcatus	1	6	6	13	NT	RR
Celestus rozellae	3	4	5	12	NT	RR
Coleonyx elegans	1	4	6	11	LC	NE
Iguana iguana	1	6	3	10	LC	NE
Norops rodriguezii	3	2	5	10	LC	RE
Norops sagrei	1	2	8	11	LC	RR
Sceloporus chrysostictus	3	2	7	12	LC	RE
Sceloporus teapensis	3	2	6	11	LC	RR
Mesoscincus schwartzei	3	1	7	11	LC	RE
Adelphicos quadrivirgatus	1	2	7	10	DD	NE
Clelia scytalina	1	4	8	13	LC	RR
Coluber mentovarius	1	4	5	10	LC	NE
Coniophanes schmidtii	3	2	8	13	LC	RE
Ficimia publia	1	2	7	10	LC	NE
Leptodeira frenata	1	2	7	10	LC	RE
Leptophis ahaetulla	1	4	5	10	LC	NE
Oxyrhopus petolarius	1	5	6	12	LC	NE
Pliocercus elapoides	1	5	4	10	LC	NE
Scaphiodontophis annulatus	1	5	7	13	LC	NE
Senticolis triaspis	1	4	6	11	LC	NE
Sibon dimidiata	1	4	5	10	LC	NE
Tantilla moesta	3	2	8	13	LC	RE
Tantillita canula	3	2	7	12	LC	RE
Thamnophis proximus	1	4	6	11	LC	NE
Tretanorhinus nigroluteus	1	4	6	11	LC	NE
Tropidodipsas fasciatus	2	2	8	12	LC	RR
Xenodon rabdocephalus	1	5	6	12	LC	NE

(continued on next page)

Table 2.5 continued.

Species	Geographic Distribution	Vulnerability to Human Persecution	Ecological Distribution	EVS	IUCN Status	Distribution Status
*Micrurus apiatus **	1	5	6	12	NA	NE
Bothrops asper	1	5	5	11	LC	NE
LOW						
Sphaerodactylus glaucus	1	3	3	7	LC	NE
Sphaerodactylus millepunctatus	1	3	3	7	LC	NE
Thecadactylus rapicauda	1	2	5	8	LC	NE
Basiliscus vittatus	1	3	1	5	LC	NE
Corytophanes cristatus	1	3	5	9	LC	NE
Corytophanes hernandezii	1	3	5	9	LC	RE
Norops beckeri	1	2	6	9	LC	NE
Norops capito	1	2	5	8	LC	NE
Norops lemurinus	1	2	4	7	LC	NE
*Norops welbornae **	1	2	4	7	LC	NE
Norops tropidonotus	1	2	6	9	LC	NE
*Norops unilobatus **	1	2	5	8	LC	NE
Plestiodon sumichrasti	1	1	6	8	LC	NE
*Marisora brachypoda **	1	2	3	6	LC	NE
Sphenomorphus cherriei	1	2	5	8	LC	NE
Holcosus festivus	1	2	5	8	LC	NE
Holcosus undulatus	1	2	1	4	LC	NE
Boa imperator	1	6	1	8	LC	NE
Coniophanes bipunctatus	1	2	5	8	LC	NE
Coniophanes imperialis	1	2	5	8	LC	NE
Drymarchon melanurus	1	4	1	6	LC	NE
Drymobius margaritiferus	1	4	2	7	LC	NE
Imantodes cenchoa	1	2	4	7	LC	NE
*Lampropeltis abnorma **	3	5	1	9	LC	NE
Leptodeira septentrionalis	1	4	1	6	LC	RE
Leptophis mexicana	1	4	4	9	LC	NE
Mastigodryas melanolomus	1	4	4	9	LC	NE
Ninia diademata	1	2	4	7	LC	NE
Ninia sebae	1	5	1	7	LC	NE
Oxybelis aeneus	1	4	3	8	LC	NE
Oxybelis fulgidus	1	4	3	8	LC	NE
Pseudelaphe flavirufa	1	2	4	7	LC	NE
Sibon nebulatus	1	4	1	6	LC	NE
Spilotes pullatus	1	4	2	7	LC	NE
Tropidodipsas sartorii	1	5	3	9	LC	NE

* reassessed from Acevedo et al. (2010) due changes in taxonomy.

2.5 Discussion

The herpetofauna of LTNP includes 93 native species, plus two non-native gekkonid lizards. The native species of LTNP represent 23.9% of Guatemala's total amphibian and reptile diversity. The nearby Sierra Lacandon mountains in Mexico that are contiguous with LTNP are reported to have a diversity of 124 species and includes 35 amphibians and 89 reptiles (Hernández-Ordóñez et al. 2014). Although the two regions are essentially part of the biogeographical unit, Lacandon has a wider altitudinal gradient (100 - 1500 m) and receives nearly twice as much precipitation than LTNP, 2894 mm compared to 1500 mm annually (Bestelmeyer 2000; Hernández-Ordóñez et al. 2014). These distinct differences between LTNP and the Lacandon region may account for differences in assemblage structure and diversity. To the north of LTNP lies the wider Yucatán Peninsula region of Mexico, the region consists of three states (Campeche, Quintana Roo, and Yucatán itself), and covers an area of 126,742 km^2 compared to the 2.89 km^2 of LTNP. Recent assessments of the conservation status of the Yucatán Peninsula identified 145 species, of which 25 are amphibians and 120 are reptiles (González-Sánchez et al. 2018). The southern portion of the Yucatán Peninsula in Mexico includes the Calakmul Biosphere Reserve (CBR), which borders the Guatemalan Mayan Biosphere Reserve to the north and includes 723,000 ha of reserve and 384,000 ha of buffer zone (Colston et al. 2015). The herpetofaunal diversity of CBR is currently understood to contain 89 species, of which 20 are amphibians and 69 are reptiles (Colston et al. 2015). The herpetofauna of LTNP represents a significant proportion of the wider Yucatán diversity (65.5% represented in LTNP), compared to that of CBR (61.3%) which is similar to LTNP in terms of habitat classification but is two and half times the size.

Although many of the species that occur in LTNP are widely distributed throughout the lowlands of Guatemala, much of that distribution is unprotected land that is subject to a wide variety of land-uses and the majority of natural habitat has already been lost (Tolisano and Lopéz 2010). Regardless of the measure used, a higher proportion of reptile species were considered to be of a vulnerable conservation status than amphibians. As such LTNP could be considered a stronghold for the conservation of widespread Guatemalan herpetofauna, especially reptile species. This pattern is reversed when compared to the assessment of

Acevedo et al. (2010) which found that a greater proportion of amphibians, compared to reptiles, were considered of vulnerable conservation status at a national level. Compared to EVS assessments both IUCN and LEA lists of endangered species underestimate the number of species of conservation interest in LTNP. This disparity between the IUCN and EVS assessments is consistent with other studies that employ the EVS methodology (Wilson et al. 2010; Johnson et al. 2015; Mata Silva et al. 2015). However, studies have shown that perceived shortcomings in the use of IUCN Red List data at the regional level is often linked to the failure to use the Regional Assessment Guidelines provided by the IUCN (Miller et al. 2007). The regional guidelines suggest that species under assessment should first be considered endemic to the country or isolated from other populations, and then secondly, it should consider whether the population in question is in contact with other populations outside of the country of interest (Gärdenfors 2001). Correct use of the IUCN regional guidelines may decrease the disparity between IUCN and EVS assessments.

The EVS methodology has been successfully applied to the herpetofauna at various geographical scales including Country, State, and more recently regional levels (Wilson et al. 2010; Johnson et al. 2015; Mata Silva et al. 2015). This chapter represents the first attempt to use the EVS methodology to assess the conservation status of the herpetofauna of a relatively small geographic unit such as a National Park and highlights the usefulness of EVS to assess the conservation status of amphibians and reptiles at various regional scales. Additionally, when considered without the use of EVS, the herpetofauna of LTNP represents relatively little conservation concern. The use of EVS however reveals that the herpetofauna of the region is of greater conservation interest than previously realised. While the herpetofauna of LTNP contains no species endemic to Guatemala itself, many are regional endemics to the Yucatán Peninsula and populations in Petén, Guatemala, represent their most southerly ranges. Due to under sampling of the region, these species are often represented by only a few specimens and their distribution and importance to the herpetofauna of the country is therefore poorly understood.

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Chapter 3 – Does low-level agriculture affect reptiles and amphibians within Laguna del Tigre National Park, Petén, Guatemala?

Guatemalan ringneck snake– *Scaphiodontophis annulatus*

3.1 Abstract

Habitat fragmentation and change in land-use are major causes of biodiversity loss, and have been shown to negatively impact amphibians and reptiles across the globe. This chapter investigates the response of the amphibian and reptile assemblages in Laguna del Tigre National Park, Northern Guatemala, to the presence of low-level subsistence agriculture that is practiced by a local community within the park. Laguna del Tigre also suffers from some of the highest rates of deforestation in Guatemala. Visual Encounter Surveys (VES) were conducted in four forest habitats in order to assess the impacts of the agriculture and fragmentation on amphibians and reptiles in the park. Species diversity was found to be consistently lower close to the agricultural edge, and the assemblages in those habitats were dominated by between two and three highly abundant species. GLMMs were used to identify the predictors of changes in diversity of the amphibian, snake, and lizard assemblages. Amphibian diversity was higher in low forest habitats, whereas snake diversity was lowest in agricultural edge habitats.

3.2 Introduction

Loss of biodiversity is one of the most pressing environmental concerns of our time (Ceballos et al. 2015). We are currently witnessing major declines in many terrestrial vertebrate populations, with many species threatened with extinction and many more populations threatened with local extirpation (Ceballos et al. 2015). The most threatened vertebrate taxa are amphibians and reptiles (Gardner et al. 2007a). Recent assessments have shown 32.5% and 19% of all known amphibian and reptile species, respectively, are threatened with extinction (Mendelson et al. 2006; Böhm et al. 2013). Many causes have been attributed to declines in amphibian and reptile populations, including, pollution, loss of habitat, collecting for the pet trade, and emerging infectious diseases (Storfer 2003; Mendelson et al. 2006; Mendelson et al. 2014; Auliya et al. 2016). Of those, habitat loss, including change in land use, is widely accepted to have the most significant effect on amphibian and reptile populations, and has been implicated as a major cause in amphibian and reptile declines (Cushman 2006; Gardner et al. 2007a). Habitat fragmentation has also been documented as an influence in the composition of reptile assemblages (Mac Nally and Brown 2001; Cabrera-Guzmán and Reynoso 2012; Medenhall et al. 2016).

Historical change in land use has resulted in a loss of 11.1% of species in vertebrate assemblages when compared to undisturbed habitats (Newbold 2018). Not only is species diversity negatively impacted by land use change, so is the functional diversity of an assemblage. This is particularly true in tropical locations where habitats and species tend to be more sensitive to changes in land use due to the lack of large-scale historical disturbances (Etard et al. 2022). Recently, Powers and Jetz (2019) predicted that Southeast Asia, South America, and Mesoamerica will undergo extreme changes in land cover by 2070. This scenario will interact with current patterns of species threat, rarity, and habitat specialization and will potentially result in between 847 and 1113 vertebrate species being newly classified as threatened with extinction, along with 570 species increasing from their current threatened status, within the same time frame due to losses in suitable habitat (Powers and Jetz 2019). Given that amphibians and reptiles are particularly sensitive to human induced land use change, it seems reasonable to assume that a disproportionately large amount of newly classified species will belong to these taxa compared to other vertebrate groups (Newbold 2018). It is important to note that while the effects of change in land use may be felt globally, they vary across taxa and locations, which highlights the need to assess relationships at a regional scale rather than at a global one (Kehoe et al. 2015).

Tropical biodiversity conservation focuses on preserving pristine primary forest areas (Gillespie et al. 2015). However, primary tropical forest continues to be degraded and lost, even within protected areas (Gillespie et al. 2015). For example, 39% of annual deforestation in Guatemala occurs within protected areas (Tolisano and López 2010). In Guatemala (Fig. 3.1), growing population and agricultural expansion are responsible for drastic changes in land-use and habitat loss (Tolisano and López 2010). Since the 1950's Guatemala's forests have been reduced by 39.6% (Tolisano and López 2010). Current estimates of forest loss in Guatemala (0.92% per yr) are the highest in Central America (Sesnie et al. 2017). Deforestation in the Department of Petén accounts for 65% of total annual deforestation in Guatemala (Tolisano and López 2010). Within Petén, the highest rates of deforestation occur within Laguna del Tigre National Park, where between 2012 and 2016, 22,927 ha of forest were lost (WCS 2016). Laguna del Tigre National Park (LTNP) is located in the north-western corner of Petén, Guatemala (Fig. 1). It is the largest core area within the Maya Biosphere

Reserve and covers 289,000 hectares (Bestelmeyer 2000). The native forest is classed as tropical humid forest (Bestelmeyer 2000). Within LTNP there are two concessional land areas (Figure 3.1) that are farmed at relatively low levels by two Mayan communities. Agriculture in LTNP consists of subsistence farming of traditional crops such as maize (*Zea mays*), squash (*Cucurbita* spp.), black beans (*Phaseolus vulgarus*), and papaya (*Carica papaya*). This is often grown in mixed crop fields (Pers. Obs.). One of these communities, Paso Caballos, has concessional lands that immediately adjoin lands owned by the Estación Biológica Las Guacamayas. Las Guacamayas stewards 5050 hectares, also within LTNP which act as an internal core protected area within the national park.

Guatemala is a mega-diverse country, with a high diversity, 387 species in total, of amphibians and reptiles, 141 and 246 species respectively (Köhler 2008*;* Acevedo et al. 2010; Köhler 2011; Sales et al. 2016). Species continue to be described either through taxonomic revisions (Rovito et al. 2012; Vásquez-Almazán and Rovito, 2014), range extensions (Griffin and Powell, 2014; Ariano-Sanchez, 2015; Morales et al. 2015), or recent discoveries (Campbell et al. 2010). Most ecological studies of Guatemala's amphibian and reptile fauna have concentrated on endangered species such as Central American river turtle (*Dermatemys mawii*), Guatemalan beaded lizard (*Heloderma charlesbogerti*), and Guatemalan black iguana (*Ctenosaura palearis*) (García Anleu et al. 2007; Coti and Ariano-Sánchez 2008; Ariano-Sánchez and Salazar 2013). Research on amphibians and reptiles in LTNP is relatively sparse and limited to *Dermatemys mawii,* and a rapid biodiversity assessment (Bestelmeyer 2000; García Anleu et al. 2007). To date no work has been conducted on the terrestrial amphibian and reptile assemblage in Laguna del Tigre National Park.

While there has been a concerted effort to understand tropical amphibian and reptile diversity and abundance, few studies have investigated the drivers of change. the effects of environmental predictors, or habitat structure on herpetofauna abundance and diversity within dispersed fragments of forest (Gardner et al. 2007b; Cabrera-Guzmán and Reynoso 2012; Souza et al. 2014; Gillespie et al. 2015).

This paper uses hierarchical modelling techniques to address the question of whether amphibian and reptile diversity and abundance is affected by the change of land use from tropical humid forest to low level agriculture within a single neotropical forest ecosystem and to identify environmental predictors of those changes.

3.3 Methods

3.3.1 Study Site

Estación Biológica Las Guacamayas (EBG) is located in the south east of Laguna del Tigre National Park (LTNP) on the banks of the Rio San Pedro (Figure 3.2). The Tropical Moist Forest (Holdridge 1967) of EBG consists of several habitat types including both primary and secondary forest, saw-grass swamp and thorn scrub. It is bordered to the east by concessional agricultural lands that belong to the nearby Quecchi Maya community of Paso Caballos. Surveys were conducted in four forest habitats, Agricultural Edge, High Forest, Low Forest and Natural Edge within the ownership of EBG (Figure 3.2). Agricultural Edge (AE) surveys were conducted in forest at the eastern border with the concessional lands of Paso Caballos approximately 2 km east of EBG. This area has been subject to relatively high levels of disturbance from the clearing activities related to the concessions and is considered to be secondary forest. High Forest (HF), known locally as Bosque Alto, is found on the top of

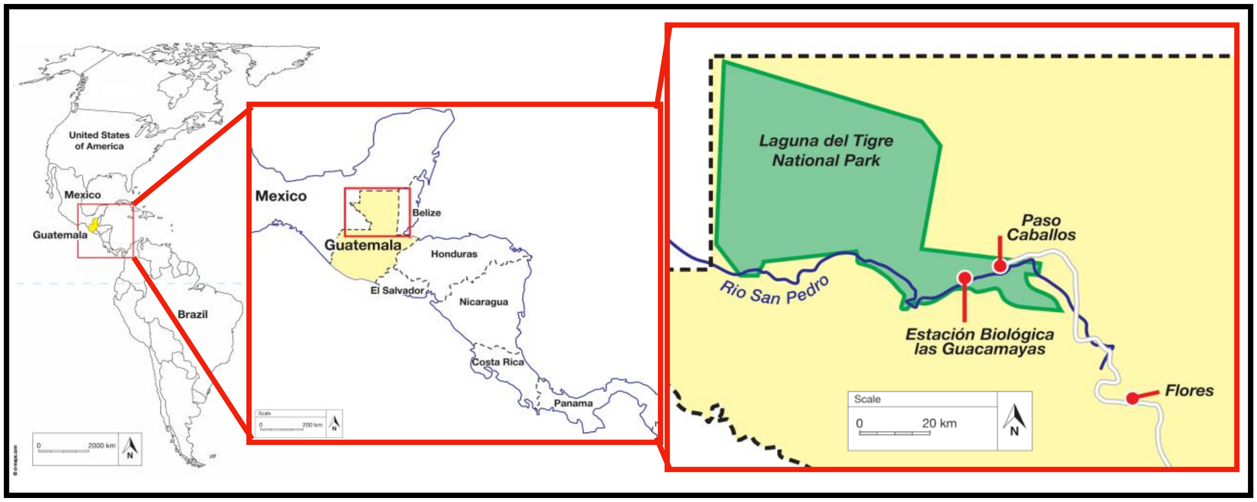

Figure 3.1: Map of the Americas, showing the location of Laguna del Tigre National Park within Guatemala. Due to the curvature of the map the scale shown is representative of the scale at the equator. Map adapted from D-Maps.com

limestone hills of LTNP. It is characterised by relatively low canopy (ca. 25 metres), sparse understorey and shallow leaf-litter and soils. HF surveys were conducted in high forest ca. 0.5 km north of EBG. Low Forest (LF), known locally as Bosque Bajo, is found in basins within the High Forest. The soils and leaf-litter are deeper in the Bajos as a result of run-off from the hills, and subsequently the understory is dense with a high canopy (ca. 35 metres). Surveys in LF were conducted in low forest ca 3.5 km west of EBG. Natural Edge (NE) were conducted on between 50 and 100 metres from top of a steep limestone cliff that rises from the northern banks of the San Pedro river. NE surveys were conducted ca. 1 km east of EBG. No change in status of the chosen habitats was observed during the study period.

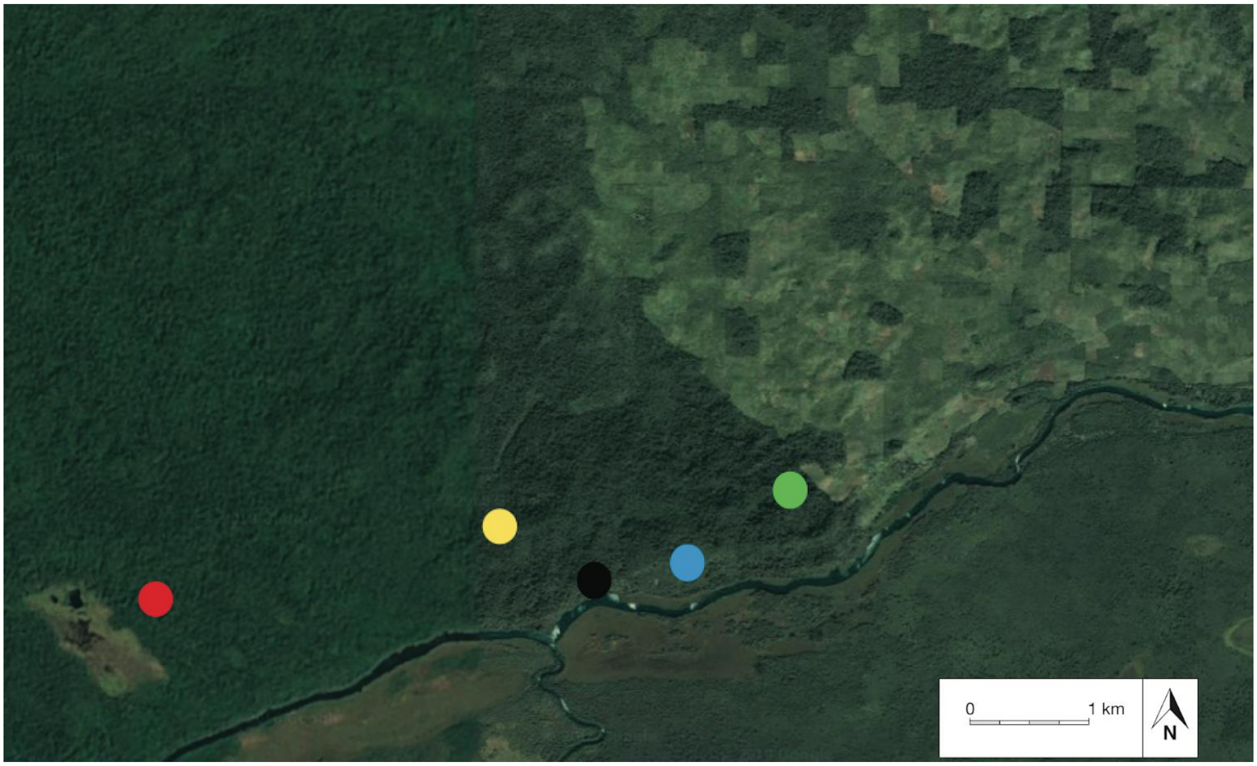

Figure 3.2: Satellite image of the southeast region of Laguna del Tigre National Park showing the location of survey sites indicated by coloured dots: Green = Agricultural Edge; Yellow = High Forest; Red = Low Forest; Blue = Natural Edge; Black = Estación Biológica las Guacamayas. The two rivers are the San Pedro River flowing east to west, and the Sacluc River flowing south to north. North of the San Pedro dark green areas indicate forest areas, lighter green indicates the concessional agricultural land of Paso Caballos. South of the San Pedro, green indicates a mixture of saw grass swamp (sabinal) and seasonally flooded thorn scrub. Image adapted from Google Maps.

3.3.2 Field Methods

In each of the four habitats, 100 m transects were conducted both along existing trail systems and on transects cut sensitively into the forest away from the trails. Transects were placed to allow a representative sample of each habitat and promote heterogeneous sampling across microhabitats for efficient detection of herpetofauna (Crump 1994; Doan 2003; Marsh and Haywood 2010). The start points for each transect (Figure 3.2) were positioned at least 50 m from the nearest forest edge to allow for any edge effects to be taken into account that may have risked biasing detection (Schlaepfer and Gavin 2001; Urbina-Cardona et al. 2006). Transects were marked every 25 m with flagging tape to indicate the path of the transect, and GPS waypoints were taken at the start and finish points using a handheld GPS device (Garmin™ GPSMap 62s) to facilitate accurate survey replication. After setup, transects were left for a minimum of two days before surveying commenced to allow for animals to resume normal activity prior to survey (Crump 1994). All transects had negligible changes in altitude and were positioned to avoid passing through broad habitat types in order to satisfy assignment of habitat categorisation (Babbitt et al. 2009). Surveys took approximately 45 minutes to one hour to complete and followed standardised protocols for Visual Encounter Surveys in tropical habitats (Rödel and Ernst 2004; Vonesh et al. 2009).

To maximise chances of detecting species with different autecology, each transect was surveyed three times, twice at night and once in the morning during each survey period (Heyer et al. 1994; McDiarmid et al. 2012). For the purposes of statistical analyses nocturnal and diurnal surveys were grouped. A minimum of two days was left between surveys of the same transect to maintain independence of sample survey periods. Surveys were conducted during seven fieldwork periods in May-June 2013, November-December 2013, June 2014, October 2014, June 2015, December 2015 and June-July 2016. A total of 86 transects were surveyed, comprising 17 in AE, 22 in HF, 23 in LF, and 24 in NE respectively. The order in which the four forest habitats were surveyed was randomized, as was the order of transects within each habitat. In some cases fieldwork was hampered by inclement weather and surveys had to be abandoned, hence the non-equal survey effort.

3.3.3 Data Collection

The following environmental data were recorded at the start and finish of each transect: time (24 hr), air temperature (ºC), relative humidity (%), and cloud cover (%). When safe and practical to do so, each animal encountered was captured and the following data recorded: time encountered (24 hr), location (recorded using a Garmin GPSmap 62s), species, age (adult, juvenile, neonate), and sex (where possible).

Visual encounter surveys are a well-known method for surveying amphibians and reptiles (Crump and Scott 1994; Lovich et al. 2012). Surveys teams consisted of between two and eight people, and included one local guide, the author and two to six field assistants. At the start of each field session, all guides and field assistants were trained in survey techniques, data collection, and species identification by the author. All biometric and environmental data collection was overseen by the author to avoid observer bias. Transects were walked at a suitably slow pace to allow detection of reptiles and amphibians by thorough examination of vegetation and refugia, such as leaf litter, fallen limbs and rocks (Crump and Scott 1994; Lovich et al. 2012). The search area was defined as up to one metre each side of the transect and up to two metres high (Crump and Scott 1994; Lovich et al. 2012). Any individual found outside of this area was recorded as a casual observation but omitted from this study. Data collection followed the method outlined above.

3.3.4 Statistical Analysis

Estimating patterns and changes in species richness and diversity is a useful tool in detecting changes in biodiversity that can inform biodiversity management (Gwinn et al. 2015). Species accumulation curves and diversity indices have been developed to address this issue (Gwinn et al. 2015). Species accumulation, or rarefaction, curves (such as Mao Tao rarefaction) are a useful way for ecologists to compare assemblage data from multiple sites. They work on the principle of extrapolating the number of new species recorded in a sample as part of a series of repeated samples. The sampling curve will naturally rise rapidly at the start of the series, and then continue to rise slowly in the later samples as increasingly rare species are added to the dataset. The curve will reach asymptote when sufficient sampling has been achieved. However, in reality this is rarely the case and for the investigator wishing to see where the asymptote lies extrapolation is necessary (Gotelli et al. 2001).

It is virtually impossible for ecologists to detect every species in a given habitat due to various sampling constraints, usually time and funding (Colwell et al. 2012). This is in part due to the fact that it can take large sampling efforts to detect all the rare species found in an ecological assemblage. This poses a problem for ecologists investigating species diversity as the total number of species observed is known to often be an underestimate of the true number present (Gwinn et al. 2015). Several methods, known as species diversity indices, have been developed to tackle the issue of estimating the number of undetected, or "unseen", species in an assemblage. Species diversity indices extrapolate the number of unseen species based on the number of rare species detected in a sample, either from abundance or sample-based incidence data. Theoretically, in the context of abundance-based diversity indices, a rare species is defined as a species with an overall abundance of either one or two, they are known as singletons and doubletons. When using an incidence-based index then a singleton or doubleton is a species that occurs in either one or two sample unit(s) (Chao et al. 2005). Whether an index uses only singletons, or both singletons and doubletons, is often indicated by the use of the suffix 1 or 2 respectively (e.g. Chao1 or Chao2). Some indices such as the abundance-based coverage estimator (ACE) and the incidence-based coverage estimator (ICE) estimate unseen species based on those species and abundance of fewer than 10 individuals, or if the species is found in fewer than 10 sample units (Chao et al. 2005).

The number of observations and species of amphibians and reptiles were recorded for each forest habitat and forest type. These data were used to create species accumulation curves, species richness indices, and model habitat association and environmental influence on amphibian and reptile species composition within each area. The length of transect and time taken to complete a transect were comparable between all years allowing the data to be pooled across years for analysis. This allowed replication of surveys (repeated surveys along the same transect) to be used as the random factor in the modelling process. Prior to analysis, the data for amphibians and reptiles was separated by Class due to the high likelihood that amphibians and reptiles would be affected in different ways by changes in habitat (Gibbons et al. 2000; Gardner et al. 2007b).

Mao Tao species accumulation curves were produced to evaluate the effectiveness of the survey methods used in relation to the target habitat types and to compare the diversity of amphibian and reptile fauna in each habitat. Species richness indices were calculated using both nonparametric incidence-based estimators (Chao2, ICE) and abundance-based data (ACE, Chao1, Jack-knife1, and Jack-knife2). Multiple indices were used because no single index presents an ideal descriptor with all of them underestimating species diversity, and most experience imprecision and suggest insufficient sampling effort, through 'sample creep' (Gotelli and Colwell 2011). Shannon-Wiener and Simpson's Diversity Indices were also calculated. Both these indices were used as the Simpson's Index is weighted towards the abundances of the commonest species in the assemblage, and calculates the probability that randomly selected individuals will belong to the same species. On the other hand the Shannon-Wiener index is weighted towards the rarest, and calculates how evenly the number of individuals are distributed between all species in the sample (Bibi and Ali 2013). Species accumulation curves and species diversity indices for each habitat were calculated in EstimateS 8.2.0 (Colwell 2006).

Classical statistical procedures are often inappropriate for use with ecological datasets (Bolker et al. 2008). For example, one such classical approach is to apply linear modelling combined with analysis of variance (ANOVA) (Guisan et al. 2002). However, for this approach to be valuable there is an assumption that the data is normally distributed, as is the case with datasets that are based on measurements of variables. Ecological datasets are frequently made up of count data, as such this assumption is frequently violated by such datasets that may contain data with several distributions, that are better handled within Poisson or binomial frameworks (Guisan et al. 2002).

Recent developments in statistical software have made alternative, and more appropriate, statistical approaches viable (Zuur et al. 2010). Generalized linear mixed models (GLMMs) are a combination of generalized linear models and linear mixed models (Bolker et al. 2008). They are widely used to explore data sets that contain non-normal data and random effects, both of which are common in ecological datasets (Guisan et al. 2002; Bolker et al. 2008). One of the advantages of using GLMMs with ecological datasets is that they are well suited to handling data with multiple variables and multiple distribution types (Warton et al. 2012).

Generating model sets of all possible sub-models from a 'global' model allows investigators to visualise the most likely model in the set by comparing a given information criterion, the most commonly used of which is the Akaike Information Criterion (AIC). If the model set is large with no clear single best model then it is also possible to use a model averaging method to account for this uncertainty (Grueber et al. 2011). Model averaging calculates weighted averages of the parameters contained in the top set of the complete model set, as defined by the information criterion being used. This approach can lead to a more stable result than selecting the top model alone (Grueber et al. 2011).

Generalized linear mixed models with Poisson distribution and model averaging were used to identify effects of habitat type on amphibian and reptile abundance (Tollington et al. 2015). Prior to model averaging, model sets were restricted to $\Delta AIC_c<2$ (amphibian species model) and $\Delta AIC_c<4$ (amphibian observations, reptile species, and reptile observation models) to eliminate unlikely models with low AIC values (Bolker et al. 2008; Tollington et al. 2015). ΔAIC thresholds were restricted to appropriate levels according to the results of the model set. The residuals of each model were then calculated to confirm if the model conformed to the assumed distribution. GLMMs were performed in the program R (R Core Team 2015). The packages lme4, arm, MuMIn, and DHARMa were used within R to fit the models.

The data for both amphibians and reptiles included two response variables: a) number of species described as the total number of species recorded in a survey, and b) number of observations described as the total number of individuals recorded in a survey. Four dummy explanatory variables were included in the model: a) Agricultural Edge (AE), b) High Forest (HF), c) Low Forest (LF), and d) Natural Edge (NE).

The data were explored prior to analysis to confirm the suitability of GLMM's using the following steps (Zuur et al. 2010): a) boxplots were used to check for outliers, b) histograms were used to check for normality. The response variables are count data and have a non-normal distribution, therefore Poisson distribution with log link functions were used (Bolker et al. 2008), and c) correlation plots and Variance Inflation Factors (VIF) were used to check for collinearity among explanatory variables, and between explanatory and response variables. No significant collinearity was detected for any of the variables as all correlations were below 0.8, and all VIFs were below 3 (Zuur et al. 2010). In the global GLM models all four explanatory variables were included as fixed factors. Because the surveys were repeated in each forest habitat, repeated surveys were also included as a random variable.

In cases where the GLMMs identified significant effects of habitat on amphibian and reptile abundance and diversity further models were created to investigate the environmental predictors. To do this generalized linear models (GLM) with Poisson errors were used. The same methodology described for GLMMs was used with $\Delta AIC_c<4$ to remove any unlikely models during model averaging (Bolker et al. 2008; Tollington et al. 2015). In the case of the amphibian models, zero counts for number of species and observations were removed to avoid bias in the models.

As before, the data for both amphibians and reptiles included two response variables: a) number of species described as the total number of species recorded in a survey, and b) number of observations described as the total number of individuals recorded in a survey. Three environmental explanatory variables that were standardized by the mean prior to running the model were included: a) temperature at start of survey, b) relative humidity at start of survey, and c) cloud cover at start of survey.

3.4 Results

A total of 49 species of herpetofauna were encountered during the survey period, consisting of 16 amphibians (Agricultural Edge [AE]: 5, High Forest [HF]: 9, Low Forest [LF]: 13, and Natural Edge [NE]: 11) and 33 reptiles (AE: 7, HF: 18, LF: 16, and NE: 16). Overall, there were 263 and 115 observations of amphibians (AE: 55, HF: 38, LF: 120, and NE:50) and reptiles (AE: 7, HF: 39, LF: 29, and NE: 40) respectively.

Table 3.1: Amphibian abundance (expressed as total observations with mean abundance and standard deviations averaged across surveys in parentheses) and diversity in four forest habitats in Laguna del National Park. AE = Agricultural Edge; HF = High Forest; LF = Low Forest; NE = Natural Edge.

Species	AE	HF	LF	NE
Plethodontidae				
Bolitoglossa mexicana	1 (0.06±0.24)	0	1 (0.04±0.21)	1 (0.04±0.20)
Bufonidae				
Incilius valliceps	13 (0.76±1.71)	12 (0.55±0.91)	23 (1.00±1.91)	8 (0.33±0.82)
Rhinella marina	0	0	4 (0.17±0.83)	0
Hylidae				
Agalychnis callidryas	1 (0.06±0.24)	0	1 (0.04±0.21)	2 (0.08±0.28)
Scinax staufferi	0	0	1 (0.04±0.21)	0
Smilisca baudinii	5 (0.29±0.85)	1 (0.5±0.21)	32 (1.39±3.30)	2 (0.08±0.28)
Trachycephalus typhonius	0	0	3 (0.13±0.46)	1 (0.04±0.20)
Leptodactylidae				
Engystomops pustulosus	0	0	7 (0.30±0.63)	2 (0.08±0.28)
Leptodactylus fragilis	0	0	1 (0.04±0.21)	1 (0.04±0.20)
Leptodactylus melanolotus	0	1 (0.5±0.21)	5 (0.22±0.85)	9 (0.38±1.10)
Microhylidae				
Gastrophryne elegans	0	0	5 (0.22±0.85)	0
Hypopachus variolosus	18 (1.06±2.54)	12 (0.55±1.14)	32 (1.39±2.04)	6 (0.25±1.22)
Ranidae				
Rana brownorum	0	3 (0.14±0.47)	6 (0.26±0.62)	5 (0.21±0.66)
Rana vaillanti	0	0	1 (0.04±0.21)	0
Total Species	5	5	14	10

For amphibians, the highest number of observations and species were recorded in low forest. The lowest number of amphibian observations were recorded in high forest, and the lowest number of species were in agricultural edge. For reptiles, the highest number of observations were recorded in natural edge, and the highest number of species were in low forest. The lowest number of both reptile observations and species were recorded in agricultural edge.

Table 3.2: Reptile abundance (expressed as total observations with mean abundance and standard deviations averaged across surveys in parentheses) and diversity in four forest habitats in Laguna del National Park. AE = Agricultural Edge; HF = High Forest; LF = Low Forest; NE = Natural Edge.

Species	AE	HF	LF	NE
Eublepharidae				
Coleonyx elegans	1 (0.06±0.24)	9 (0.41±1.10)	1 (0.04±0.21)	0
Corytophanidae				
Basiliscus vittatus	0	1 (0.05±0.21)	1 (0.04±0.21)	0
Corytophanes cristatus	0	1 (0.05±0.21)	0	0
Corytophanes hernandesii	0	0	0	0
Dactyloidae				
Norops capito	3 (0.18±0.39)	5 (0.23±0.53)	1 (0.04±0.21)	1 (0.04±0.20)
Norops lemurinus	1 (0.06±0.24)	2 (0.09±0.43)	0	1 (0.04±0.20)
Norops sp.	0	4 (0.18±0.50)	1 (0.04±0.21)	1 (0.04±0.20)
Norops tropidonotus	0	0	0	0
Norops uniformis	0	1 (0.05±0.21)	0	1 (0.04±0.20)
Phrynosomatidae				
Sceloporus chrysostictus	0	1 (0.05±0.21)	0	0
Sphenomorphidae				
Sphenomorphus cherriei	0	3 (0.14±0.47)	4 (0.17±0.49)	0
Teiidae				
Holcosus festiva	0	0	0	3 (0.13±0.45)
Holcosus undulatus	1 (0.06±0.24)	0	0	0
Boidae				
Boa imperator	0	1 (0.05±0.21)	0	0
Colubridae				
Colubrinae				
Drymobius margaritiferus	0	0	0	0
Oxybelis aeneus	0	1 (0.05±0.21)	0	0
Spilotes pullatus	0	0	0	1 (0.04±0.20)
Dipsadinae				
Adelphicos quadrivirgatus	0	0	1 (0.04±0.21)	0
Clelia scytalina	0	0	0	1 (0.04±0.20)

(continued on next page)

Table 3.2 continued.

Species	AE	HF	LF	NE
Coniophanes imperialis	0	0	8 (0.35±0.57)	0
Coniophanes schmidtii	1 (0.06±0.24)	0	2 (0.09±0.42)	1 (0.04±0.20)
Imantodes cenchoa	0	2 (0.09±0.29)	2 (0.09±0.29)	4 (0.17±0.48)
Leptodeira septentrionalis	1 (0.06±0.24)	1 (0.05±0.21)	2 (0.09±0.42)	5 (0.21±0.66)
Ninia diademata	0	0	1 (0.04±0.21)	0
Ninia sebae	1 (0.06±0.24)	3 (0.14±0.47)	1 (0.04±0.21)	8 (0.33±0.92)
Oxyrhopus petolarius	0	1 (0.05±0.21)	0	0
Pliocercus elapoides	0	1 (0.05±0.21)	0	0
Sibon dimidiata	0	0	0	0
Sibon nebulatus	0	1 (0.05±0.21)	0	1 (0.04±0.20)
Tropidodipsas sartorii	0	0	1 (0.04±0.21)	0
Xenodon rabdocephalus	0	0	1 (0.04±0.21)	0
Elapidae				
Micrurus diastema	1 (0.06±0.24)	2 (0.09±0.29)	0	0
Viperidae				
Bothrops asper	0	0	2 (0.09±0.29)	3 (0.13±0.45)
Kinosternidae				
Kinosternon acutum	0	1 (0.05±0.21)	1 (0.04±0.21)	3 (0.13±0.34)
Kinosternon leucostomum	0	0	0	3 (0.13±0.34)
Geomydidae				
Rhinoclemmys areolata	0	0	0	3 (0.13±0.34)
Total Species	8	19	16	16

Abundance data of each amphibian and reptile species detected are reported in Tables 3.1 and 3.2 respectively.

3.4.1 Species Accumulation and Diversity

Species accumulation curves were produced for both amphibians and reptiles in all four habitats (Figure 3.3). Only the curve for amphibians in Agricultural Edge was close to reaching asymptote, although it does indicate that some species remain to be found. For both amphibians and reptiles, species richness indices were consistently lower in Agricultural Edge (Tables 3.3 and 3.4). Species richness indices showed higher diversity than recorded

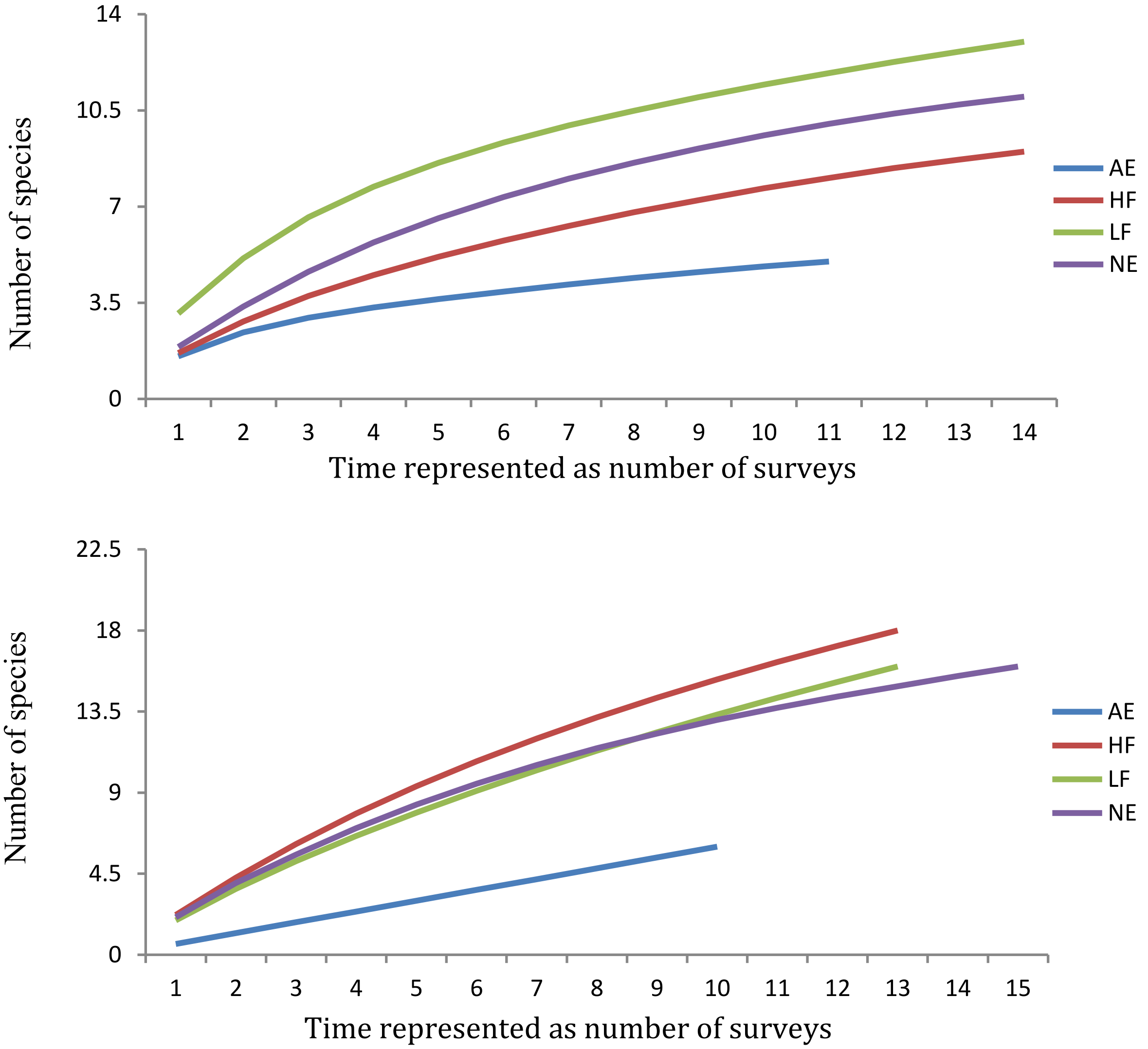

Figure 3.3: Species accumulation curves for amphibians (above) and reptiles (below). AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

Table 3.3: Species richness indices of the amphibian assemblage at Las Guacamayas. See section 3.2.4 for explanations of the indices.

	Habitat			
Species Richness Index	**Agricultural Edge**	**High Forest**	**Low Forest**	**Natural Edge**
ACE	9.00	13.82	15.75	14.98
ICE	7.24	15.14	17.99	14.41
Chao 1	6.00	17.00	19.00	12.13
Chao 2	7.00	11.67	19.25	13.00
Jack 1	6.82	12.71	17.64	14.71
Jack 2	7.72	13.77	20.35	14.98
Shannon-Weiner	1.04	1.71	1.96	2.00
Simpson’s	2.37	4.56	5.58	7.40
Observed Species	5	5	14	10

Table 3.4: Species richness indices of the reptile assemblage at Las Guacamayas. See section 3.2.4 for explanations of the indices.

	Habitat			
Species Richness Index	**Agricultural Edge**	**High Forest**	**Low Forest**	**Natural Edge**
ACE	21.00	34.04	37.62	25.13
ICE	19.50	33.79	45.17	22.84
Chao 1	21.00	34.67	28.50	44.00
Chao 2	19.50	33.13	36.17	32.00
Jack 1	11.40	28.15	26.15	23.47
Jack 2	16.20	34.36	33.13	28.79
Shannon-Weiner	1.79	2.61	2.52	2.52
Simpson’s	6.00	13.98	13.10	13.22
Observed Species	8	19	16	16

by this study in all four forest habitats (Tables 3.3 and 3.4). However, the most conservative species richness indices for amphibians were closer to the number of observed species than those for reptile species (Tables 3.3 and 3.4).

Based on the indices for amphibian species richness (Table 3.3), predictions for amphibian diversity range from 6 to 9 species in Agricultural Edge (5 species observed), 11 to 17 in High Forest (9 species observed), 17 to 20 in Low Forest (13 species observed), and 12 to 15 in Natural Edge (11 species observed). Predictions for reptile diversity (Table 3.4) range from 11 to 21 species in Agricultural Edge (7 species observed), 28 to 34 in High Forest (18 species observed), 26 to 45 in Low Forest (16 species observed), and 23 to 44 in Natural Edge (16 species observed). Both Shannon-Weiner and Simpson's indices were lowest in Agricultural Edge.

3.4.2 Predictors of Amphibian and Reptile Abundance and Diversity

Averaged variable estimates, standard errors, lower and upper confidence intervals, and the relative importance factors of the variable are reported in Table 3.5. The models for both amphibian observations and amphibian species identified that amphibian abundance and diversity were positively associated with low forest ($P = <0.001$ and $P = 0.0002$ respectively) (Table 3.5). The models for reptile observations and reptile species identified that reptile abundance and diversity were negatively associated with agricultural edge ($P = 0.003$ and $P = 0.02$ respectively) (Table 3.5).

3.4.3 Environmental Predictors of Amphibian and Reptile Abundance and Diversity

GLMMs identified four instances where habitat had a significant effect on amphibian and reptile abundance and, or, diversity. In these cases, GLMs were used to investigate the effect of three environmental variables (temperature, relative humidity, and cloud cover) on amphibian and reptile abundance and diversity. Averaged variable estimates, standard errors, lower and upper confidence intervals, and the relative importance factors of the variable are reported in Table 3.6.

The models identified that amphibian observations in low forest were positively associated with temperature ($P = 0.003$, RIF = 1.00) (Table 3.6). However, all other models failed to show any significant association with any of the environmental variables (Table 3.6).

Table 3.5: Results of model averaged GLMMs with Poisson errors to investigate predictors of amphibian and reptile abundance in Laguna del Tigre National Park. Intercept is Natural Edge. LCI = Lower Confidence Interval, UCI = Upper Confidence Interval.

Response Variable	Predictor	Averaged Variable Estimate	SE	p-value	LCI	UCI	Relative Importance Factors
Amphibian Observations	Intercept	0.834	0.077	<0.001	0.681	0.986	
	Agricultural Edge	0.198	0.242	0.416	-0.078	0.797	0.55
	Low Forest	**1.151**	**0.184**	**<0.001**	**0.786**	**1.515**	**1**
	High Forest	-0.15	0.23	0.516	-0.801	0.155	0.47
Amphibian Species	Intercept	0.072	0.109	0.512	-0.144	0.289	
	Low Forest	**0.828**	**0.22**	**0.0002**	**0.39**	**1.265**	**1**
	High Forest	-0.077	0.207	0.712	-0.862	0.368	0.31
	Agricultural Edge	0.002	0.161	0.989	-0.632	0.649	0.25
Reptile Observations	Intercept	0.283	0.099	0.005	0.086	0.48	
	Agricultural Edge	**-1.028**	**0.34**	**0.003**	**-1.704**	**-0.353**	**1**
	Low Forest	-0.091	0.18	0.615	-0.684	0.202	0.38
	High Forest	0.056	0.144	0.699	-0.242	0.59	0.32
Reptile Species	Intercept	0.109	0.106	0.311	-0.102	0.319	
	Agricultural Edge	**-0.798**	**0.338**	**0.02**	**-1.47**	**-0.126**	**1**
	High Forest	0.024	0.113	0.834	-0.332	0.554	0.22
	Low Forest	-0.019	0.112	0.864	-0.552	0.365	0.21

Significantly explanatory variables, where confidence intervals do not cross zero, are highlighted in bold.

Table 3.6: Results of model averaged GLMs with Poisson errors to investigate environmental predictors of amphibian and reptile abundance and diversity in selected habitats in Laguna del Tigre National Park. Intercept is Time at Start of Survey. LCI = Lower Confidence Interval, UCI = Upper Confidence Interval

Response Variable	Predictor	Averaged Variable Estimate	SE	p-value	LCI	UCI	Relative Importance Factors
Amphibian Observations In Low Forest	Intercept	2.14	0.102	<0.001	1.913	2.366	
	Cloud Cover	-0.596	0.345	0.104	-1.263	-0.157	0.84
	Temperature	**0.997**	**0.298**	**<0.001**	**0.342**	**1.652**	**1**
	Relative Humidity	-0.096	0.294	0.756	-1.472	0.614	0.22
Amphibian Species In Low Forest	Intercept	1.207	0.159	<0.001	0.857	1.557	
	Temperature	0.651	0.51	0.231	-0.053	1.759	0.76
	Cloud Cover	-0.019	0.129	0.897	-0.961	0.621	0.11
	Relative Humidity	0.038	0.488	0.713	-0.848	1.239	0.19
Reptile Observations In Agricultural Edge	Intercept	-0.573	0.331	0.11	-1.276	0.13	
	Relative Humidity	-0.356	0.497	0.489	-1.758	0.197	0.46
	Temperature	-0.029	0.297	0.927	-1.656	1.316	0.17
	Cloud Cover	0.013	0.268	0.963	-1.31	1.47	0.17
Reptile Species In Agricultural Edge	Intercept	-0.564	0.327	0.112	-1.259	0.132	
	Relative Humidity	-0.277	0.456	0.556	-1.722	0.193	0.36
	Temperature	-0.006	0.22	0.981	-1.441	1.341	0.11
	Cloud Cover	0.001	0.218	0.995	-1.373	1.399	0.11

Significantly explanatory variables, where confidence intervals do not cross zero, are highlighted in bold.

3.5 Discussion

The species accumulation curves for both amphibians and reptiles show that further fieldwork is needed to detect all amphibian and reptile species in the four habitats. Surveys of amphibians and reptiles can be affected by low detection rates and as such it can take many years to build up a full picture of a species assemblage for a given area (MacKenzie et al. 2003; Bailey et al. 2004; Durso et al. 2011). For example, at a single site in the south-eastern Peruvian Amazon it took 992 person/days of survey conducted over eight years to detect 141 of 151 known species from that site (Duellman 2005). Other less intensive studies from the same site showed that after 202 person/days of survey 45% of known species had been detected (Doan and Arizábal 2002). In the current work species continue to be detected for the first time after four years of extensive study.

Accumulation curves and richness indices consistently showed that diversity of amphibians and reptiles was lower in the agricultural edge, a secondary forest habitat, when compared to the other three forest habitats. The value of the Shannon-Weiner Diversity Index usually falls between 1.5 and 3.5, the higher the value the more even the distribution of individuals across species (Bibi and Ali 2013). The low values of the Shannon-Weiner index for both amphibians (1.04) and reptiles (1.79) in Agricultural Edge (AE) indicate that individuals are highly unevenly distributed amongst species in this habitat. This is corroborated by low Simpson's Diversity Index values which suggest that it is unlikely that two individuals in a random sample will belong to the same species. This suggests that a small number of amphibian and reptile species in the AE habitat are more abundant than others. This is consistent with other studies on the effects of land use on amphibian and reptile diversity. For example, Gardner el al. (2007*b*) found significantly higher diversity in primary forest compared to either secondary or plantation forest in the Jari region of Brazil. Additionally, they found one third of all amphibian and lizard species only occurred in primary forest. Conversely, in a highly fragmented protected forest in Mexico, forest edge habitat showed an increase in amphibian and reptile diversity, while the number of observations increased in the forest interior (Urbina-Cardona et al. 2006). It is clear that the effects of land-use can affect the amphibian and reptile assemblages of different regions in different way (Gibbons et al. 2000; Gillespie et al. 2015).

The averaged GLMM amphibian observations model showed a significant positive association between amphibian abundance and diversity and low forest. The higher abundance of amphibians in low forest was positively associated with temperature, however the predictors of increased diversity could not be identified. The associations between amphibian abundance and diversity and low forest may be due to this habitat providing more suitable resources for amphibians than other forest habitats. The presence of permanent water bodies in low forest may provide greater breeding opportunities. The deeper leaf litter and soil layer, and subsequently denser vegetation, may provide increased microhabitats suitable for amphibian survival.

Interestingly, no effect on amphibian abundance or diversity was found in Agricultural Edge. However, the species diversity indices showed agricultural edge to have lower diversity than the other three habitats. This chapter does not take species composition of forest habitats into account (see Chapter 4) and it is possible that while the number of species is lower in agricultural edge, the species that are found there occur in high abundances. This could be due to lower competition from other amphibian species. Further work is needed to investigate species composition of forest habitats (see Chapter 4). The averaged GLMMs for reptile observations and reptile species identified negative associations between reptile abundance, and diversity, and agricultural edge. These models suggest that reptile numbers are lower in the agricultural edge habitat compared to other forest habitats. However, the averaged GLMs did not identify any environmental predictors driving these negative associations. Reptile diversity and abundance in LTNP may be driven by factors other than the environmental variables tested in this work. Variables such as habitat structure and heterogeneity are also known to influence amphibian and reptile assemblages (Souza et al. 2014; Gilespie et al. 2015).

The positive association of amphibians with low forest, and the negative association of reptiles with agricultural edge are consistent with other studies that show primary forests to be higher in abundance and diversity (Gardner et al. 2007*b*; Gillespie et al. 2015; Cabrera-

Guzmán and Reynoso 2012). Gillespie et al. (2015) showed that in the Juli region of Brazil increased habitat heterogeneity had a greater influence on both amphibian and reptile diversity than anthropogenic effects. In this study the same seems to be true for amphibians, with greater diversity in low forest, however conversely it seems that the anthropogenic effects of agriculture have a greater influence on lowering reptile abundance and diversity. This result is consistent with the concept that amphibian and reptile populations may respond differently to change in land use (Gibbons et al. 2000; Gardner et al 2007*b*; Urbina-Cardona et al. 2006).

The results of the current work show that both diversity and abundance of amphibians and reptiles in Laguna del Tigre National Park are higher in low forest, a primary forest habitat. As such it is reasonable to suggest that if conversion of primary forest to agriculture continues to expand in Laguna del Tigre it will significantly affect the amphibian and reptile assemblage held within the National Park.

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Chapter 4 - Changes in Amphibian and Reptile Assemblage Composition in Response to Natural and Anthropogenic Forest Edges

Painted treefrog – *Tlalocohyla picta*

4.1 Abstract

Natural habitats are becoming increasingly fragmented, this is especially true in the tropics. Fragmentation is known to impact diversity and abundance, but its effect on different species varies. This chapter used hierarchical GLMs to investigate the effect of fragmentation and agriculture on species within the amphibian and reptile assemblages of Laguna del Tigre National Park. The assemblages of both amphibians and reptiles displayed significant dominance effects in forest close to agriculture, with between 1 and 3 species accounting for more than 75% of individuals in the assemblage. The assemblage of amphibians and reptiles present in the disturbed habitat is dominated by five 'winning' species: two amphibians, one snake, and two lizards. It also showed that the effects of the presence of agriculture can be felt on the amphibian and reptile assemblage, particularly snakes, up to 7 km from the agricultural edge. However, overall habitat fragmentation had a stronger impact on the assemblage than did agriculture.

4.2 Introduction

Biodiversity declines have been widely reported throughout the world and are accelerating (Cardinale et al. 2012; Horváth et al. 2019; Semper-Pascual et al. 2019). There are a wide range of causes influencing these declines, including pollution (Qian et al. 2019), emerging disease (Scheele et al. 2019), and introduced species (Milardi et al. 2020). One of the most widespread threats to biodiversity loss, both in terms of range of taxonomic groups affected and geographic spread, is landscape modification and habitat fragmentation (Fischer and Lindenmeyer 2007). A modified landscape refers to an alteration of native vegetation caused by human activity that can lead to fragmentation of habitat available to a given species (Nichols et al. 2007), and there is a wealth of information discussing the effects of landscape modification on biodiversity (McWilliams et al. 2019; Salgado et al. 2019; Li et al. 2020). Broadly speaking, these studies fill a conceptual spectrum from a species-oriented approach to a pattern-oriented one (Fischer and Lindenmeyer 2007). A species-oriented approach allows for the investigation of the effects of landscape modification on an individual species' autoecology. Effects may range from disturbance to migration routes, changes in access to food and shelter, disruption of breeding behaviour, and alteration to species interactions such as predation, parasitism, competition, and mutualism (Bovo et al. 2018). The species-oriented approach is limited in most instances by the ability of researchers to investigate more than one species at a time, however details about the response of an individual species to landscape modification can prove vital to its conservation (Manning et al. 2004; Fischer and Lindenmeyer 2006). On the other end of the spectrum, a pattern-oriented approach allows a landscape-scale investigation into the relationship between habitat conditions, such as edge effects, habitat connectivity, and landscape heterogeneity, and the occurrence of species within that landscape, and as such can reveal patterns of species' response across a wider geographic scale (Haddad et al. 2015). However, a pattern-oriented approach tends to require the aggregation of the entire species assemblage being investigated, and consequentially finer detail on the responses of individual species within the assemblage is lost, and this can lead to the oversimplification of the ecological processes being investigated (Fischer and Lindenmeyer 2007).

Most studies investigating the effects of landscape modification have focused on biodiversity loss (Benítez-Malvido et al. 2016). However, understanding how a species assemblage responds to landscape modification is important to conservation management in tropical regions where levels of biodiversity and modification are both high. Within a species assemblage, different species may respond in varied ways to modification. Studies of tropical bird assemblages suggest that habitat fragmentation is linked to declines, and extirpations of larger-sized seed-dispersing bird species, which is then followed by increases in abundances of smaller birds that disperse smaller seeds. In time, this can lead to changes in vegetation structure (Terborgh et al. 2008; Bomfim et al. 2018; Bovo et al. 2018). This response may be more pronounced as fragment size decreased (Bovo et al. 2018). Studies of arthropods in tropical forest fragments have found increased abundances of herbivorous ants within the arthropod assemblage, whereas beetle abundance was highest in continuous forest (Benítez-Malvido et al. 2016). In bats, a species assemblage may respond to habitat fragmentation based on the way echolocation is adapted to hunting in forest interiors or edges: bats that specialize on hunting along forest edges may increase in abundance with increasing fragmentation (Nuñez et al. 2019). The responses of amphibians and reptiles to landscape modification have been studied in a wide variety of habitats, and have been found in some cases to be characterized by a lowered functional diversity and absence of forest specialist species in disturbed areas (Gallmetzer and Schulze 2015), with increases of total abundance in remaining fragments (McAlpine et al. 2015).

The objectives of the current study are to: a) describe the response of the amphibian and reptile assemblage of Laguna del Tigre National Park to landscape modification; and b) explore how individual species within the assemblage respond to those modifications.

4.3 Methods

4.3.1 Study Site

Estación Biológica Las Guacamayas (EBG) is located in the south east of Laguna del Tigre National Park (LTNP) on the banks of the Rio San Pedro (Figure 4.1). The Tropical Moist Forest (Holdridge 1967) of EBG consists of several habitat types including both primary and secondary forest, saw-grass swamp and thorn scrub. It is bordered to the east by concessional agricultural lands that belong to the nearby Quecchi Maya community of Paso Caballos. This area has been subject to relatively high levels of disturbance from the clearing activities related to the concessions and is considered to be secondary forest. High Forest (HF), known locally as Bosque Alto, is found on the top of limestone hills of LTNP. It is characterized by relatively low canopy (ca. 25 metres), sparse understorey, and shallow leaf-litter and soils. HF surveys were conducted in high forest ca. 0.5 km north of EBG. Low Forest (LF), known locally as Bosque Bajo, is found in basins between the High Forest. The soils and leaf-litter are deeper in the Bajos as a result of run-off from the hills, and subsequently the understory is dense with a high canopy (ca. 35 metres). Surveys in LF were conducted in low forest ca 3.5 km west of EBG. Natural Edge (NE) were conducted between 50 and 100 metres from the top of a steep limestone cliff that rises from the northern banks of the San Pedro river. NE surveys were conducted ca. 1 km east of EBG. No change in status of the chosen habitats was observed during the study period.

4.3.2 Data Collection

Surveys were conducted in four forest habitats, Agricultural Edge, High Forest, Low Forest and Natural Edge within the ownership of EBG (Figure 4.2). Agricultural Edge (AE) surveys were conducted in forest at the eastern border with the concessional lands of Paso Caballos approximately 2 km east of EBG. In each of the four habitats, 100 m transects were conducted both along existing trail systems and on transects cut sensitively into the forest away from the trails. Transects were placed to allow a representative sample of each habitat and promote heterogeneous sampling across microhabitats for efficient detection of herpetofauna (Crump 1994; Doan 2003; Marsh and Haywood 2010). The start points for each transect (Figure 4.2) were chosen to allow for any edge effects to be taken into account that may have risked biasing detection (Schlaepfer and Gavin 2001; Urbina-Cardona et al. 2006). Transects were marked every 25 m with flagging tape to indicate the path of the transect, and GPS waypoints were taken at the start and finish points using a handheld GPS device (Garmin™ GPSMap 62s) to facilitate accurate survey replication. After setup, transects were left for a minimum of two days before surveying commenced to allow for animals to resume normal activity prior to survey (Crump 1994). All transects had negligible changes in altitude (+/- 5 m) and were positioned to avoid passing through broad habitat types in order to satisfy assignment of habitat categorization (Babbitt et al. 2009). Transects took

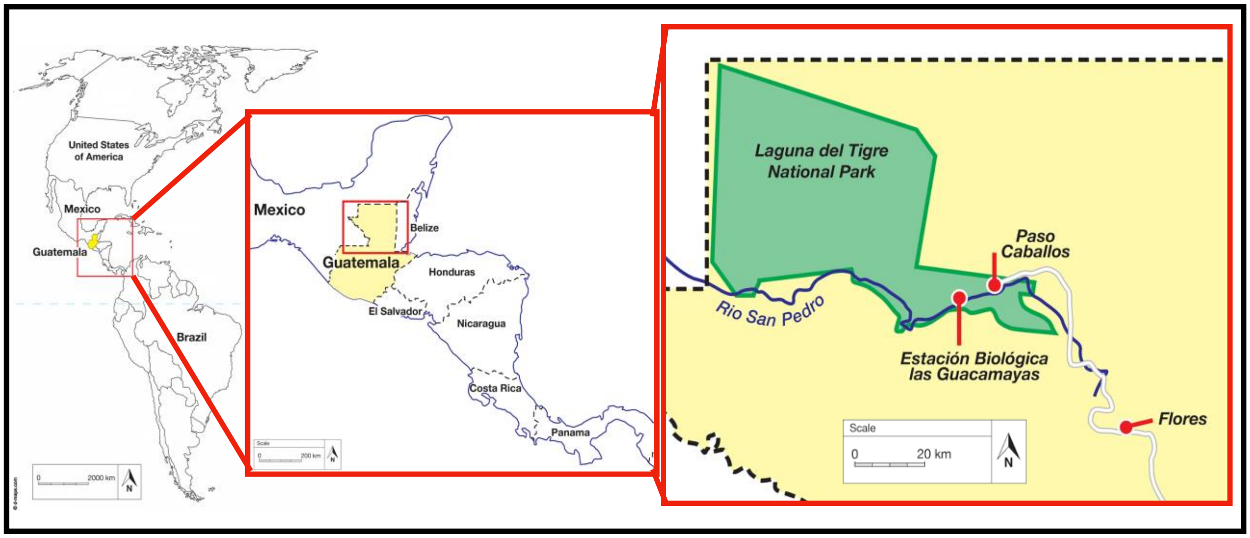


Figure 4.1: Map of the Americas, showing the location of Laguna del Tigre National Park within Guatemala. Red box indicates area shown in Figure 2. Due to the curvature of the map the scale shown is representative of the scale at the equator. Map adapted from D-Maps.com

approximately 45 minutes to one hour to complete and followed standardized protocols for Visual Encounter Surveys in tropical habitats (Rödel and Ernst 2004; Vonesh et al. 2009).

To maximize chances of detecting species with different autecology, each transect was surveyed three times, twice at night and once in the morning during each survey period (Heyer et al. 1994; McDiarmid et al. 2012). For the purposes of statistical analyses, nocturnal and diurnal surveys were grouped. A minimum of two days was left between surveys of the same transect to maintain independence of sample survey periods. Surveys were conducted

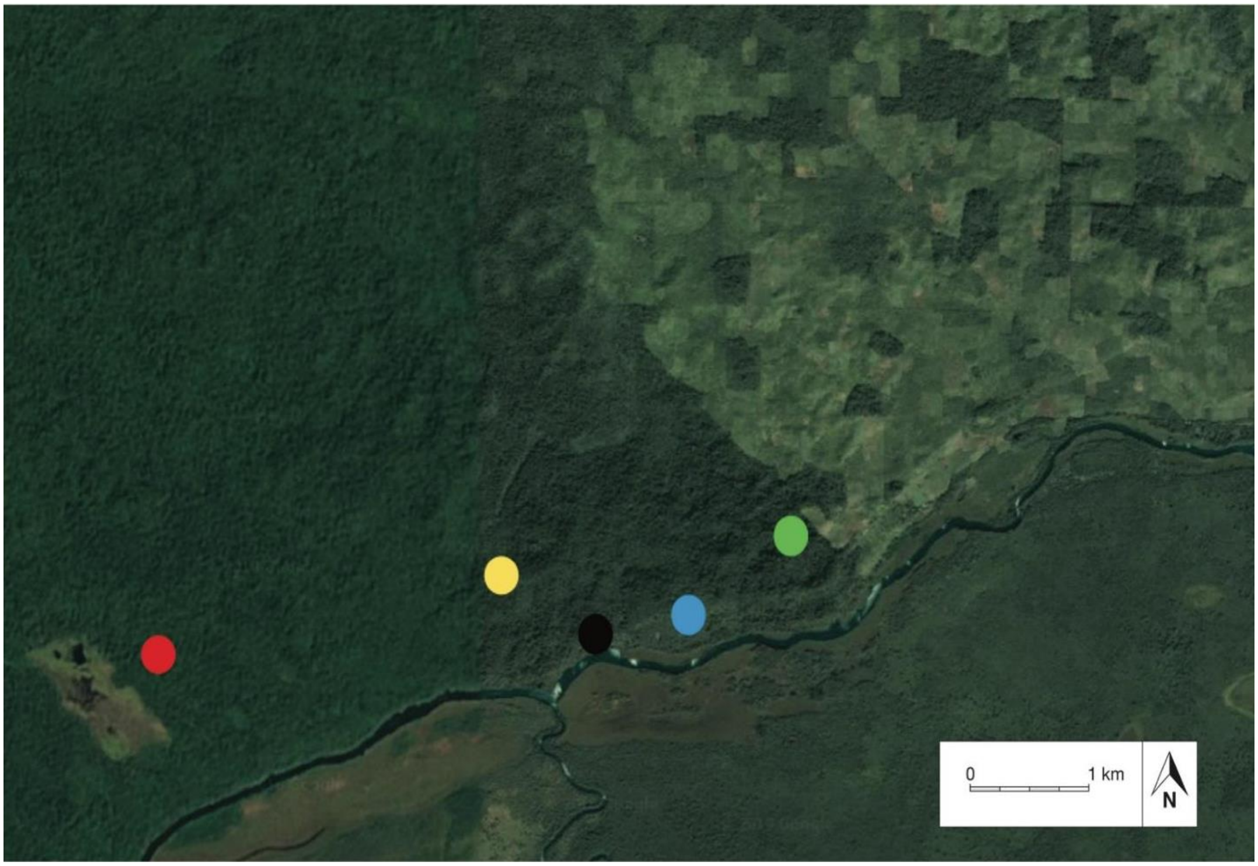


Figure 4.2: Satellite image of the southeast region of Laguna del Tigre National Park showing the location of survey sites indicated by coloured dots: Green = Agricultural Edge; Yellow = High Forest; Red = Low Forest; Blue = Natural Edge; Black = Estación Biológica las Guacamayas. The two rivers are the San Pedro River flowing east to west, and the Sacluc River flowing south to north. North of the San Pedro dark green areas indicate forest areas, lighter green indicates the concessional agricultural land of Paso Caballos. South of the San Pedro, green indicates a mixture of saw grass swamp (sabinal) and seasonally flooded thorn scrub. Image adapted from Google Maps.

during seven fieldwork periods in May-June 2013, November-December 2013, June 2014, October 2014, June 2015, December 2015 and June-July 2016.

Visual encounter surveys are a regularly used method for surveying amphibians and reptiles (Crump and Scott 1994; Lovich et al. 2012). Survey teams consisted of between two and eight people, and included one local guide, the author and two to six field assistants. At the start of each field session, all guides and field assistants were trained in survey techniques, data collection, and species identification by the author. All biometric and environmental data collection was overseen by the author to avoid observer bias. Transects were walked at a suitably slow pace to allow detection of reptiles and amphibians by thorough examination of vegetation and refugia, such as leaf litter, fallen limbs and rocks (Crump and Scott 1994; Lovich et al. 2012). The search area was defined as up to one metre each side of the transect and up to two metres high (Crump and Scott 1994; Lovich et al. 2012). Any individual found outside of this area was recorded as a casual observation but omitted from this study. In total 120 VES were conducted, comprising 18 in AE, 30 in HF, 36 in LF, and 36 in NE respectively. The order in which the four forest habitats were surveyed was randomized, as was the order of transects within each habitat. In some cases, fieldwork was hampered by inclement weather and surveys had to be abandoned.

The following environmental data were recorded at the start and finish of each transect: time (24 hr), air temperature (ºC), relative humidity (%), and cloud cover (%). When safe and practical to do so, each animal encountered was captured for identification purposes, and the following data recorded: time encountered (24 hr), location (recorded using a Garmin GPSmap 62s), species, age (adult, juvenile, neonate), and sex (where possible).

4.3.3 Statistical Analysis

Species and abundance of amphibians and reptiles were recorded for each forest habitat and forest type. Length of transect and time taken to complete a transect were comparable between all years allowing the data to be pooled across years for analysis. This allowed replication of surveys (repeated surveys along the same transect) to be used as the random factor in the modelling process. Prior to analysis, the data for amphibians and reptiles was separated by Class due to the high likelihood that amphibians and reptiles would be affected in different ways by changes in habitat (Gibbons et al. 2000; Gardner et al. 2007b).

The amphibian and reptile assemblage composition was analysed for each habitat by calculating the dominance and persistence of each species detected. Dominance (D) was calculated by dividing the number of detections of a given species by the total number of observations for that taxon. Persistence (P) was calculated by dividing the number of surveys a given species was detected in by the total number of observations for that taxon. Both D and P were expressed as percentages. Similarity Percentage analysis (SIMPER) was conducted to assess dissimilarity between the amphibian and reptile assemblages in the four habitats. SIMPER with Bray-Curtis similarity measure was conducted using the PAST3 software (Hammer et al. 2001).

Multivariate GLM were used in both frequentist and Bayesian frameworks to contrast the response of amphibian, snake, and lizard abundance, described as total number of observations of a species, to distances from agriculture and forest edge within specific habitat types that taxa were detected in. All models were performed in the program R version 3.6.0. (R Core Team 2019). For each taxon, data for frequentist GLMs were placed in an abundance response matrix format. Two predictor variables were used: a) 'distance found from agriculture', defined as the shortest distance measured from the mid-point of a transect to the edge of agriculture, and b) 'distance found from forest edge', defined as the shortest distance measured from the mid-point of a transect to the nearest forest edge. Straight-line distances were calculated using GIS software (Google Maps) and ranged from: 50 m in both cases for AE; 1200 m to agricultural edge and 700 m to forest edge for HF; 2000 - 7000 m to agricultural edge and 400 - 4500 m for LF; and 1200 m to agricultural edge and 100 to forest edge for NE. For each taxon, two multivariate GLM models were made, one for distance to agriculture and one for distance to edge. For both these models the function manyglm in the package mvabund was used to assess relationships of both the assemblage as a whole, and also the relationships of individual species within the assemblage (Wang et al. 2012). The manyglm models were fitted with both Poisson and negative binomial distributions. The data for amphibian, snake, and lizard models included the response variable: a) abundance (as a multi-species matrix), with two explanatory variables: a) distance to agriculture (Dist_to_Agri), and b) distance to forest edge (Dist_to_Edge). The models also included four additive terms that were used to assess their interaction with the explanatory variables: a) Agricultural Edge (AE), b) High Forest (HF), c) Low Forest (LF), and d) Natural Edge (NE). Due to the use of additive terms, and to avoid over-parameterisation, each distance variable was modelled separately. In each case the models used the same abundance data, as such they are considered nested models and are directly comparable through the use of AIC values. Additionally, adjusted R-squared values were calculated for each predictor variable using the function best.r.sq within manyglm, which returns a matrix of the most influential model variables in a step-wise method during which the most influential variable is removed from the following step. Model assumptions of mean-variance and log-linearity were examined using Dunn-Smyth residuals vs. fit plots and normal quantile plots (Dunn and Smyth 1996).

For the corresponding Bayesian GLMM models, data was transformed using package reshape2 (Wickham 2007) into long-format with Dist_to_Agri and Dist_to_Edge variables being centred to reduce range. Estimation was performed using Markov Chain Monte Carlo (MCMC) routines in software JAGS version 4.3.0 (Plummer 2003) through the package runjags (Denwood 2016) in R version 3.6.0. (R Core Team 2019). The models comprised both Poisson and negative binomial families, ran 40000 iterations with 10000 discarded for burn-in (negative binomial comprises 4000 with 1000 for adaptation) with four MCMC chains. Priors were set using templates within runjags modest automated uniform gamma distribution, detected and set through JAGS (priors = ~ dnorm (0, 10^-6)). Convergence was assessed using MCMC trace plots of iterations retrieved from runjags and inspection of the Gelman statistic potential scale reduction factor (PSRF) (Gelman et al. 2013). Model assumptions of mean-variance, log-linearity and potential autocorrelation were examined using residuals vs. fit plots, and a correlation plot function within runjags. MCMC draws from posterior distributions were used for assessing model component relations. Across all GLM and GLMM models, both frequentist and Bayesian, negative binomial distributions represented a better fit than Poisson. Therefore, only results from the negative binomial models are presented here.

4.4 Results

4.4.1 Amphibian Assemblage

Dominance and persistence of amphibians are reported in Figures 4.3 and 4.4 respectively. The overall amphibian assemblage in LTNP was dominated by three species *Hypopachus variolosus, Incilius valliceps,* and *Smilsica baudinii,* that account for 62.6% of total amphibian encounters. Four amphibian species, *Agalychnis callidryas, H. variolosus, I. valliceps,* and *S. baudinii,* were encountered in all four forest habitats and accounted for 67% of the total assemblage in LTNP.

The amphibian assemblage in the Agricultural Edge forest habitat, represented by five species, showed the greatest dominance affect. Two species (*H. variolosus* and *I. valliceps*) represented 87.3% of the entire assemblage. The remaining three species represented 9.1% in the case of *Smilisca baudinii*, and 1.8% for both *Agalychnis callidryas* and *Bolitoglossa mexicanus* (Figure 4.3). The dominance effect in the other three forest assemblage of 16 species) forest habitats *H. variolosus* and *I. valliceps* represented 58.8% and 44.3% of the respective assemblages. In the High Forest habitat, no other species represented more than 10% of the assemblage (Figure 4.3). Two species in Low Forest represented more than 10% of the total assemblage. Although only encountered on one occasion, the aggregation of 24 individuals of *Rhinophrynus dorsalis* accounted for 11.4% of the assemblage. A further 17.1% of the Low Forest assemblage was represented by the hylid frog *S. baudinii* (Figure 4.3). The most evenly distributed assemblage was the Natural Edge habitat, represented by 14 species. The most frequently encountered amphibians were *Rana brownorum* (18.9%), *S. baudinii* (17.9%), *H. variolosus* (14.2%), *A. callidryas* (13.2%), and *I. valliceps* (13.2%). The remaining 22.6% of the Natural Edge assemblage is represented by nine species (Figure 4.3). Additionally, *H. variolosus* and *I. valliceps* showed the highest levels of persistence in all four habitats, ranging from 38.9% (LF) to 16.7% (NE) for *H. variolosus,* and from 41.7% (LF) to 22.2% (NE) for *I. valliceps* (Figure 4.4). Three other species of anuran also showed high levels of persistence, ranging from 25% (NE) to 22.2% (LF) for *Smilisca baudinii*, and from 22.2% (LF) to 11.1% (NE) for *Engystomops pustulosus*, and from 19.4% (LF) to 13.9% (NE) for *Rana*

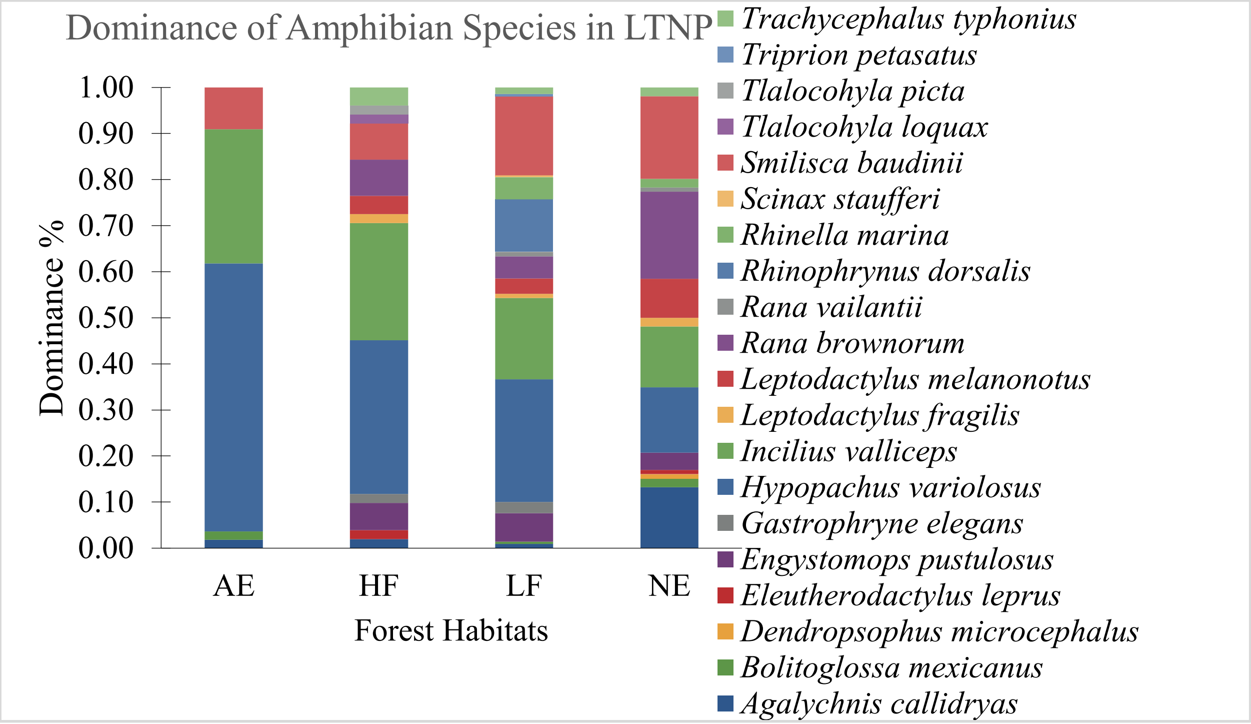


Figure 4.3: Dominance of amphibian species in four forest habitats in Laguna del Tigre National Park, expressed as a percentage. AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

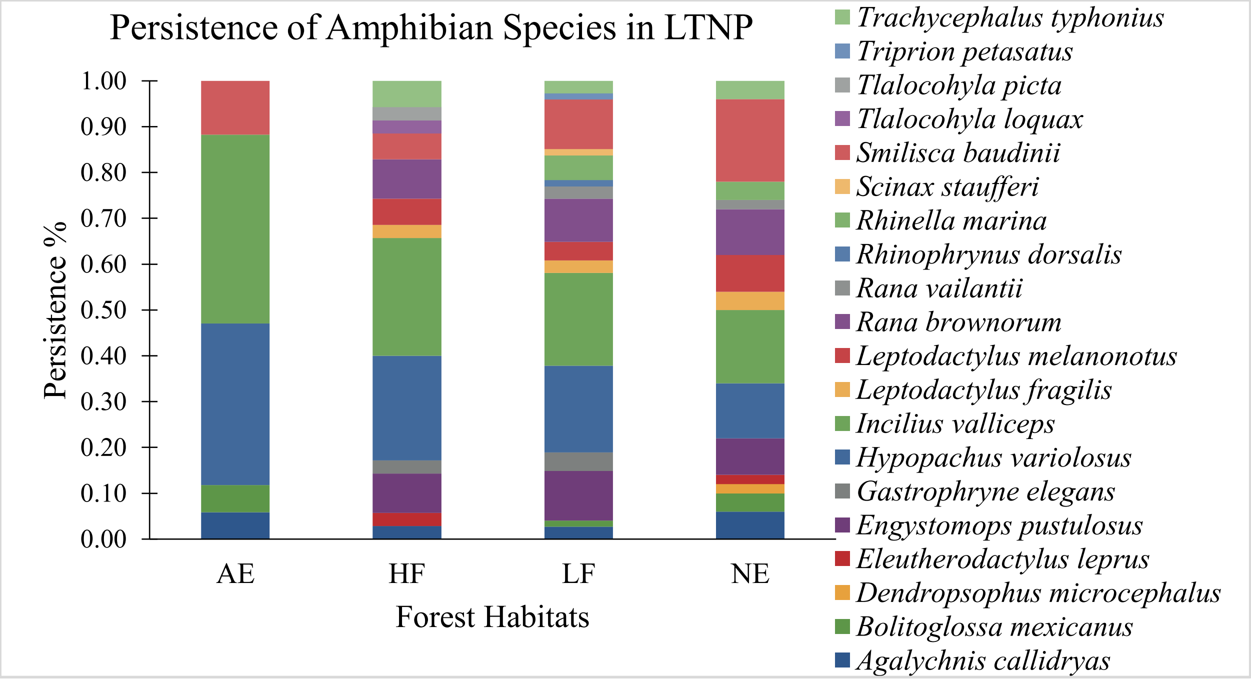


Figure 4.4: Persistence of amphibian species in four forest habitats in Laguna del Tigre National Park, expressed as a percentage. AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

Table 4.1: Analysis of overall percentage dissimilarity of amphibian assemblages found in four forest habitats in Laguna del Tigre National Park. AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

	AE	**HF**	**LF**	**NE**
AE		69.78	75.38	87.64
HF	69.78		80.7	89.27
LF	75.38	80.7		88.29
NE	87.64	89.27	88.29	

brownorum (Fig. 4.4). SIMPER analysis of the amphibian assemblages showed that in terms of overall dissimilarity the HF and NE habitats exhibited the greatest dissimilarity (89.27%), and the least dissimilar assemblages were AE and HF (69.78%) (Table 4.1). In all combinations of comparisons, *H. variolosus*, *I. valliceps*, and *S. baudinii* contributed the most to the dissimilarity between assemblages.

Frequentist GLMs showed that species within the amphibian assemblage of LTNP respond in different ways to 'distance to agriculture' and 'distance to forest edge' (Table 4.2). Overall, Distance to Edge has a greater significance to the amphibian assemblage than Distance to Agriculture (Table 4.2). Inspection of R-squared values revealed that distance to forest edge accounted for more variance in the structure of the amphibian assemblage than distance to agriculture. Step-down comparison identified distance to edge, HF, and LF as the variables with the greatest explanatory power (Table 4.3). Additionally, the effect of Distance to Edge was felt significantly in all four forest habitats, whereas the effect of Distance to Agriculture was only felt significantly in three of them (Table 4.2). In both Edge and Agriculture models, effects of the Forest Habitats themselves on the structure of the amphibian assemblage were observed, but they were not as strongly expressed as the effects of Distance to Edge or Agriculture. These combined results suggest that creation of more edge through the fragmentation of habitat has a more profound effect on the amphibian assemblage in LTNP than the presence of agriculture itself.

Univariate outputs from the frequentist models highlighted that individual species within the amphibian assemblage respond differently to both distance to agriculture (Figure 4.5) and distance to forest edge (Figure 4.6). *Gastrophryne elegans* shows a significant negative

Table 4.2: Multivariate frequentist GLM results showing the relationship between the amphibian assemblage of LTNP and distance to agriculture and distance to forest edge. Res.Df = residual degrees of freedom; Df.diff = degrees of freedom difference; Dev = likelihood ratio test (LRT) result; Pr(>Dev) = probability the variable is greater than LRT. AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

Distance to Agri Multivariate test	AIC 36.72517 : df -15.15758				**Distance to Edge Multivariate test**	AIC 36.18545 ; df -15.43012			
	Res.Df	**Df. diff**	**Dev**	**Pr(>Dev)**		**Res.Df**	**Df. diff**	**Dev**	**Pr(>Dev)**
(Intercept)	119				(Intercept)	119			
Dist_to_Agri	118	1	36.23	**0.017**	Dist_to_Edge	118	1	47.37	**0.001**
AE	117	1	35.14	**0.007**	AE	117	1	30.44	**0.015**
HF	116	1	30.72	**0.037**	HF	116	1	26.88	0.112
LF	115	1	31.32	**0.005**	LF	115	1	27.28	**0.046**
NE	114	1	-0.02	0.97	NE	114	1	0	0.875
Dist_to_Agri:AE	113	1	30.66	**0.001**	Dist_to_Edge:AE	113	1	32.94	**0.001**
Dist_to_Agri:HF	112	1	25	**0.001**	Dist_to_Edge:BA	112	1	33.47	**0.001**
Dist_to_Agri:LF	111	1	-0.01	0.685	Dist_to_Edge:BB	111	1		**0.001**
Dist_to_Agri:NE	113	1		**0.001**	Dist_to_Edge:NE	113	1		**0.001**

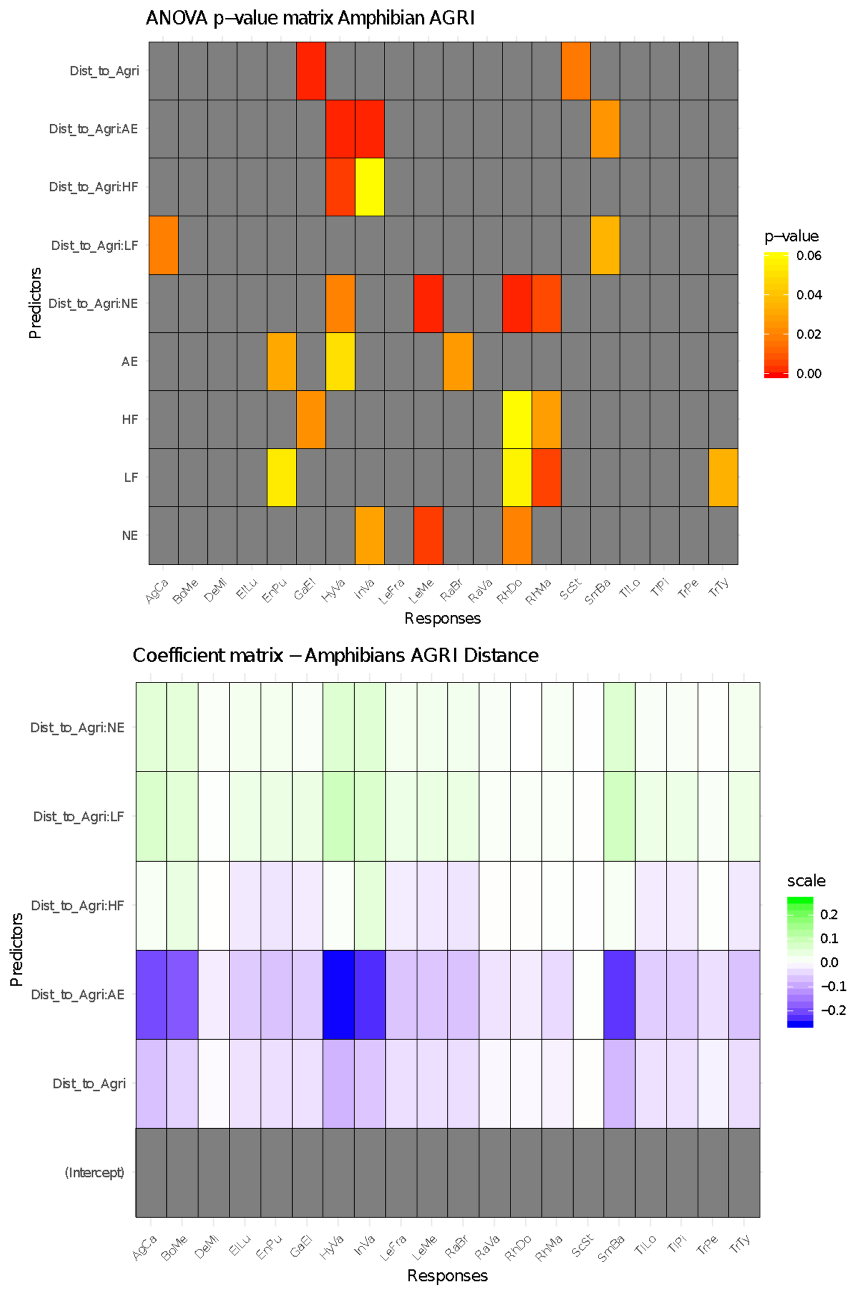
response to the presence of agriculture. The three most common species of amphibian, *Hypopachus variolosus*, *Smilisca baudinii* and *Incilius valliceps*, dominate the assemblage in AE forest habitat (Figure 4.3), however, they show differing responses to the presence of agriculture in that habitat. The first two show a negative response, while the latter shows a positive response. Additionally, *I. valliceps* shows a positive response to agriculture in HF forest habitat. This suggests that *I. valliceps* benefits in some way from the presence of agriculture in LTNP. The presence of agriculture affects the assemblage of the LF forest habitat with the abundance of the hylid frogs, *Agalychnis callidryas* and *S. baudinii* increasing positively with increased distance from the agricultural edge. In NE forest habitat, two species of terrestrial frog, *H. variolosus* and *Leptodactylus melanonotus* also show increasing abundances as a response to increased distance from agricultural edge. *Incilius valliceps* shows a negative response to distance to forest edge (Figure 4.6). Negative responses to the presence of a forest edge were seen in AE forest habitat in the abundances of four amphibian

Table 4.3: Step-wise matrix of R-squared values retrieved from frequentist models showing the three predictor variables (in bold) that explain the most variance in the amphibian assemblage of LTNP.

	Step 1	**Step 2**	**Step 3**
Distance to Edge	**0.061699081**	NA	NA
Distance to Agriculture	0.02111938	0.06852524	0.08318161
AE	0.005970858	0.06887964	0.07999588
HF	0.007999604	**0.07284488**	NA
LF	0.017060697	0.07267244	**0.08433108**
NE	0.009035905	0.07187256	0.08224212

species (80% of species in the AE assemblage), *A. callidryas*, *H. variolosus, I. valliceps, Rhinella marina,* and *S. baudinii.* As distance from forest edge increases, positive responses to the presence of a forest edge were seen in the abundances of two species in NE, and four species in HF. Additionally, two species, *Rhinophrynus dorsalis* and *R. marina* show a positive association with LF (Figure 4.6). The response of multiple amphibian species abundance is positively correlated with increased distance from a forest edge.

Bayesian modelling of the amphibian assemblages facilitated analysis of the response of an individual species in a particular habitat to both 'distance to agriculture' and 'distance to forest edge'. For ease of interpretation the data from the Bayesian models were split into two, those with low value distributional means and those with high values. The high value results represent species that were found in the respective habitat (Figure 4.7). The two most abundant species in all four habitat types, *H. variolosus* and *I. valliceps*, both showed no effect of distance to agriculture in any habitat type, indicated by the credible intervals crossing zero. Other species for which no effect was found included *S. baudinii* in AE, LF, and NE, *R. dorsalis* in LF, and *R. brownorum* and *A. callidryas* in NE. All other species showed a negative effect of distance to agriculture regardless of which forest habitat they were encountered in (Figure 4.7). No amphibian species showed a positive effect of distance to agriculture. All species that were not present in the habitat being analysed showed a negative effect of the presence of agriculture (Appendix I.1 to I.4).



ANOVA p–value matrix Amphibian AGRI

Coefficient matrix – Amphibians AGRI Distance

Figure 4.5: Univariate GLM heat matrices showing significant effects of distance to agriculture on the amphibian assemblage of LTNP. Significant p-values are shown at the top (yellow to red shows increasing significance) which matched to the coefficient matrix at the bottom indicate significant positive (green) and negative (blue) responses of amphibian species to the presence of agriculture. The coefficient matrix shows species responses to interactions between distance to agriculture and how that is expressed in different forest habitats Species codes; AgCa = *Agalychnis callidryas*, BoMe = *Bolitoglossa mexicanus*, DeMi = *Dendropsophus microcephalus*, ElLe = *Eleutherodactylus leprus*, EnPu = *Engystomops pustulosus*, GaEl = *Gastrophyryne elegans*, HyVa = *Hypopachus variolosus*, InVa = *Incilius valliceps*, LeFra = *Leptodactylus fragilis*, LeMe = *Leptodactylus melanonotus*, RaBr = *Rana brownorum*, RaVa = *Rana vailantii*, RhDo = *Rhinophrynus dorsalis*, RhMa = *Rhinella marina*, ScSt = *Scinax staufferi*, SmBa = *Smilisca baudinii*, TlLo = *Tlalocohyla loquax*, TlPi = *Tlalocohyla picta*, TrPe = *Triprion petasatus*, TrTy = *Trachycephalus typhonius*. Forest Habitat codes; AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

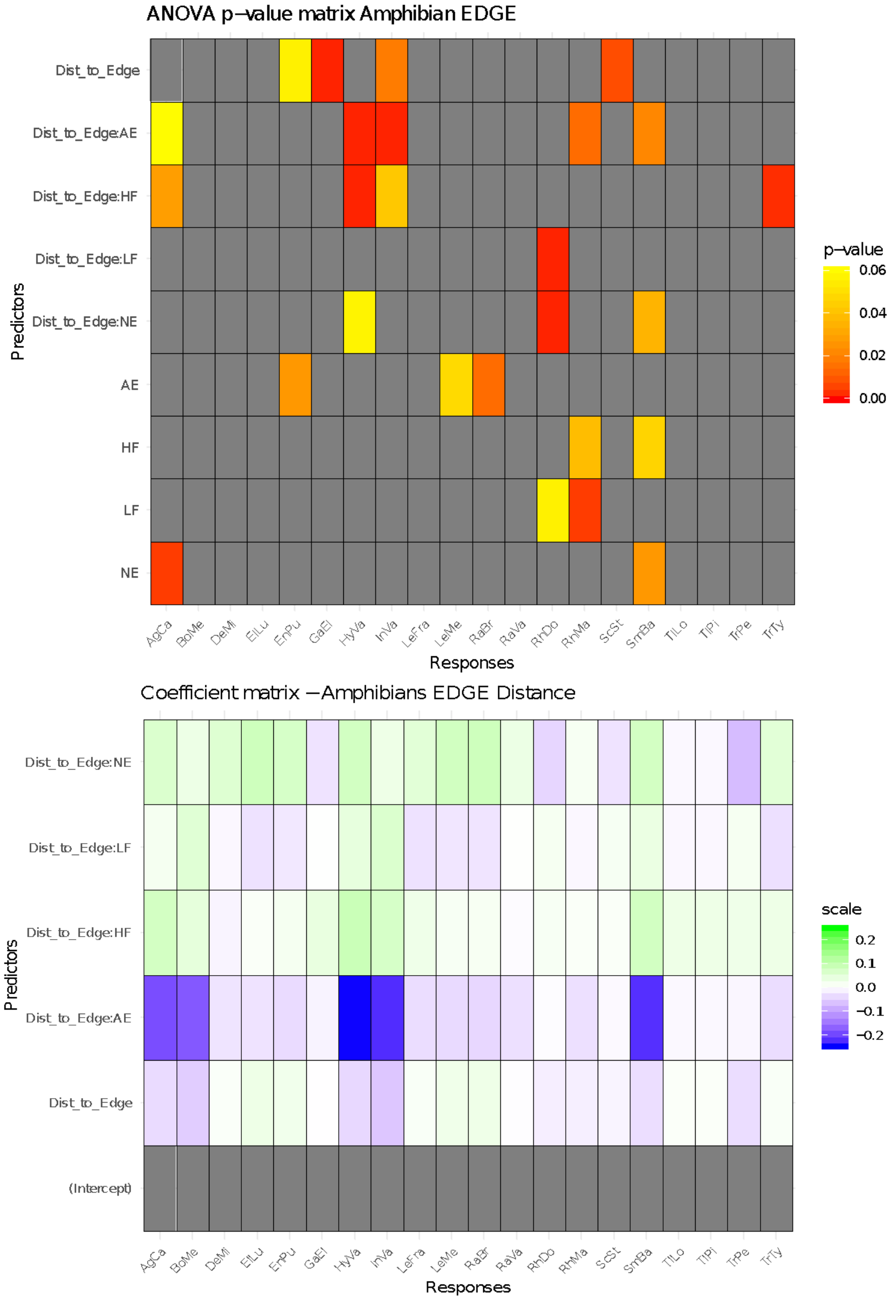


Figure 4.6: Univariate GLM heat matrices showing significant effects of distance to edge on the amphibian assemblage of LTNP. Significant p-values are shown at the top (yellow to red shows increasing significance) which matched to the coefficient matrices indicate significant positive (green) and negative (blue) responses of amphibian species to the presence of agriculture. Coefficient matrix bottom of this page shows species responses to interactions between distance to forest edge and how that is expressed in different forest habitats. Coefficient matrix on the following page shows species responses to the different forest habitats themselves. Species codes; AgCa = *Agalychnis callidryas*, BoMe = *Bolitoglossa mexicanus*, DeMi = *Dendropsophus microcephalus*, ElLe = *Eleutherodactylus leprus*, EnPu = *Engystomops pustulosus*, GaEl = *Gastrophyryne elegans*, HyVa = *Hypopachus variolosus*, InVa = *Incilius valliceps*, LeFra = *Leptodactylus fragilis*, LeMe = *Leptodactylus melanonotus*, RaBr = *Rana brownorum*, RaVa = *Rana vailantii*, RhDo = *Rhinophrynus dorsalis*, RhMa = *Rhinella marina*, ScSt = *Scinax staufferi*, SmBa = *Smilisca baudinii*, TlLo = *Tlalocohyla loquax*, TlPi = *Tlalocohyla picta*, TrPe = *Triprion petasatus*, TrTy = *Trachycephalus typhonius*. Forest Habitat codes; AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge. Continued on next page.

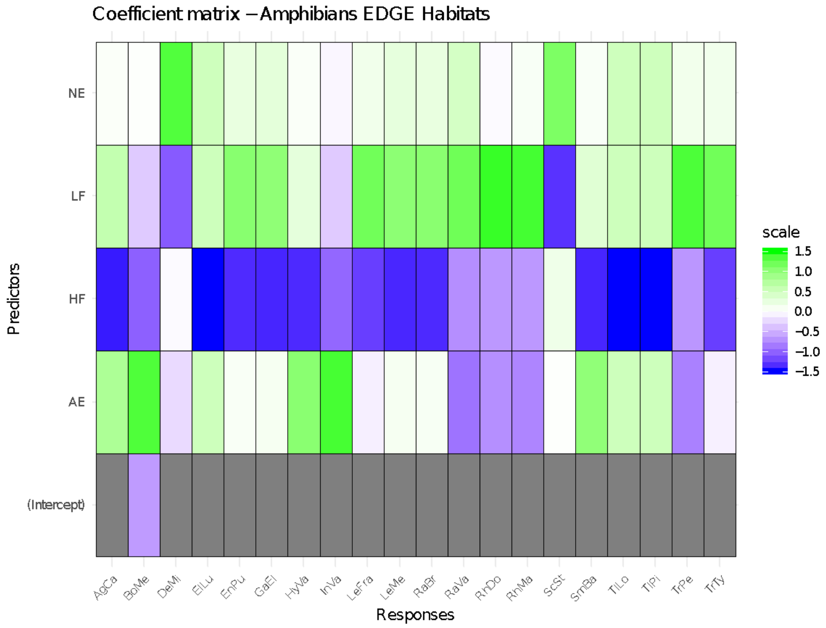
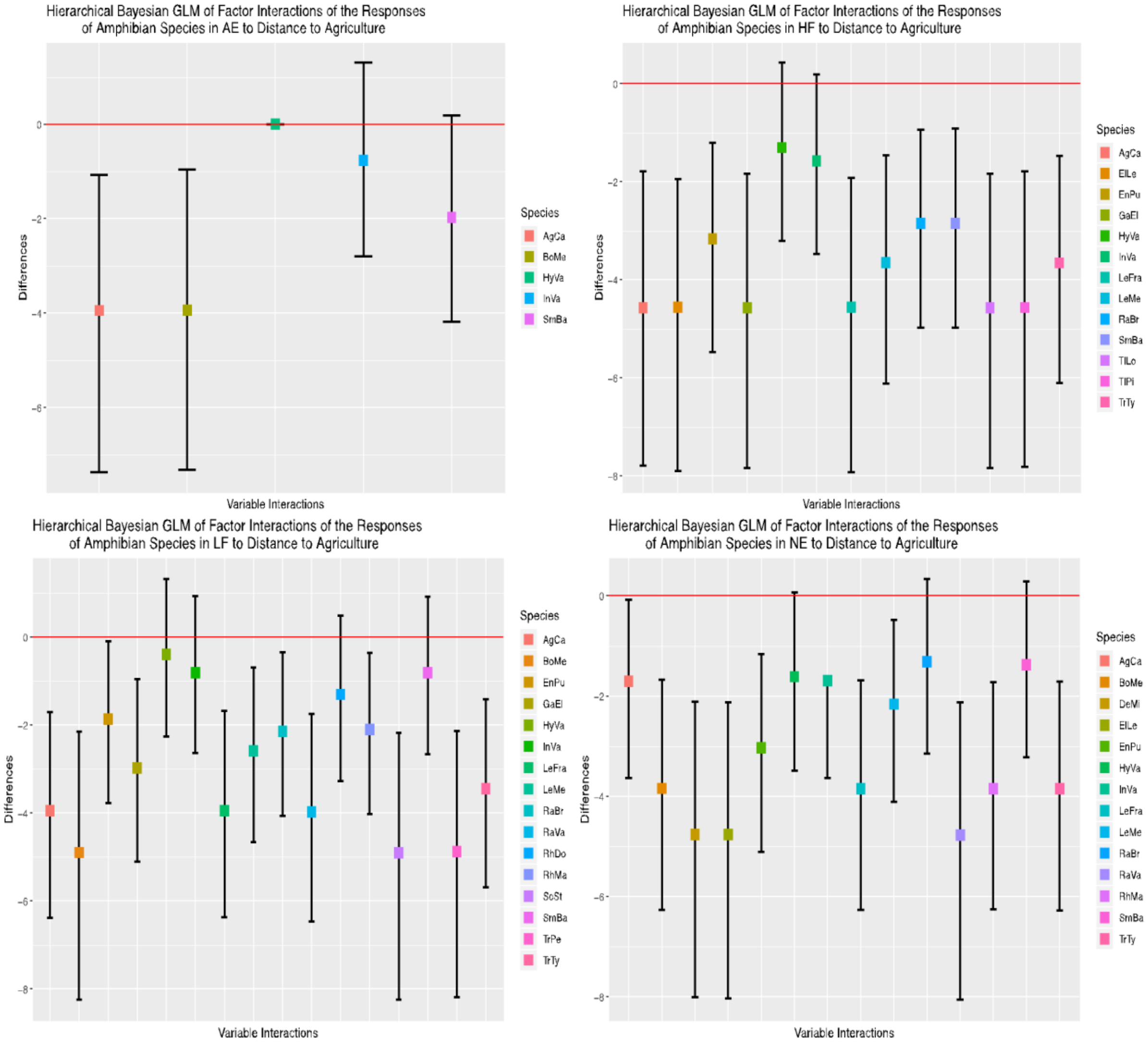


Figure 4.6 continued.

Bayesian GLM's that modelled the response of the amphibian assemblage to the 'distance to forest edge' showed that most species responded negatively to the presence of a forest edge (Figure 4.8). In AE *A. callidrays* and *Bolitoglossa mexicanus* showed no response to forest edge. In HF, *H. variolosus* and possibly *I. valliceps* showed no response to forest edge. In theLF forest habitat, *H. variolosus, I. valliceps, R. dorsalis,* and *S. baudinii* all showed no response to forest edge. Five species in NE showed no response to forest edge, they were *A. callidryas, H. variolosus, I. valliceps, R. brownorum,* and *S. baudinii*. All species that were not present in the habitat being analyzed showed a negative effect of the presence of forest edge (Appendix I.5 to I.8). The agricultural edge amphibian assemblage is dominated by a few species, this is compared to the other forest habitats with higher diversity and a more even distribution of species abundances. The abundances of most amphibian species were negatively affected by distance to edge and distance to agriculture, although the abundance of one species, *Incilius valliceps,* benefitted from the presence of agriculture. Overall, distance to forest edge accounts for most of the variance in the amphibian assemblage of LTNP.


Hierarchical Bayesian GLM of Factor Interactions of the Responses of Amphibian Species in AE to Distance to Agriculture

Hierarchical Bayesian GLM of Factor Interactions of the Responses of Amphibian Species in HF to Distance to Agriculture

Hierarchical Bayesian GLM of Factor Interactions of the Responses of Amphibian Species in LF to Distance to Agriculture

Hierarchical Bayesian GLM of Factor Interactions of the Responses of Amphibian Species in NE to Distance to Agriculture

Figure 4.7: Caterpillar plots with credible intervals (CI) of Bayesian GLM model with a negative binomial distribution showing the effect of distance to agriculture on the amphibian assemblage composition in Laguna del Tigre National Park. Red line represents the zero line, those credible intervals that do not cross zero are not significant, those are below zero are negative responses, and those that are above zero are positive respsones. Species codes; AgCa = *Agalychnis callidryas*, BoMe = *Bolitoglossa mexicanus*, DeMi = *Dendropsophus microcephalus*, ElLe = *Eleutherodactylus leprus*, EnPu = *Engystomops pustulosus*, GaEl = *Gastrophyrene elegans*, HyVa = *Hypopachus variolosus*, InVa = *Incilius valliceps*, LeFra = *Leptodactylus fragilis*, LeMe = *Leptodactylus melanonotus*, RaBr = *Rana brownorum*, RaVa = *Rana vailantii*, RhMa = *Rhinella marina*, RhDo = *Rhinophrynus dorsalis*, ScSt = *Scinax staufferi*, SmBa = *Smilisca baudinii,* TlLo = *Tlalocohyla loquax*, TlPi = *Tlalocohyla picta*, TrPe = *Triprion petasatus*, TrTy = *Trachycephalus typhonius*. Forest Habitat codes; AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

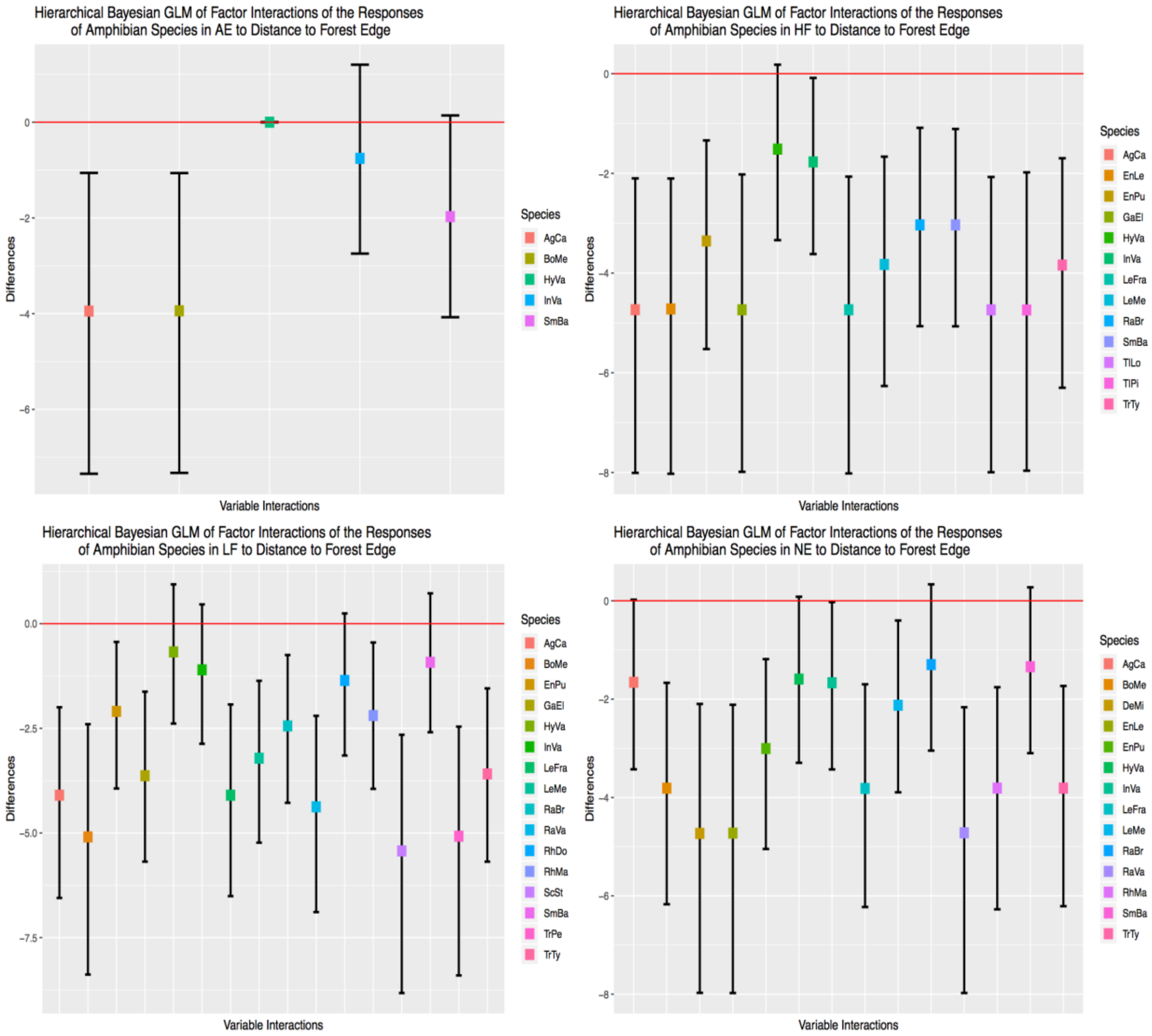


Figure 4.8: Caterpillar plots with credible intervals (CI) of Bayesian GLM model with a negative binomial distribution showing the effect of distance to forest edge on the amphibian assemblage composition in Laguna del Tigre National Park. Red line represents the zero line, those credible intervals that do not cross zero are not significant, those are below zero are negative responses, and those that are above zero are positive respsones.Species codes; AgCa = *Agalychnis callidryas,* BoMe = *Bolitoglossa mexicanus,* DeMi = *Dendropsophus microcephalus,* ElLe = *Eleutherodactylus leprus,* EnPu = *Engystomops pustulosus,* GaEl = *Gastrophyryne elegans,* HyVa = *Hypopachus variolosus,* InVa = *Incilius valliceps,* LeFra = *Leptodactylus fragilis,* LeMe = *Leptodactylus melanonotus,* RaBr = *Rana brownorum,* RaVa = *Rana vailantii,* RhMa = *Rhinella marina,* RhDo = *Rhinophrynus dorsalis,* ScSt = *Scinax staufferi,* SmBa = *Smilisca baudinii,* TlLo = *Tlalocohyla loquax,* TlPi = *Tlalocohyla picta,* TrPe = *Triprion petasatus,* TrTy = *Trachycephalus typhonius.* Forest Habitat codes; AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

4.4.2 Snake Assemblage

Dominance and persistence for the snake assemblage in LTNP are reported in Figures 4.9 and 4.10 respectively. The overall assemblage of snakes was dominated by four species that accounted for 48.5% of all snake encounters. These consisted of one viperid (*Bothrops asper*) and three colubrids (*Imantodes cenchoa*, *Leptodeira septentrionalis*, and *Ninia sebae*). Additionally, six species of snake were encountered across all four forest habitats, and cumulatively they accounted for 58.3% of the total snake assemblage. They were *C. schmidti, I. cenchoa, L. septentrionalis, Micrurus diastema, N. sebae,* and *Tropidodipsas sartorii*. Of all snake encounters in AE two species (*Coniophanes schmidti* and *L. septentrionalis*) dominated the assemblage, accounting for 54.5% of the assemblage. The remaining five snake species encountered in AE were all represented by a single individual. The colubrid snake, *Leptophis ahaetulla* was only encountered in AE habitat. In HF the snake assemblage was represented by 17 species, four of which each contributed greater than 10% to the total individuals encountered. Those species, *B. asper*, *I. cenchoa*, *L. septentrionalis,* and *N. sebae*, cumulatively contributed 52.73% to the HF snake assemblage. Six snake species were only encountered in HF, *Boa imperator, Coluber mentovarius, Leptophis mexicanus, Oxybelis aeneus,* and *Tantilla moesta*. The LF snake assemblage was represented by 16 species, and was also dominated by four species, *B. asper*, *C. imperialis, L. septentrionalis*, and *N. sebae,* that accounted for 57.2% of the total individuals encountered. Five species encountered in LF, *Adelphicos quadrivigattus, Coniophanes bipunctatus, Pseudelaphe flavirufa, Sibon dimidiata,* and *Xenodon rabdocephalus,* were only found in this habitat. Of the 14 snake species encountered in NE, four species accounted for 69.4% of the assemblage. They were *B. asper*, *I. cenchoa*, *L. septentrionalis,* and *N. sebae*. Three snake species, *Clelia scytalina, Lampropeltis abnorma,* and *Spilotes pullatus,* were only found in the NE forest habitat.

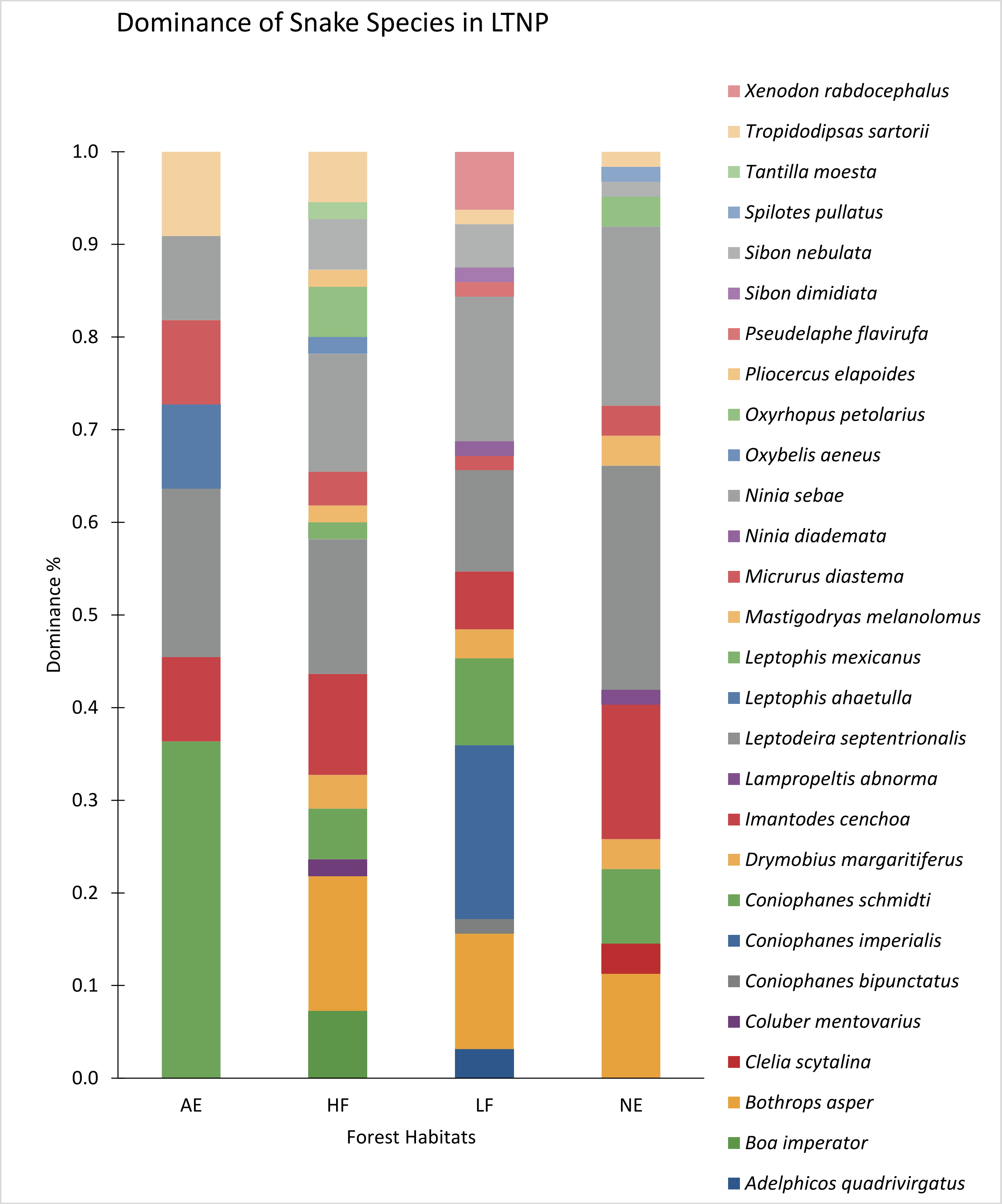


Figure 4.9: Dominance of snake species in four forest habitats in Laguna del Tigre National Park, expressed as a percentage. AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

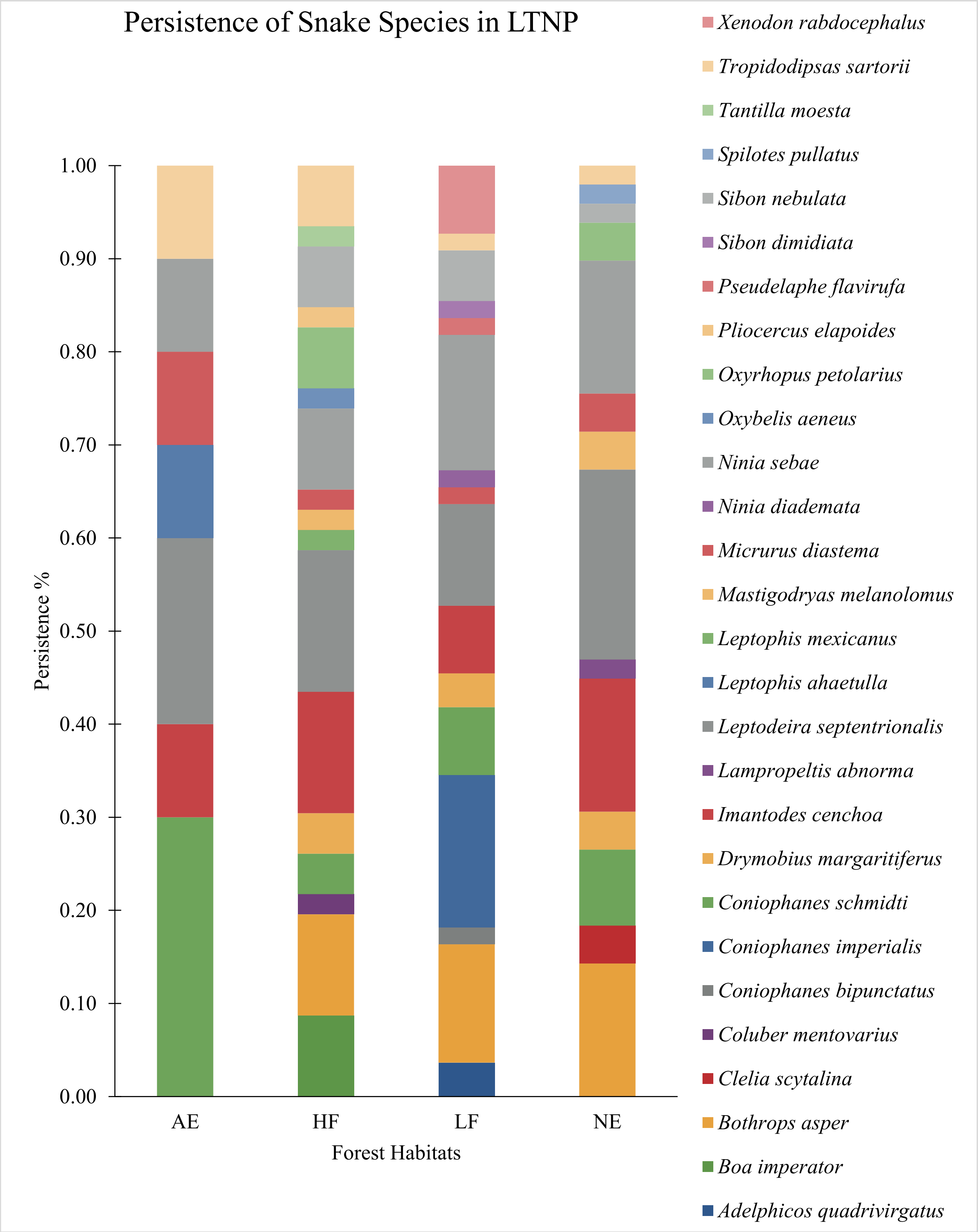


Figure 4.10: Persistence of snake species in four forest habitats in Laguna del Tigre National Park, expressed as a percentage. AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

Table 4.4: Analysis of overall percentage dissimilarity of snake assemblages found in four forest habitats in Laguna del Tigre National Park. AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

	AE	HF	LF	NE
AE		73.17	74.54	72.16
HF	73.17		82.46	80.35
LF	74.54	82.46		81.65
NE	72.16	80.35	81.65	

Persistence levels ranged from 15% to 10% in AE, from 18% to 10.3% in HF, from 23.1% to 10.3% in LF, and from 21.7% to 15.2% in NE. In AE two species were the most persistent, being *C. schmidti* and *L. septentrionalis*. In HF, five species were the most persistent, with *L. septentrionalis* occurring in the most surveys. In LF, seven species occurred regularly, with the most persistent being *C. imperialis*. In NE, four species occurred regularly, with the most persistent being *L. septentrionalis* (Figure 4.10). SIMPER analysis showed that the snake assemblages of HF and LF were the most dissimilar (82.46%), and those of AE and NE were the least (72.16%) (Table 4.4). In all analyses *N. sebae* was included in the top three species that contributed to the dissimilarity between assemblages. Other species that were included in the top three contributions were (in no order) *B. asper*, *C. schmidti*, *C. imperialis*, *L. septentrionalis*, and *I. cenchoa.*

The frequentist multivariate GLMs showed that although neither Distance to Agriculture nor Distance to Edge had a significant effect on the structure of the snake assemblage, AIC values indicate that Distance to Edge is the better fitting model (Table 4.5). Inspection of R-squared values revealed that distance to forest edge accounted for more variance in the structure of the snake assemblage than distance to agriculture. Step-down comparison identified distance to edge, HF, and LF as the variables with the greatest explanatory power (Table 4.6). The effect of agriculture was felt on the structure of the localized assemblages in three forest habitats, and the effect of edge was felt in two (Table 4.5). In both models the greatest significance in the snake assemblage of LTNP was felt by forest habitat itself, LF in the case of Distance to Agriculture and HF in the case of Distance to Edge. Both LF and HF are primary

Table 4.5: Multivariate frequentist GLM results showing the relationship between the snake assemblage of LTNP and distance to agriculture and distance to forest edge. Res.Df = residual degrees of freedom; Df.diff = degrees of freedom difference; Dev = likelihood ratio test (LRT) result; Pr(>Dev) = probability the variable is greater than LRT AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

Distance to Agri Multivariate test	AIC -104.4632 : df -59.71287				**Distance to Edge Multivariate test**	AIC -107.7830 : df -60.28363			
	Res.Df	**Df. diff**	**Dev**	**Pr(>Dev)**		**Res.Df**	**Df. diff**	**Dev**	**Pr(>Dev)**
(Intercept)	143				(Intercept)	143			
Dist_to_Agri	142	1	29.66	0.309	Dist_to_Edge	142	1	28.8	0.245
AE	141	1	47.58	**0.005**	AE	141	1	30.02	0.164
HF	140	1	38.71	0.054	HF	140	1	47.68	**0.006**
LF	139	1	51.44	**0.001**	LF	139	1	40.39	**0.005**
NE	138	1	-0.03	0.977	NE	138	1	-0.01	0.919
Dist_to_Agri:AE	137	1	10.86	**0.012**	Dist_to_Edge:AE	137	1	13.48	**0.003**
Dist_to_Agri:HF	136	1	20.2	**0.004**	Dist_to_Edge:HF	136	1	39.97	**0.001**
Dist_to_Agri:LF	135	1	0	**0.016**	Dist_to_Edge:LF	135	1	0	0.07
Dist_to_Agri:NE	137	1	0	0.123	Dist_to_Edge:NE	137	1	0	0.064

forest habitats suggesting that secondary or disturbed habitats have less influence over the structure of the snake assemblage in LTNP.

Univariate outputs for the frequentist models show that the abundance of multiple species in the snake assemblage are significantly, and positively correlated with increasing distance

Table 4.6: Step-wise matrix of R-squared values retrieved from frequentist models showing the three predictor variables (in bold) that explain the most variance in the snake assemblage of LTNP.

	Step 1	**Step 2**	**Step 3**
Distance to Edge	**0.061699081**	NA	NA
Distance to Agriculture	0.02111938	0.06852524	0.08318161
AE	0.005970858	0.06887964	0.07999588
HF	0.007999604	**0.07284488**	NA
LF	0.017060697	0.07267244	**0.08433108**
NE	0.009035905	0.07187256	0.08224212

from agriculture (Figure 4.11). The results show that some snake abundances respond negatively to the presence of agriculture in forest habitats that are close to agriculture. For example, *Leptophis ahaetulla* shows a general negative response to the presence of agriculture, *Coniophanes schmidtii* responds negatively to the presence of agriculture in AE, and *Bothrops asper* responds negatively in HF. Other species respond positively with increased distance from agriculture, such as *Ninia sebae* in HF and LF, and *Leptodeira septentrionalis* in NE (Figure 4.11). The significant positive response of *Xenodon rabdocephalus* in LF suggests that this species prefers primary forest, whereas the negative response of *Sibon nebulata* in the same habitat could show a preference for edge habitats. There were a greater number of significant responses in the univariate outputs in response to distance to forest edge: again, the responses of individual snake species suggest a positive correlation between increasing snake abundance and increasing distance from a forest edge (Figure 4.12). The abundances of *Adelphicos quadrivigattus* and *Coniophanes imperialis* respond negatively to the presence of a forest edge, additionally the abundances of *C. schmidtii* and *B. asper* respond negatively to the presence of a forest edge in AE and HF respectively. In three forest habitats the abundances of several snake species increased with increasing distance from a forest edge, *Imantodes cenchoa, Micrurus diastema, N. sebae,* and *S. nebulata* in HF, *C. schmidtii* and *Lampropeltis abnormal* in LF, and *I. cenchoa* and *N. sebae* in NE (Figure 4.12).

Bayesian GLMs showed that, with the exception of *C. imperialis* in LF, which showed a positive response to distance to agriculture, the snake assemblages of all forest habitats were not affected by either distance to agriculture or distance to forest edge, (Figures 4.13 and

4.14). However, the models also showed that a number of species were absent in a given habitat due to the effect of distance to agriculture and anthropogenic forest edges (Appendix I.9 to I.16). The models showed that in NE, 14 species of snakes exhibited significant, or near significant, negative responses and were absent from the assemblage due to the presence of agriculture (Appendix I.12). In two forest habitats, AE and HF, the models suggested that 10 species exhibited significant, or near significant, negative responses and were absent from those habitats due to the presence of agriculture (Appendix I.19 and I.10). The LF forest habitat was the least affected by the presence of agriculture with only five absent species exhibiting significant, or near significant, negative responses (Appendix I.11). The models also showed that the snake assemblage of the AE forest habitat was the most affected by the presence of a forest edge, with 16 absent species exhibiting significant, or near significant, negative responses (Appendix I.13). In the NE forest habitat, 14 absent species showed the same response, whereas in HF and LF, 11 absent species showed significant, or near significant, negative responses (Appendix I.16, I.14, and I.15 respectively). The snake assemblage in agricultural edge is dominated by a single species, *Coniophanes schmidtii*, whereas the other forest habitats contain a greater diversity of species and display a more even distribution of abundance among those species. Most variation in the snake assemblage is caused by the presence of agriculture, in particular, the absence of a species from a forest habitat assemblage is often related to the presence of agriculture.

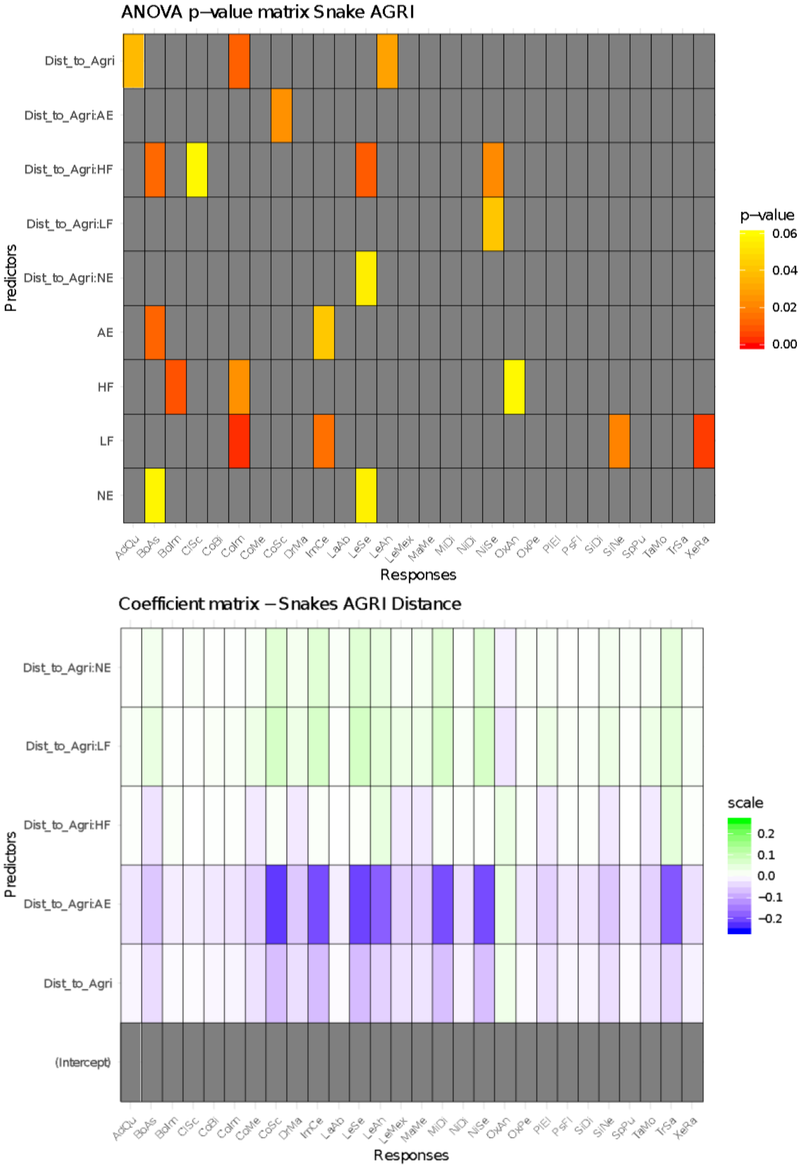
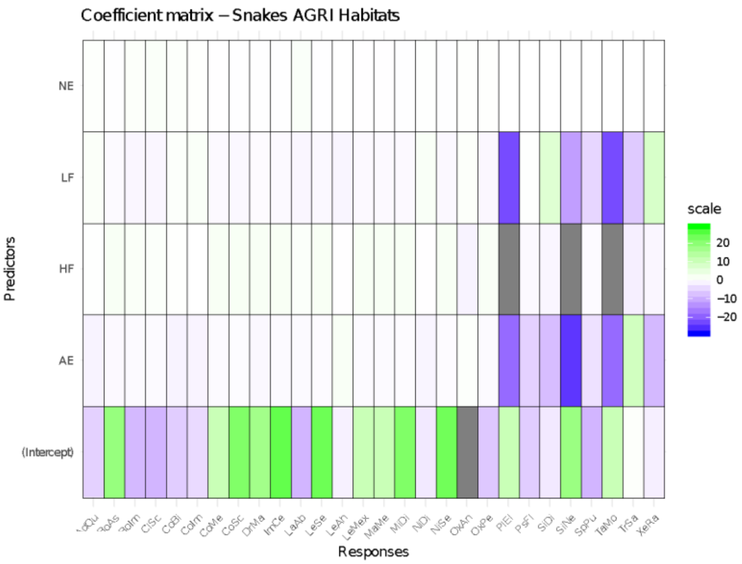


Figure 4.11: Univariate GLM heat matrices showing significant effects of distance to agriculture on the snake assemblage of LTNP. Significant p-values are shown at the top (yellow to red shows increasing significance) which matched to the coefficient matrices indicate significant positive (green) and negative (blue) responses of amphibian species to the presence of agriculture. Coefficient matrix bottom of this page shows species responses to interactions between distance to forest edge and how that is expressed in different forest habitats. Coefficient matrix on the following page shows species responses to the different forest habitats themselves. Species codes; AdQu = *Adelphicos quadrivigattus*, BoAs = *Bothrops asper,* BoIm = *Boa imperator*, ClSc = *Clelia scytalina*, CoBi = *Coniophanes bipunctatus*, CoIm = *Coniophanes imperialis*, CoMe = *Coluber mentovarius*, CoSc = *Coniophanes schmidtii*, DrMa = *Drymobius margaritiferus*, ImCe = *Imantodoes cenchoa*, LaAb = *Lampropeltis abnorma*, LeAh = *Leptophis ahaetulla*, LeMex = *Leptophis mexicanus*, LeSe = *Leptodiera septentrionalis*, MaMe = *Mastigodryas melanonomus*, MiDi = *Micrurus diastema*, NiDi = *Ninia diademata*, NiSe = *Ninia sebae*, OxAe = *Oxybelis aeneus*, OxPe = *Oxyrhopus petolarius*, PlEl = *Pliocercus elapoides*, PsFl = *Psuedelaphe flavirufa*, SiDi = *Sibon dimidiata*, SiNe = *Sibon nebulata*, SpPu = *Spilotes pullatus*, TaMo = *Tantilla moesta*, TrSa = *Tropidodipsas sartorii*, XeRa = *Xenodon rabdocephalus*. Forest Habitat codes; AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge. Continued on next page.



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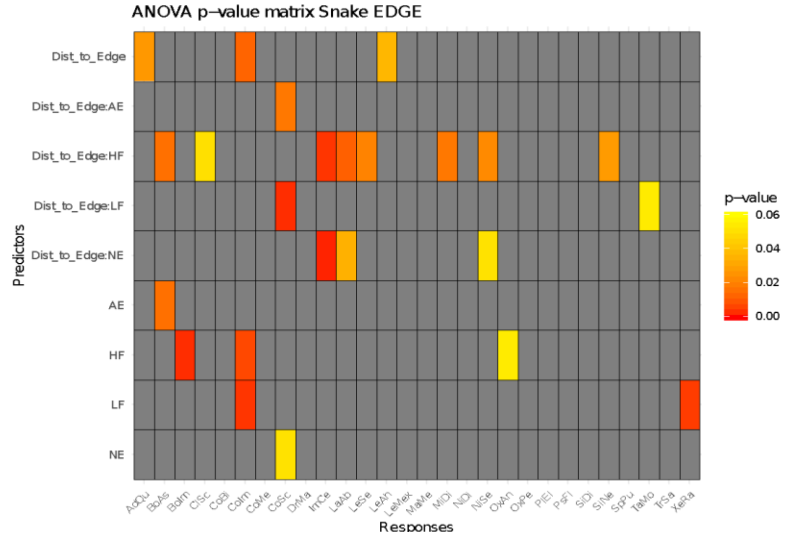

Figure 4.12: Univariate GLM heat matrices showing significant effects of distance to edge on the snake assemblage of LTNP. Significant p-values are shown (yellow to red shows increasing significance) which matched to the coefficient matrices indicate significant positive (green) and negative (blue) responses of amphibian species to the presence of agriculture. Coefficient matrix top of next page shows species responses to interactions between distance to forest edge and how that is expressed in different forest habitats. Coefficient matrix on the bottom of the following page shows species responses to the different forest habitats. Species codes; AdQu = *Adelphicos quadrivigattus*, BoAs = *Bothrops asper,* BoIm = *Boa imperator*, ClSc = *Clelia scytalina*, CoBi = *Coniophanes bipunctatus*, CoIm = *Coniophanes imperialis*, CoMe = *Coluber mentovarius*, CoSc = *Coniophanes schmidtii*, DrMa = *Drymobius margaritiferus*, ImCe = *Imantodoes cenchoa*, LaAb = *Lampropeltis abnorma*, LeAh = *Leptophis ahaetulla*, LeMex = *Leptophis mexicanus*, LeSe = *Leptodiera septentrionalis*, MaMe = *Mastigodryas melanonomus*, MiDi = *Micrurus diastema*, NiDi = *Ninia diademata*, NiSe = *Ninia sebae*, OxAe = *Oxybelis aeneus*, OxPe = *Oxyrhopus petolarius*, PlEl = *Pliocercus elapoides*, PsFl = *Psuedelaphe flavirufa*, SiDi = *Sibon dimidiata*, SiNe = *Sibon nebulata*, SpPu = *Spilotes pullatus*, TaMo = *Tantilla moesta*, TrSa = *Tropidodipsas sartorii*, XeRa = *Xenodon rabdocephalus*. Forest Habitat codes; AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge. Continued on next page.

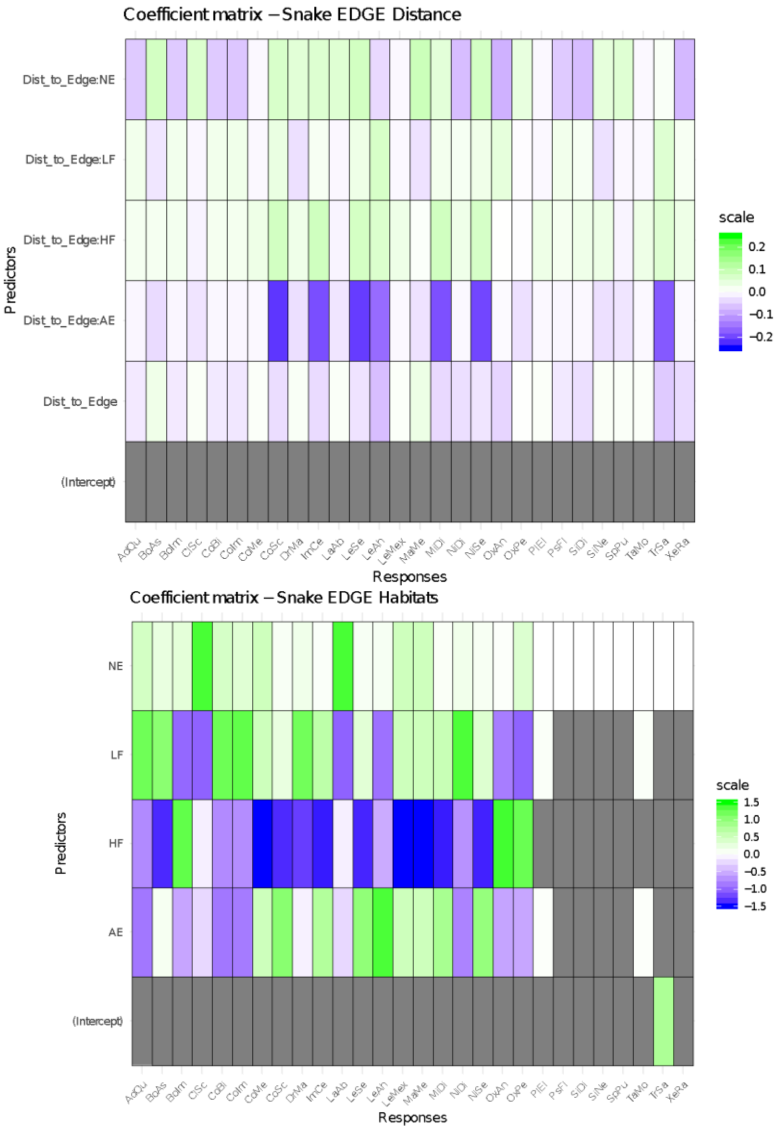

Figure 4.12 continued.

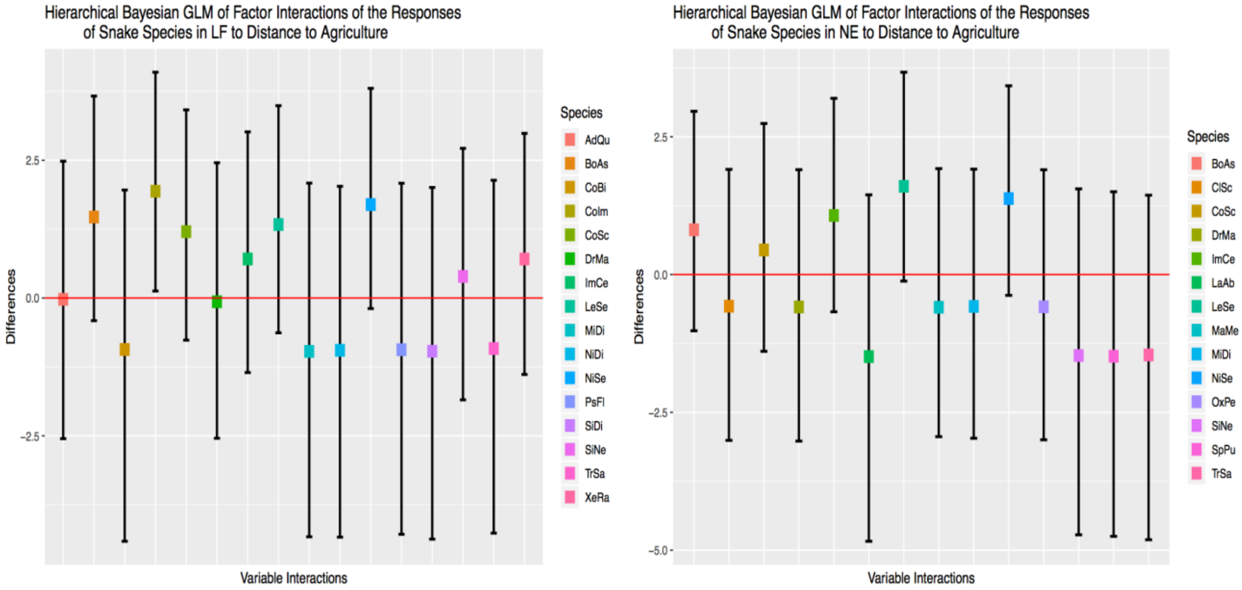

Figure 4.13: Caterpillar plots with credible intervals (CI) of Bayesian GLM model with a negative binomial distribution showing the effect of distance to agriculture on the snake assemblage composition in Laguna del Tigre National Park. Red line represents the zero line, those credible intervals that do not cross zero are not significant, those are below zero are negative responses, and those that are above zero are positive respsones. Species codes; AdQu = *Adelphicos quadrivigattus*, BoAs = *Bothrops asper*, BoIm = *Boa imperator*, ClSc = *Clelia scytalina*, CoBi = *Coniophanes bipunctatus*, CoIm = *Coniophanes imperialis*, CoSc = *Coniophanes schmidtii*, DrMa = *Drymobius margaritiferus*, ImCe = *Imantodoes cenchoa*, LaAb = *Lampropeltis abnorma*, LeSe = *Leptodiera septentrionalis*, LeAh = *Leptophis ahaetulla*, LeMex = *Leptophis mexicanus*, MaMe = *Mastigodryas melanonomus*, MiDi = *Micrurus diastema*, NiDi = *Ninia diademata*, NiSe = *Ninia sebae*, OxAe = *Oxybelis aeneus*, OxPe = *Oxyrhopus petolarius*, PlEl = *Pliocercus elapoides*, PsFl = *Psuedelaphe flavirufa*, SiDi = *Sibon dimidiata*, SiNe = *Sibon nebulata*, SpPu = *Spilotes pullatus*, TaMo = *Tantilla moesta*, TrSa = *Tropidodipsas sartorii*, XeRa = *Xenodon rabdocephalus*. Forest Habitat codes; AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

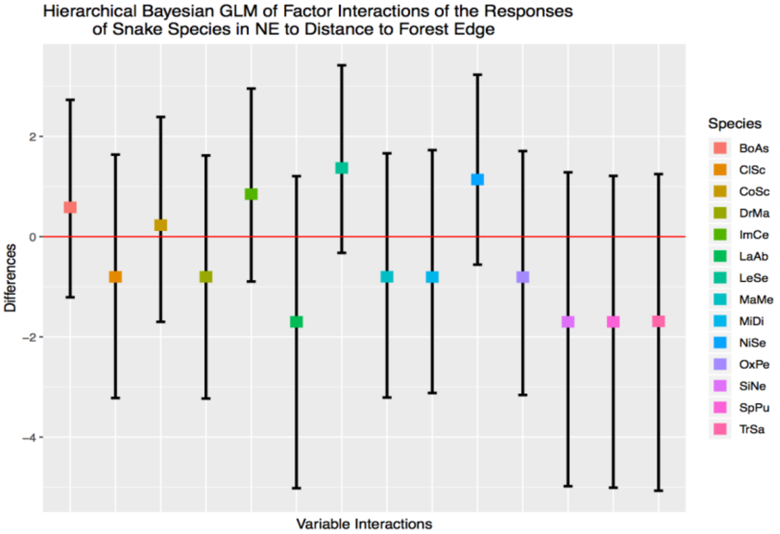

Figure 4.14: Caterpillar plots with credible intervals (CI) of Bayesian GLM model with a negative binomial distribution showing the effect of distance to forest edge on the snake assemblage composition in Laguna del Tigre National Park. Red line represents the zero line, those credible intervals that do not cross zero are not significant, those are below zero are negative responses, and those that are above zero are positive respsones. Species codes; AdQu = *Adelphicos quadrivigattus*, BoAs = *Bothrops asper*, BoIm = *Boa imperator*, ClSc = *Clelia scytalina*, CoBi = *Coniophanes bipunctatus*, CoIm = *Coniophanes imperialis*, CoSc = *Coniophanes schmidtii*, DrMa = *Drymobius margaritiferus*, ImCe = *Imantodoes cenchoa*, LaAb = *Lampropeltis abnorma*, LeSe = *Leptodiera septentrionalis*, LeAh = *Leptophis ahaetulla*, LeMex = *Leptophis mexicanus*, MaMe = *Mastigodryas melanonomus*, MiDi = *Micrurus diastema*, NiDi = *Ninia diademata*, NiSe = *Ninia sebae*, OxAe = *Oxybelis aeneus*, OxPe = *Oxyrhopus petolarius*, PlEl = *Pliocercus elapoides*, PsFl = *Psuedelaphe flavirufa*, SiDi = *Sibon dimidiata*, SiNe = *Sibon nebulata*, SpPu = *Spilotes pullatus*, TaMo = *Tantilla moesta*, TrSa = *Tropidodipsas sartorii*, XeRa = *Xenodon rabdocephalus*. Forest Habitat codes; AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

4.4.4 Lizard Assemblage

Dominance and persistence for the lizard assemblage are reported in Figures 4.15 and 4.16. The overall lizard assemblage of LTNP was dominated by three species that accounted for 61% of all encounters, *Coleonyx elegans* (23.2%), *Norops capito* (20.7%), and *Norops lemurinus* (17.1%). The lizard species were encountered in all four forest habitats, they were *C. elegans, N. capito*, and *N. undulata.* Cumulatively they accounted for 47% of total encounters in the lizard assemblage of LTNP. In the AE habitat four lizard species showed high levels of dominance and accounted for 92.9% of all encounters, the fifth species (*Holcosus undulata*) was represented by a single individual (7.1% of encounters). Although, the assemblage was dominated by two species (*N. capito* and *Corytophanes cristatus*) accounting for 64.3% of encounters. *Coleonyx elegans* and *N. capito* dominated the HF assemblage, accounting for 58.3% of all encounters in this habitat. Two lizard species,

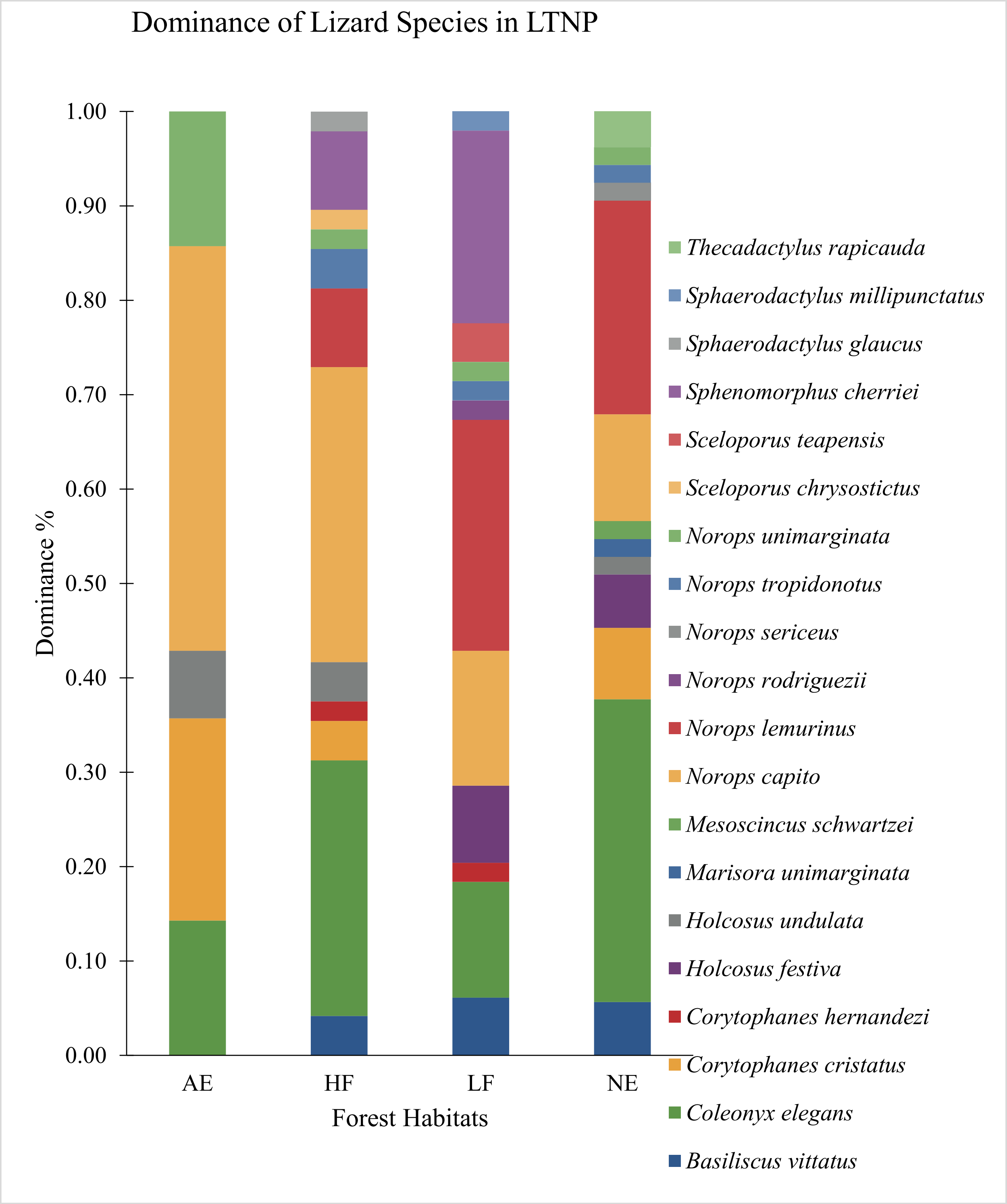

Figure 4.15: Dominance of lizard species in four forest habitats in Laguna del Tigre National Park, expressed as a percentage. AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

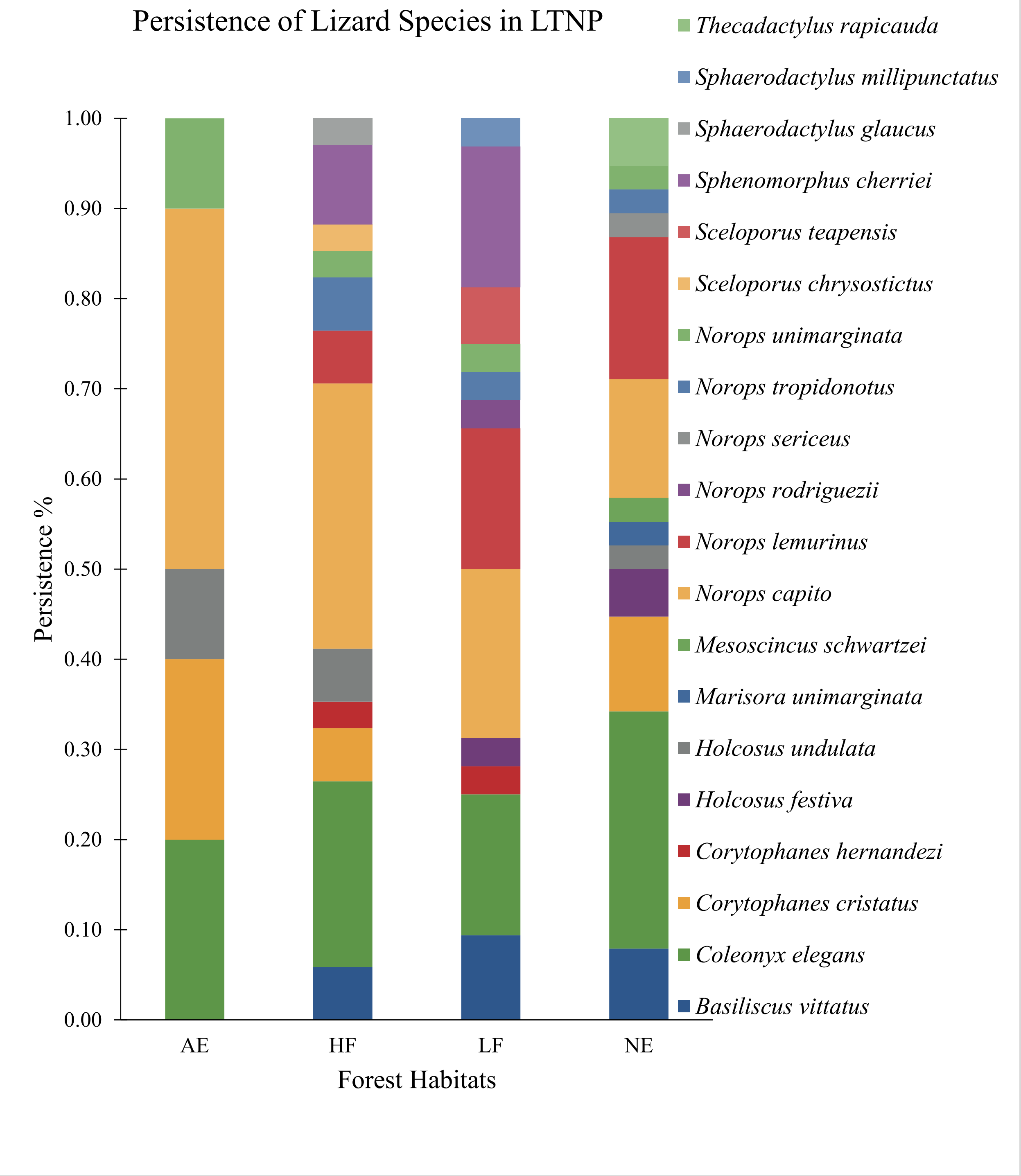

Figure 4.16: Persistence of lizard species in four forest habitats in Laguna del Tigre National Park, expressed as a percentage. AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

Table 4.7: Analysis of overall percentage dissimilarity of lizard assemblages found in four forest habitats in Laguna del Tigre National Park. AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

	AE	HF	LF	NE
AE		81.22	86.35	86.78
HF	81.22		80.04	84.31
LF	86.35	80.04		83.65
NE	86.78	84.31	83.65	

Sceloporus chrysostictus and *Sphaerodactylus glaucus,* were only encountered in HF and both were represented by a single individual. The LF assemblage was also dominated by two species (*N. lemurinus* and *Sphenomorphus cherriei*) that accounted for 45% of all encounters. Two species, *N. rodriguezii* and *Sphaerodactylus millipunctatus*, were only encountered in LF and were both encountered once. The assemblage in NE was dominated by three species (*C. elegans, N. capito*, and *N. lemurinus*) that accounted for 66% of all encounters. The lizard assemblage in NE contained four species - *Marisora unimarginata, Mesoscincus schwartzei, Norops sericeus,* and *Thecadactylus rapicauda* - that were not encountered in any other forest habitat. Persistence levels in the lizard assemblages were generally quite low, with the most persistent species being *N. capito* (20.0%, AE; 25.6%, HF; 15.4%, LF), and *C. elegans* (21.7%, NE). *N. capito* was also encountered in 10.9% of surveys in NE. SIMPER analyses of the lizard assemblages showed that the most dissimilarity occurred between AE and LF (86.35%), and AE and NE (86.78%). The lowest dissimilarity was found between the assemblages of HF and LF (80.04%) (Table 4.7). Two species, *C. elegans* and *N. capito*, were included in the top three contributions to dissimilarity between assemblages in all analyses. Three other species, *C. cristatus*, *N. lemurinus*, and *S. cherriei,* were also variously included in the top three contributions.

In both frequentist models most significant effect in the structure of the lizard assemblage was shown in LF forest habitat, with no significant effect of either Distance to Agriculture of Distance to Edge (Table 4.8). Inspection of R-squared values revealed that distance to agriculture accounted for more variance structure of the lizard assemblage than distance to forest edge. Step-down comparison identified LF, NE, and distance to agriculture, as the

Table 4.8: Multivariate frequentist GLM results showing the relationship between the lizard assemblage of LTNP and distance to agriculture and distance to forest edge. Res.Df = residual degrees of freedom; Df.diff = degrees of freedom difference; Dev = likelihood ratio test (LRT) result; Pr(>Dev) = probability the variable is greater than LRT AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

Distance to Agri Multivariate test	AIC -2.417065 : df -28.56128				**Distance to Edge Multivariate test**	AIC -2.413644 : df -28.56128			
	Res.Df	**Df. diff**	**Dev**	**Pr(>Dev)**		**Res.Df**	**Df. diff**	**Dev**	**Pr(>Dev)**
(Intercept)	143				(Intercept)	143			
Dist_to_Agri	142	1	11.41	0.818	Dist_to_Edge	142	1	14.34	0.521
AE	141	1	26.4	0.103	AE	141	1	21.004	0.153
HF	140	1	21.89	0.349	HF	140	1	19.608	0.215
LF	139	1	37.17	**0.001**	LF	139	1	27.268	**0.008**
NE	138	1	0	0.453	NE	138	1	-0.002	0.559
Dist_to_Agri:AE	137	1	8.99	**0.019**	Dist_to_Edge:AE	137	1	6.061	0.089
Dist_to_Agri:HF	136	1	7.92	**0.022**	Dist_to_Edge:HF	136	1	23.99	**0.001**
Dist_to_Agri:LF	135	1	0	0.272	Dist_to_Edge:LF	135	1	-0.001	0.99
Dist_to_Agri:NE	137	1	0	0.538	Dist_to_Edge:NE	137	1	0	0.105

variables with the greatest explanatory power (Table 4.9). Significant effects of agriculture were felt in AE and HF, and significant effects of edge were felt in HF. This suggests that forest habitat itself has more influence over the lizard assemblage than the presence of edge or agriculture.

Univariate outputs for the frequentist models revealed that only four lizard species showed significant responses to distance to agriculture (Figure 4.17). The abundances of *Corytophanes cristatus*, *Norops lemurinus*, and *Sphenomorphus cherriei* were negatively affected by distance to agriculture, whereas *Norops uniformis* responded positively in AE.

Table 4.9: Step-wise matrix of R-squared values retrieved from frequentist models showing the three predictor variables (in bold) that explain the most variance in the lizard assemblage of LTNP.

	Step 1	**Step 2**	**Step 3**
Distance to Edge	0.00282116	0.01288454	0.01879399
Distance to Agriculture	0.003019542	0.0161886	**0.02360353**
AE	0.004540283	0.01355914	0.02056304
HF	0.005828031	0.01568181	0.02056304
LF	**0.009818053**	NA	NA
NE	0.007706563	**0.01699133**	NA

The abundances of three lizard species showed a significant negative response to distance to forest edge, *C. cristatus* and *Holcosus festiva* in AE, and *N. uniformis* in HF, and the abundance five species showed a positive response in forest habitats with greater distance to agriculture, *Coleonyx elegans, N. lemurinus,* and *Norops tropidonotus* in HF, and *H. festiva* and *Norops sericeus* in NE (Figure 4.18).

Bayesian analysis showed that for most lizard species there is no effect on the assemblage from either distance to agriculture or forest edge. However, *C. elegans* showed a positive response to distance to agriculture in HF, LF, and NE forest habitats. *N. capito* showed a positive response to distance to agriculture in HF and LF, and both *N. lemurinus* and *S. cherriei* showed a positive response to distance from agriculture in LF. Bayesian GLMs showed that several species present in three habitats (HF, LF, and NE) exhibited significant positive responses to the presence of agriculture (Figure 4.19). *Coleonyx elegans* responded positively in all three of those habitats. *Norops capito* responded positively in both HF and LF, and *N. lemurinus* and *S. cherriei* responded positively in LF. Of the absent species, five in AE and four in NE showed significant, or near significant, negative responses to the presence of agriculture (Appendix I.17 and I.20).

No species in HF or LF showed negative responses to agriculture (Appendix I.18 and I.19). The models also showed that no species of lizard present in the assemblage of a forest habitat was affected by the presence of a forest edge (Appendix I.21 to I.24). However, there were eight species absent from both HF and LF habitats the showed significant, or near significant, negative responses to the presence of forest edge. Significant, or near significant, negative responses to the presence of forest were also seen in seven species absent from NE, and

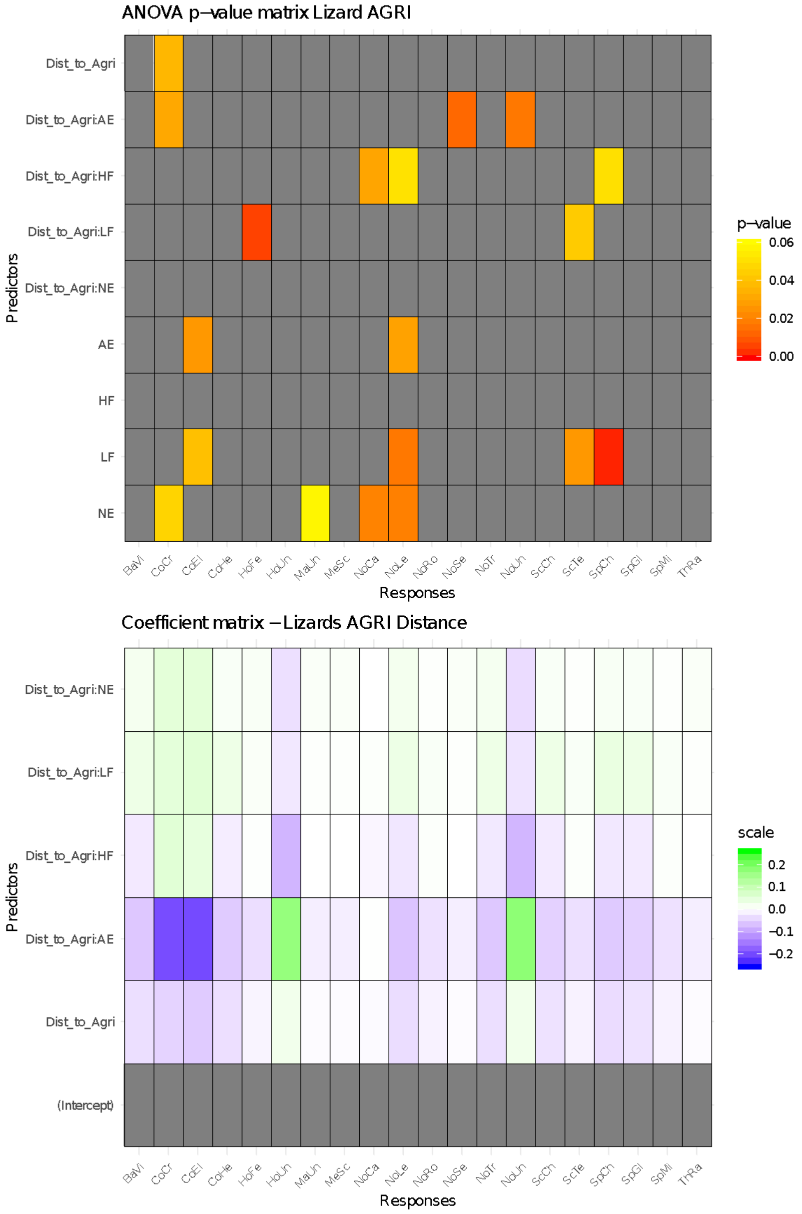

Figure 4.17: Univariate GLM heat matrices showing significant effects of distance to agriculture on the lizard assemblage of LTNP. Significant p-values are shown above (yellow to red shows increasing significance) which matched to the coefficient matrix sown below indicate significant positive (green) and negative (blue) responses of amphibian species to the presence of agriculture. The coefficient matrix shows species responses to interactions between distance to agriculture and how that is expressed in different forest habitats. Species codes; BaVi = *Basiliscus vittatus*, CoCr = *Corytophanes cristatus*, CoHe = *Corytophanes hernandezii*, HoFe = *Holcosus festiva*, HoUn = H*olcosus undulata*, MaUn = Marisora unimarginata*,* MeSc = *Mesoscincus schwartzei*, NoCa = *Norops capito*, NoLe = *Norops lemurinus*, NoRo = *Norops rodriguezii*, NoSe = *Norops sericeus*, NoTr = *Norops tropidonotus*, NoUn = *Norops uniformis*, ScCh = *Sceloporus chrysostictus*, ScTe = *Sceloporus teapensis*, SpCh = *Sphenomorphus cherriei*, SpGl = *Sphaerodactylus glaucus*, SpMi = *Sphaerodactylus millepunctatus*, ThRa = *Thecadactylus rapicauda*. Forest Habitat codes; AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

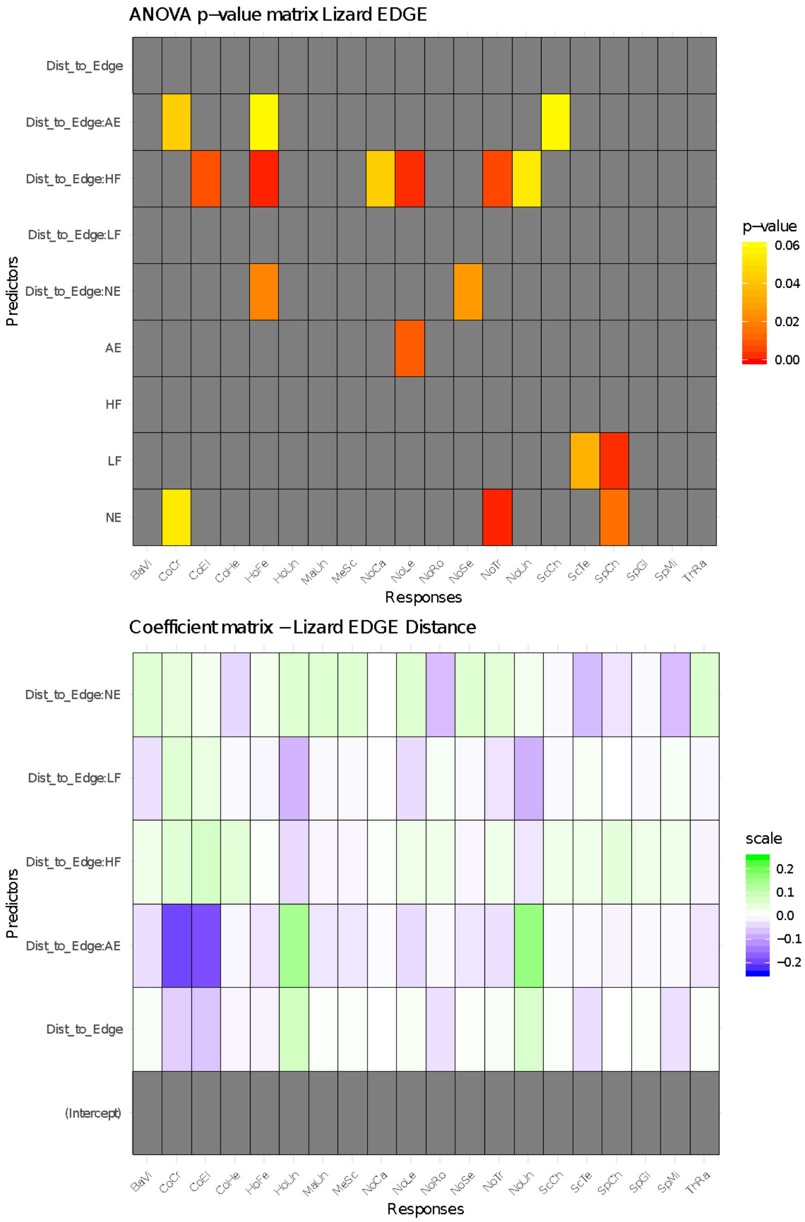

Figure 4.18: Univariate GLM heat matrices showing significant effects of distance to agriculture on the lizard assemblage of LTNP. Significant p-values are shown above (yellow to red shows increasing significance) which matched to the coefficient matrices indicate significant positive (green) and negative (blue) responses of amphibian species to the presence of agriculture. Coefficient matrix on this page shows species responses to interactions between distance to forest edge and how that is expressed in different forest habitats. Coefficient matrix on the following page shows species responses to the different forest habitats themselves Species codes; BaVi = *Basiliscus vittatus*, CoCr = *Corytophanes cristatus*, CoHe = *Corytophanes hernandezii*, HoFe = *Holcosus festiva*, HoUn = H*olcosus undulata*, MaUn = Marisora unimarginata*,* MeSc = *Mesoscincus schwartzei*, NoCa = *Norops capito*, NoLe = *Norops lemurinus*, NoRo = *Norops rodriguezii*, NoSe = *Norops sericeus*, NoTr = *Norops tropidonotus*, NoUn = *Norops uniformis*, ScCh = *Sceloporus chrysostictus*, ScTe = *Sceloporus teapensis*, SpCh = *Sphenomorphus cherriei*, SpGl = *Sphaerodactylus glaucus*, SpMi = *Sphaerodactylus millepunctatus*, ThRa = *Thecadactylus rapicauda*. Forest Habitat codes; AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge. Contiued on next page.

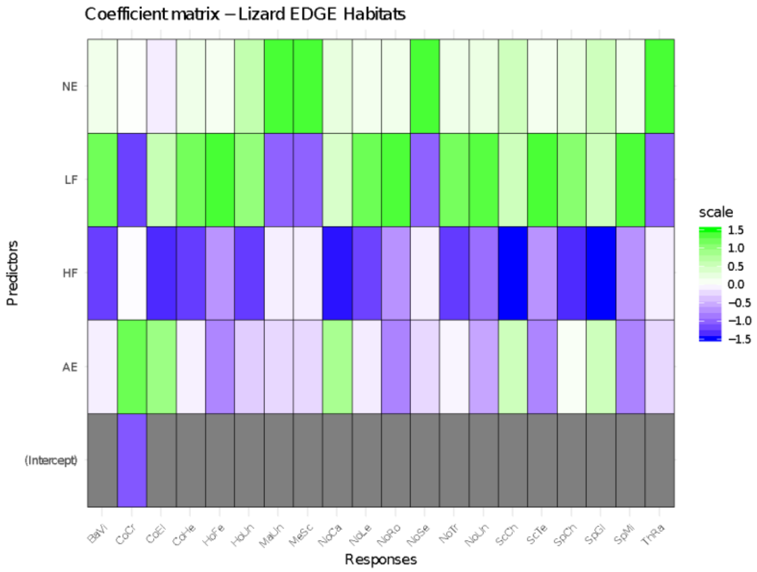

Figure 4.18 continued.

species from AE. Although lizard diversity is lowest at the agricultural edge and the assemblage in that forest habitat type exhibits high dominance effects, habitat type plays a more significant role in the lizard assemblage structure than does either distance to forest edge or distance to agricultural edge.

4.5 Discussion

This study showed that presence of both agriculture and forest edges influence the composition of amphibian and reptile assemblages in LTNP. That influence has the possibility to affect not only the species composition but also assemblage structure in terms of species abundances relative to one another. Elucidating patterns in the response of a species assemblage at the landscape scale is an important tool in understanding the effects of habitat modification (Fischer and Lindenmeyer 2007). This study shows that a multi-framework approach can also highlight the intricacies of that response by individual species within a given assemblage, and that compared to using either a species or pattern-oriented

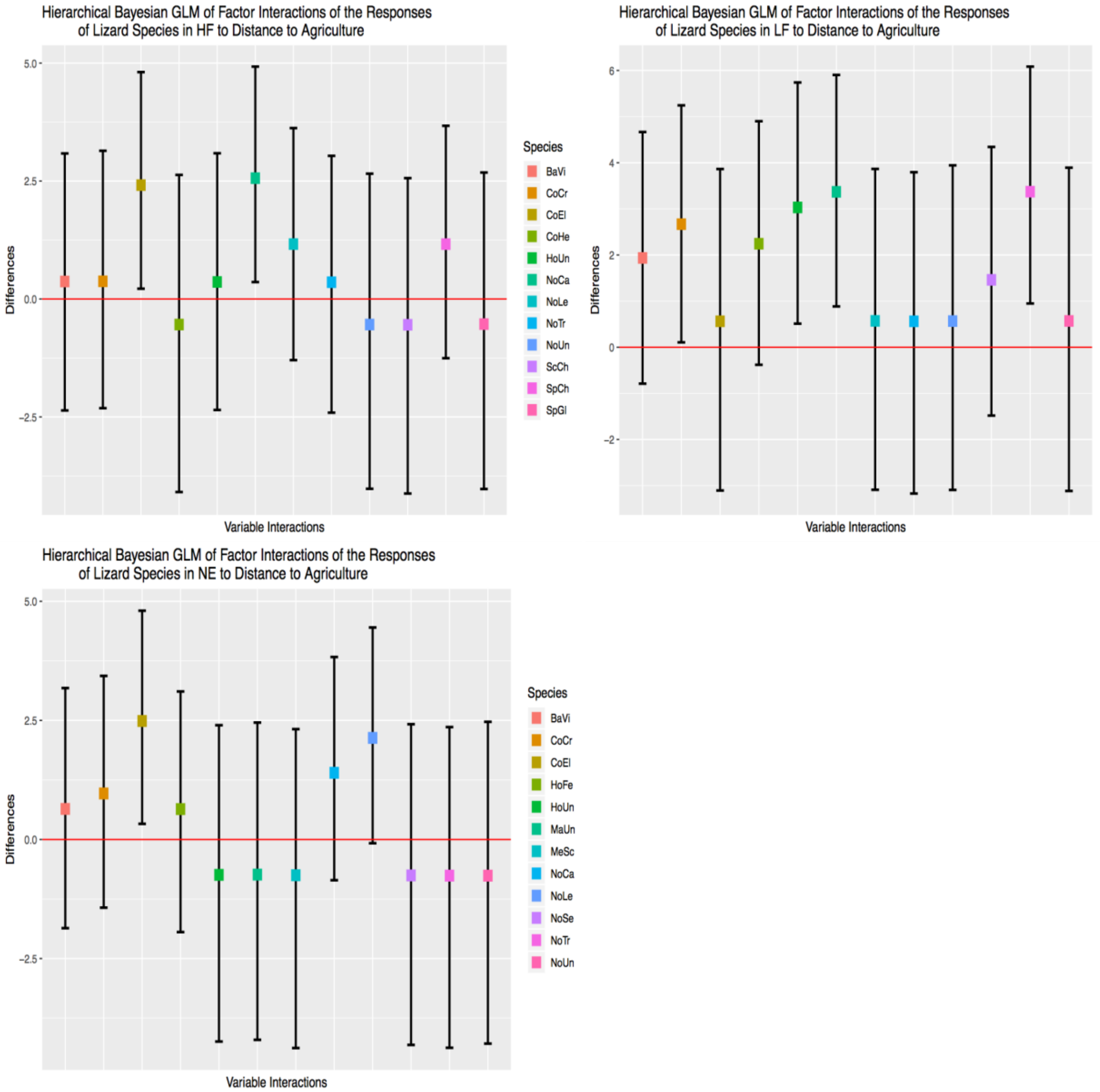

Figure 4.19: Caterpillar plots with credible intervals (CI) of Bayesian GLM model with a negative binomial distribution showing the effect of distance to agriculture on the lizard assemblage composition in Laguna del Tigre National Park . Red line represents the zero line, those credible intervals that do not cross zero are not significant, those are below zero are negative responses, and those that are above zero are positive respsones. Species codes; BaVi = *Basiliscus vittatus*, CoCr = *Corytophanes cristatus*, CoHe = *Corytophanes hernandezii*, HoFe = *Holcosus festiva*, HoUn = *Holcosus undulata*, MaUn = *Marisora unimarginata,* MeSc = *Mesoscincus schwartzei*, NoCa = *Norops capito*, NoLe = *Norops lemurinus*, NoRo = *Norops rodriguezii*, NoSe = *Norops sericeus*, NoTr = *Norops tropidonotus*, NoUn = *Norops uniformis*, ScCh = *Sceloporus chrysostictus*, ScTe = *Sceloporus teapensis*, SpCh = *Sphenomorphus cherriei*, SpGl = *Sphaerodactylus glaucus*, SpMi = *Sphaerodactylus millepunctatus*, ThRa = *Thecadactylus rapicauda*. Forest Habitat codes; AE = Agricultural Edge, HF = High Forest, LF = Low Forest, NE = Natural Edge.

approaches in isolation to each other, it can give a higher resolution of detail into the response of that assemblage to increasing habitat modification and fragmentation.

Analysis of the dominance and persistence of species within the four forest habitats showed that the highest effects were observed in the disturbed AE habitat. This was consistent across the whole amphibian and reptile assemblage and manifested in one or two species dominating the species assemblage in AE. The effects were not as pronounced in the snake assemblage as species diversity was higher than for amphibians and lizards in AE. The results of SIMPER analysis did not show a consistent pattern across the assemblages of amphibians, snakes, and lizards. For example, the highest dissimilarity between forest habitats in the amphibian assemblage was found in NE, this is probably due to the number of ephemeral pools in this habitat that are suitable for amphibian breeding activity. In the snake assemblage there was a clear association for LF, as this forest habitat consistently showed the highest percentage dissimilarity when compared to the other three forest habitats. In the lizard assemblage, the presence of an edge (both agricultural and natural) seems to have the most pronounced effect on the dissimilarity seen between forest habitats. There are, however, confounding issues regarding mean-variance within SIMPER analysis that can lead to a bias towards those taxa with the highest variances, as such these results may in fact by indicative of variance within an assemblage of a particular forest habitat, rather than variance between forest habitats (Warton et al. 2012).

This study is consistent with previous studies that have reported differing responses to fragmentation and habitat modification in reptiles and amphibians (Gibbons et al. 2000; Bell and Donnelly 2006; Gardner et al. 2007; Watling and Donnelly 2007). A complementary frequentist and Bayesian modelling approach was used to elucidate how individual species with the amphibian and reptile assemblages respond to both distance to agriculture and distance to forest edge. Frequentist models show that most variation in amphibian and snake assemblages is explained by forest edge, whereas in lizards most variation is explained by agriculture. However, the effect on the abundances of individual species is a more complex. Overall, Bayesian models yielded more significant results than did the frequentist models. Bayesian models showed that in all four forest habitats, the same amphibian species responded negatively to both distance to agriculture and distance to nearest forest edge, which suggests that 'edge' of any kind is the driving factor on the presence and abundance of species within the amphibian assemblages of LTNP. This is corroborated by the frequentist results that show more amphibian species responded to distance to forest edge than to distance to agriculture. This result is mirrored in the lizard assemblage of LTNP, where 45% of species showed a negative response to the presence of agriculture compared to 75% that responded negatively to the presence of a forest edge. However, both frequentist and Bayesian models suggested that the snake assemblage of LTNP is heavily impacted by the presence of agriculture, more so than the amphibian and lizard assemblages. While species present in a forest habitat show no response to the presence of agriculture and seemingly tolerate the disturbance, those snake species that are absent from a forest habitat are so in response to the presence of agriculture. The strength of that response decreases with increasing distance from the agricultural edge. Additionally, the distance to forest edge model for snakes suggests that the AE snake assemblage, which is the closest habitat to a forest edge, is the most heavily impacted by the presence of a forest edge.

Studies in the nearby Mexican Biosphere Reserve of Montes Azules (MABR) show that assemblage evenness increases as the successional state of the forest increases. Although some species common to both locations responded differently: e.g. in MABR, *Norops uniformis* is dominant in older forests, whereas in LTNP it is associated with disturbed edge habitat (Hernandez-Ordoñez et al. 2015). The study found that species richness and diversity recovered faster than species composition and concluded that the amphibian and reptile assemblages of MABR are severely affected by land-use practices in secondary forest habitats (Hernandez-Ordoñez et al. 2015). Whilst the amphibian and reptile assemblages of LTNP are all negatively affected by the presence of agriculture, the amphibian and snake assemblages are affected most by the presence of a forest edge, suggesting that fragmentation plays a more significant role. The differing responses of amphibian, snake, and lizard assemblages to change in land-use in LTNP highlight the need to carefully consider how data are organised for analysis. The traditional split into amphibians and reptiles seen in many studies may hide more intricate relationships between taxa and predictor variables

(Gardner et al. 2007; Watling and Donnelly 2007; Hernandez-Ordoñez et al. 2015; Schneider-Maunoury et al. 2016).

The negative effects of habitat modification and fragmentation on multiple taxa are well documented throughout the tropics (Ghose et al. 2017; Storck-Tonon and Peres 2017; Akani et al. 2018; Deere et al. 2020). This study shows that increasing habitat modification and fragmentation will have an increasingly negative effect on the amphibian and reptile assemblage of LTNP. While forest edge seems to have a more significant impact on the assemblage than the presence of agriculture, agricultural impact was observed up to 7 km into the forest of LTNP. This is a huge increase in the distance at which effects of fragmentation can be felt by amphibian and reptile assemblages, which in some cases been estimated at extending to just 250 m (Schneider-Maunoury et al. 2016). In LTNP the presence of forest edge, a proxy for fragmentation, has a greater influence on the amphibian and reptile assemblage than the presence of agriculture, which can lead to an assemblage of only a few species that is dominated by one or two of those species. Fragmentation, leading to increased edge, pushes Neotropical forests towards a prolonged and stable early successional state with lower structural diversity (Tabarelli et al. 2008). Species diversity and assemblage composition of herpetofauna communities has been shown to be influenced more by changes in habitat structure then by anthropogenic presence (Gillespie et al. 2015). It is important to note however, that the assemblage response on a species level can be highly variable, and traditional multivariate approaches may miss the subtleties of species interactions within the assemblage.

This study highlights the effects of change in land use and habitat fragmentation on Neotropical amphibian and reptile assemblages and shows that a combined pattern and species-oriented approach can be adopted from the same modelling techniques in order to identify the differences and intricacies of assemblage and species-specific responses to landscape modification.

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Chapter 5 - Relationships between life history traits and distribution of the amphibian and reptile assemblage in Laguna Del Tigre National Park.

Yucatán banded gecko – *Coleonyx elegans*

5.1 Abstract

Habitat alteration can lead to a few ‘winning’ species outcompeting many ‘losing’ species, an affect commonly termed as ‘Winner-Loser-Replacements’ or WLRs. This can lead to homogenisation of species assemblages at genetic, taxonomic, and functional levels. However, these studies have only analyzed the response of species to the study’s chosen predictors. This chapter uses fourth corner modelling techniques to investigate the interaction between the ecological data and trait information. Five guilds of amphibians, 12 of snakes, and 7 of lizards were identified. Overall, this study identified a greater diversity of ecological traits in Forest and Edge habitats compared to the Disturbed habitat at the edge of the forest close to agricultural land. Amphibian species that have significant or near significant associations with Bare Ground and / or Leaf Litter in one or more forest habitats are more likely to be found in Disturbed habitat where the vegetation is less dense in the other two habitat types. In amphibians and snakes the association with bare ground is what allows a species to win in the disturbed habitat. Continued forest fragmentation in LTNP and the wider Mayan Biosphere Reserve will result in increased edge effects, a greater proportion of remaining forest kept in an early successional state, and with a highly reduced, and homogenized, amphibian and reptile assemblage of Northern Guatemala.

5.2 Introduction

Habitat alteration is one of the most widespread causes of biodiversity loss, directly affecting the species occurring in the altered habitat, as well as indirectly affecting species in neighbouring intact habitat (Laurance 2008). The loss of habitat resulting from a change in land use often creates unnatural forest edges. In tropical forests, the floral assemblage of so-called edge habitat is often kept in an early successional state, with a highly altered habitat structure and reduced diversity of species, trait diversity, and ecosystem functions (Taberelli and Lopes 2008; Pütz et al. 2011). This reduction in diversity is often driven by increases of native pioneer generalist species rather than by invasion of non-natives through Winner-Loser Replacements, or WLRs, where so called ‘losing’ species are replaced by ‘winning’ species (Tabarelli et al. 2012). Losing species tend to exhibit traits such large size, low fecundity, limited geographical ranges and specialized ecology, combined with low dispersal rates, and poor adaption to human disturbance. Conversely, winning species tend to be widespread generalists with high fecundity and rapid dispersal rates that are well adapted to human disturbance (Tabarelli et al. 2012). Over 50% of all species could be considered to be losers that are adversely affected by human activity compared to estimates 5 to 29% of native species considered to be winners with either stable or expanding ranges (McKinney and Lockwood 1999). A further 1-2% of species could be considered non-native invasive winners. Therefore, there is an overall effect of replacing many losing species with a few winning species. This leads to assemblage homogenization of genetic, taxonomic, and functional levels at both local and global scales (McKinney and Lockwood 1999; Olden et al. 2004; Newbold et al. 2008).

Global meta-analyses indicate that homogenization is occurring globally and across taxonomic groups (McKinney and Lockwood 1999; Newbold et al. 2008). Studies have shown, however, that the process is currently more pronounced in the tropics (Newbold et al. 2008). This is thought to be due to: a) distributional ranges that are smaller than the global average; b) a higher degree of ecological specialization; and c) that temperate zones have already experienced the large-scale homogenization that the tropics are currently experiencing (Newbold et al. 2008). The homogenizing effect of WLRs has been recorded in invertebrates (Oliveira et al. 2016; Mangels et al. 2017; Filgueiras et al. 2019), anurans (Cunha Bitar et al. 2015), birds (Villegas Vallejos et al. 2016), mammals (Palmeirim et al. 2020), and plants (Tabarelli et al. 2012; Leal et al. 2015). However, these studies have only analyzed the response of species to the study’s chosen predictors. This is due in part to the fact that until recently, modelling and ordination techniques were limited to analyzing and predicting the response of abundance - or presence/absence - data to some form of observed data (Ter Braak 1986). In ecology it is well known that species often respond to the interactions between two or more variables (Brown et al. 2014). The interaction between ecological and trait data is termed as the fourth corner (Brown et al. 2014). The advent of fourth corner modelling techniques allow the modelling of abundance data as a response to observed ecological data and recorded trait data, as well as abundance as a function of the interaction between ecological and trait data. Recently, it has been recognized that not only is trait data essential for informing the conservation of species, but also that there is a paucity of trait data available for amphibians and reptiles (Etard et al. 2020

Populations of amphibians and reptiles are in global decline and are considered among the most threatened vertebrate taxa (Gibbons et al. 2000; Collins and Storfer 2003). Understanding the dynamics of amphibian and reptile declines is hampered as many species undergo natural fluctuations in populations that often require long-term data collected over decades to identify (Pechmann et al. 1991; Alford and Richards 1999; Whitfield et al. 2007). The diversity of amphibian and reptile species is highest in the tropics, as are the level of threats to their populations and habitats (Vitt and Caldwell 2014; Newbold et al. 2018). Several studies have identified WLRs in tropical amphibian and reptile assemblages in response to anthropogenic pressures (Gallmetzer and Schulze 2015; Hirschfeld et al. 2017; Nowakowski el al. 2018). This study extends on these previous studies by utilizing fourth corner modelling techniques to identify WLRs between amphibian and reptile species, the environment, and their traits. This is first time this approach as been used in a full amphibian and reptile assemblage.

The objectives of this study were to: a) identify which natural history traits were significant in enabling amphibian and reptile species to live in disturbed habitat; and b) identify relationships between observed behaviour in amphibians and reptiles, their natural history traits, and microhabitat selection.

5.3 Methods

5.3.1 Study Site

Estación Biológica Las Guacamayas (EBG) is located in the south-east of Laguna del Tigre National Park (LTNP) on the banks of the Rio San Pedro (Figure 5.1). The Tropical Moist Forest (Holdridge 1967) of EBG consists of several habitat types including both primary and secondary forest, saw-grass swamp and thorn scrub. It is bordered to the east by concessional agricultural lands that belong to the nearby Quecchi Maya community of Paso Caballos.

5.3.2 Field Methods

In each of the four habitats, 100 m transects were conducted both along existing trail systems and on transects cut sensitively into the forest away from the trails. Transects were placed to allow a representative sample of each habitat and promote heterogeneous sampling across microhabitats for efficient detection of herpetofauna (Crump 1994; Doan 2003; Marsh and Haywood 2010). The start points for each transect (Figure 5.2) were chosen to allow for any edge effects to be taken into account that may have risked biasing detection (Schlaepfer and Gavin 2001; Urbina-Cardona et al. 2006). Transects were marked every 25 m with flagging tape to indicate the path of the transect, and GPS waypoints were taken at the start and finish points using a handheld GPS device (Garmin™ GPSMap 62s) to facilitate accurate survey replication. After setup, transects were left for a minimum of two days before surveying commenced to allow for animals to resume normal activity prior to survey (Crump 1994). All transects had negligible changes in altitude and were positioned to avoid passing through broad habitat types in order to satisfy assignment of habitat categorization (Babbitt et al. 2009). Surveys took approximately 45 minutes to one hour to complete and

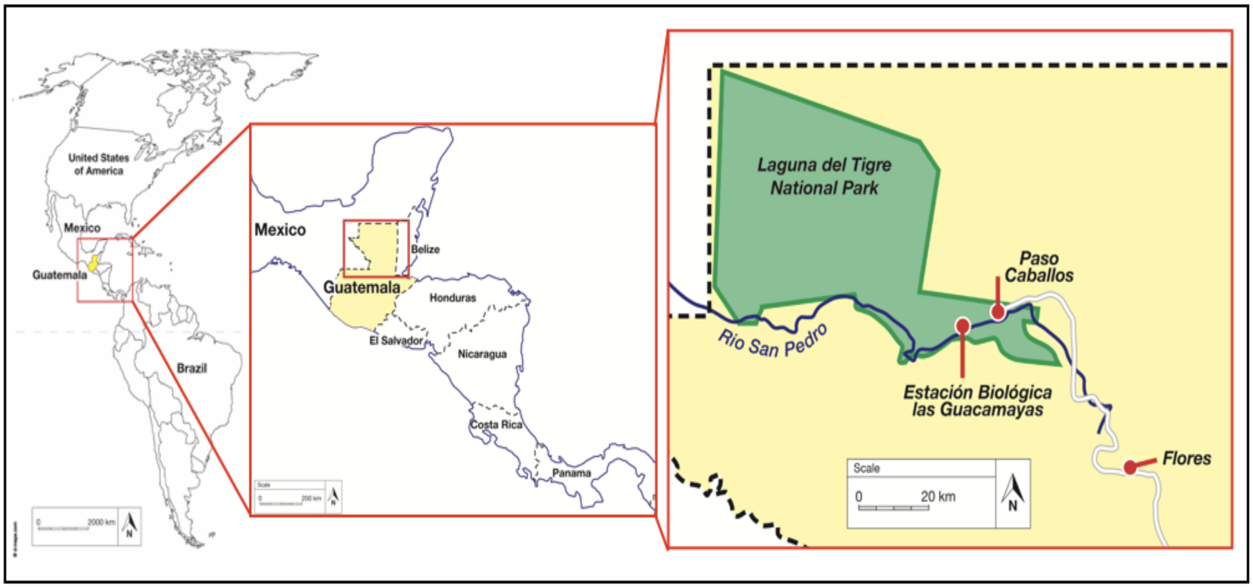


Figure 5.1: Map of the Americas, showing the location of Laguna del Tigre National Park within Guatemala. Red box indicates area shown in Figure 2. Due to the curvature of the map the scale shown is representative of the scale at the equator. Map adapted from D-Maps.com

followed standardized protocols for Visual Encounter Surveys in tropical habitats (Rödel and Ernst 2004; Vonesh et al. 2009).

To maximize chances of detecting species with different autecology, each transect was surveyed three times, twice at night and once in the morning during each survey period (Heyer et al. 1994; McDiarmid et al. 2012). For the purposes of statistical analyses nocturnal and diurnal surveys were pooled. A minimum of two days was left between surveys of the same transect to maintain independence of sample survey periods. Surveys were conducted during seven fieldwork periods in May-June 2013, November-December 2013, June 2014, October 2014, June 2015, December 2015 and June-July 2016. A total of 120 transects were surveyed, comprising 18 in Disturbed habitat (MH1), 66 in Forest habitat (MH2), and 36 in

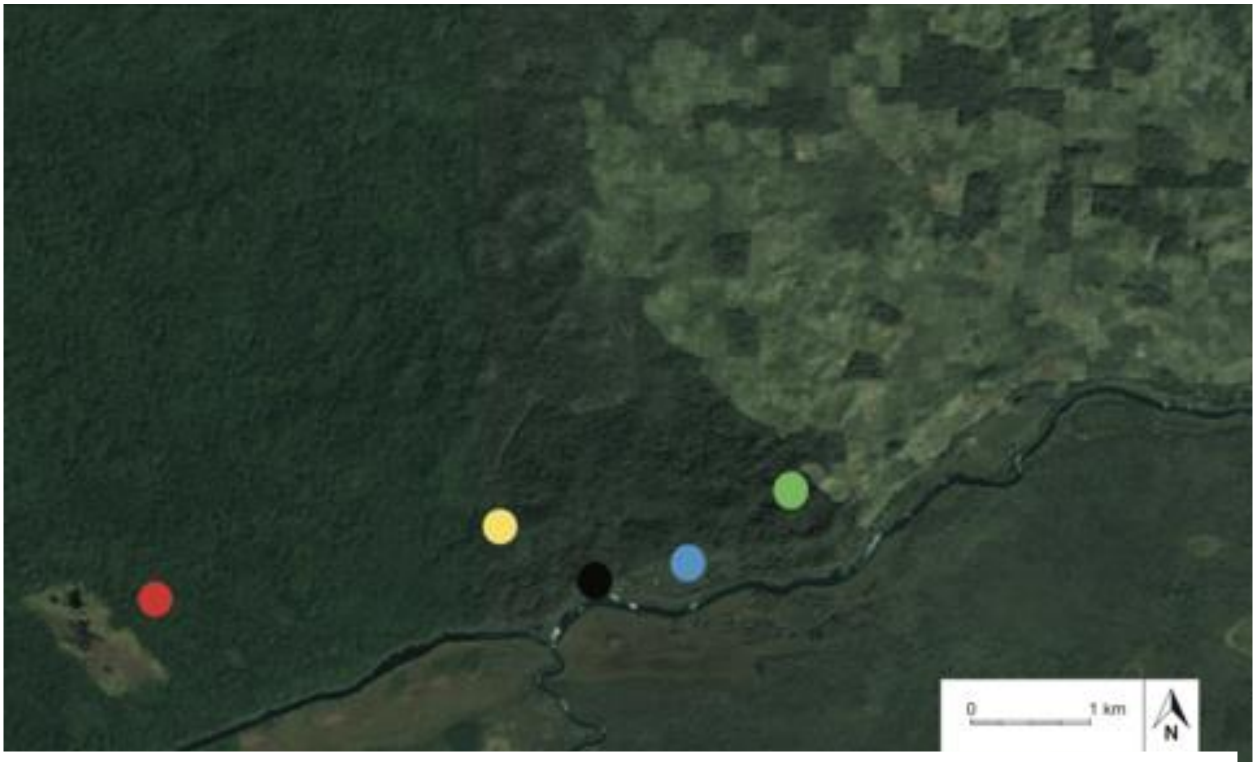


Figure 5.2: Satellite image of the south-east region of Laguna del Tigre National Park showing the location of survey sites indicated by coloured dots: Green = Disturbed Habitat MH1; Yellow and Red = Forest Habitat MH2; Blue = Edge Habitat MH3; Black = Estación Biológica Las Guacamayas. The two rivers are the San Pedro River flowing east to west, and the Sacluc River flowing south to north. North of the San Pedro dark green areas indicate forest areas, lighter green indicates the concessional agricultural land of Paso Caballos. South of the San Pedro, green indicates a mixture of saw grass swamp (sabinal) and seasonally flooded thorn scrub. Image adapted from Google Maps™.

Edge habitat (MH3) respectively. The order in which the three forest habitats were surveyed was randomized, as was the order of transects within each habitat. On some occasions, fieldwork was hampered by inclement weather and surveys had to be abandoned and were removed from the dataset prior to analyses.

5.3.3 Data Collection

Upon location of an amphibian or reptile the following data were recorded: time encountered (24 hr), location (recorded using a Garmin GPSmap 62s), species, microhabitat (aquatic, aquatic margin, bare ground, leaf litter, leaf, tree limb, and tree trunk), behaviour at time of first observation (active, ambush, amplexus [amphibians only], calling [amphibians only], feeding, and resting). If safe and practical to do so, individuals were captured to confirm identification when needed; if a positive species identification was not possible the individual was excluded from the dataset. Natural history traits were also recorded from the literature (Lee 1996) and included: diel activity patterns (diurnal, nocturnal, nocturnal/diurnal, and in the case of diurnal lizards, shade loving or heliophilic), prey preference, and mass categorized into ranges appropriate for each taxa.

Visual encounter surveys are a regularly used method for surveying amphibians and reptiles (Crump and Scott 1994; Lovich et al. 2012). Survey teams consisted of between two and eight

people, and included one local guide, the author and two to six field assistants. At the start of each field session, all guides and field assistants were trained in survey techniques, data collection, and species identification by the author. All biometric and environmental data

collection was overseen by the author to avoid observer bias. Transects were walked at a suitably slow pace to allow detection of reptiles and amphibians by thorough examination of vegetation and refugia, such as leaf litter, fallen limbs and rocks (Crump and Scott 1994; Lovich et al. 2012). The search area was defined as up to one metre each side of the transect and up to two metres high (Crump and Scott 1994; Lovich et al. 2012). Any individual found outside of this area was recorded as a casual observation but omitted from this study.

Table 5.1: Categories used for variables in the Environmental Matrix for GLLVM models of the amphibian, snake, and lizard assemblages of LTNP.

	Models Categories		
Environmental Variable	**Amphibians**	**Snakes**	**Lizards**
Microhabitat	Aquatic	Aquatic	Bare Ground
	Bare Ground	Bare Ground	Leaf Litter
	Leaf Litter	Leaf Litter	Tree Limb
	Tree Limb	Logs	Tree Trunk
	Tree Trunk	Tree Limb	
		Tree Trunk	
Activity	Active	Active	Active
	Ambush	Ambush	Ambush
	Amplexus	Feeding	Basking
	Calling	Resting	Resting
	Feeding		
	Resting		

5.3.4 Statistical Analysis

Guilds for the amphibian and reptile assemblages were assigned following Duellman (2005) as appropriate and based on diel activity, microhabitat preferences, and diet. The data used to form the guilds were derived from a combination of field observations and information contained in Lee (1996).

Generalised Linear Latent Variable Modelling (GLLVM) was performed in the package gllvm (Niku et al. 2019a) to model relationships between factors affecting the amphibian and reptile assemblage of LTNP, and to contrast responses of different species to forest habitat selection and natural history traits. GLLVM extend basic generalized linear models on multivariate data using a factor analytic approach by incorporating latent variables to combine values with factor loadings that model correlation between responses. These latent variables have a natural interpretation as ordination axes and can predict new values, control for known variables, and assist model selection (Hui et al. 2015; 2017). When initial environmental predictors of interest are combined with morphology and natural history information a third matrix can be bound to predictors to illicit a trait covariate model, also

Table 5.2: Categories used for variables in the Trait Matrix for GLLVM models of the amphibian, snake, and lizard assemblages of LTNP.

	Models		
Trait Variable	**Amphibians**	**Snakes**	**Lizards**
Diel Activity	Nocturnal	Nocturnal	Diurnal Shade loving
	Diurnal and Nocturnal	Diurnal and Nocturnal	Diurnal Sun loving
		Diurnal	Nocturnal
Prey Preference	Ants	Amphibians	Arachnids
	Insects	Birds	Insects
	Fish	Earthworms	Larval Insects
	Frogs	Mammals	Small Insects
	Mammals	Snakes	Frogs
	Termites	Lizards	Fruit
		Snails	Lizards
		Fish	
		Reptile Eggs	
Mass	<2g	<5g	<2g
	2-9.9g	11-25g	2-5g
	10-29.9g	26-50g	10-20g
	30-100g	101-300g	21-50g
		301-1000g	51-100g
		1001-2000g	>100g
		>2000g	
Foraging Mode	Sit and Wait	Active	Active
		Sit and Wait	Sit and Wait
Prey Consumption		Constrictor	
		Grab and Swallow	
		Venom	

known as a fourth corner model (Brown et al. 2014, Warton et al. 2015). Models were performed for amphibians, snakes, and lizard assemblages separately.

Each model consisted of three matrices: a) Abundance Matrix (the response variable) - the abundances of each species encountered in each of the three forest habitat categories; b) Environment Matrix (the predictor variable) - the frequency a given microhabitat was used, and the frequency a given behaviour was observed (Table 5.1); and c) Trait Matrix (the fourth corner) - natural history traits for each species encountered based on a combination of observed traits and traits recorded in the literature (Lee 1996), variables used were diel activity, foraging mode (except in amphibians where all species encountered were classed as sit and wait predators), prey consumption (snakes only), prey preferences, and mass (Table 5.2).

The GLLVM regressed the mean species abundances against a matrix of predictor factors such as microhabitat selection and observed behaviours as variables. The response (Abundance) and predictor (Environment) matrices were then coupled to a third trait covariate (natural history traits) matrix to create a full fourth corner model.

Models were fitted to negative binomial and Poisson family distributions and applied to variation approximation method (Hui et al. 2017). Package gllvm deploys factor analysis on Dunn-Smyth residuals to obtain starting values for the latent variable that are close to an anticipated solution. Dunn-Smyth residuals fits and Q-Q plots were used to inspect model fit. In all cases residual fits and Q-Q plots were more robust for Poisson distributed models, and so only those are presented here. The ideal number of latent variables was investigated using BIC scores. GLLVM fit can be sensitive to the choice of initial latent variable values as they are unobserved. This limitation was overcome by integrating the latent variable values and maximising approximation to the log-likelihood. For each taxon, the two models were run multiple times with a best of five run routines and selected out the highest log-likelihood value for different distribution families (Niku et al. 2019b). Latent variables induce correlation across response variables and provide estimation of correlation patterns, and the extent to which these are explained by variables, with the aim of achieving the lowest correlation in a model, and therefore identify the most influential predictors in the model. The getResidualCor function was used within gllvm to estimate correlation of the linear predictors across amphibian and reptile presence and was visualized using package corrplot (Wei and Simco 2017). The getResidualCor function in gllvm was utilised to quantify (co)variation by individual predictor factors (natural history traits). The estimated coefficients for predictors, and their confidence intervals, were plotted using the coefplot function in gllvm to reveal the nature of the predictor factors relating to each species. Coefficients for the natural history traits (the fourth corner) were extracted from the model

Table 5.3: Amphibian guilds in Laguna del Tigre National Park, Guatemala.

Guild Number	Guild Description	Species	Family
1	Nocturnal Terrestrial Ants/termites	*Gastrophryne elegans*	Microhylidae
		Hypopachus variolosus	Microhylidae
		Rhinophrynus dorsalis	Rhynophrynidae
2	Nocturnal Terrestrial other insects	*Eleutherodactylus leprus*	Eleutherodactylidae
		Engystomops pustulosus	Leiuperidae
		Incilius valliceps	Bufonidae
		Leptodactylus fragilis	Leptodactylidae
		Leptodactylus melanonotus	Leptodacylidae
3	Nocturnal Terrestrial insects/vertebrates	*Rhinella marina*	Bufonidae
4	Nocturnal aquatic insects/vertebrates	*Rana brownorum*	Ranidae
		Rana vailantii	Ranidae
5	Nocturnal arboreal insects	*Bolitoglossa mexicanus*	Plethodontidae
		Agalychnis callidryas	Hylidae
		Dendropsophus microcephalus	Hylidae
		Scinax staufferi	Hylidae
		Smilisca baudinii	Hylidae
		Tlalocohyla loquax	Hylidae
		Tlalocohyla picta	Hylidae
		Trachycephalus typhonius	Hylidae

and plotted using package lattice (Sarkar 2020) to visualize the relationship of observed behaviour and microhabitat selection and natural history traits.

5.4 Results

5.4.1 Amphibian Assemblage

The amphibian assemblage was categorized into five guilds using published data contained in Lee (1996) (Table 5.3): 1. Nocturnal terrestrial amphibians that feed primarily on ants and termites (3 species); 2. Nocturnal terrestrial amphibians that feed on other insects (5 species); 3. Nocturnal terrestrial amphibians that feed on insects and vertebrates (1 species); 4. Nocturnal aquatic species that feed on both aquatic and terrestrial insects and vertebrates (2 species); and 5. Nocturnal arboreal amphibians that feed on insects (8 species). Based on BIC values, two latent variables were selected for the modelling process. Dunn-Smyth

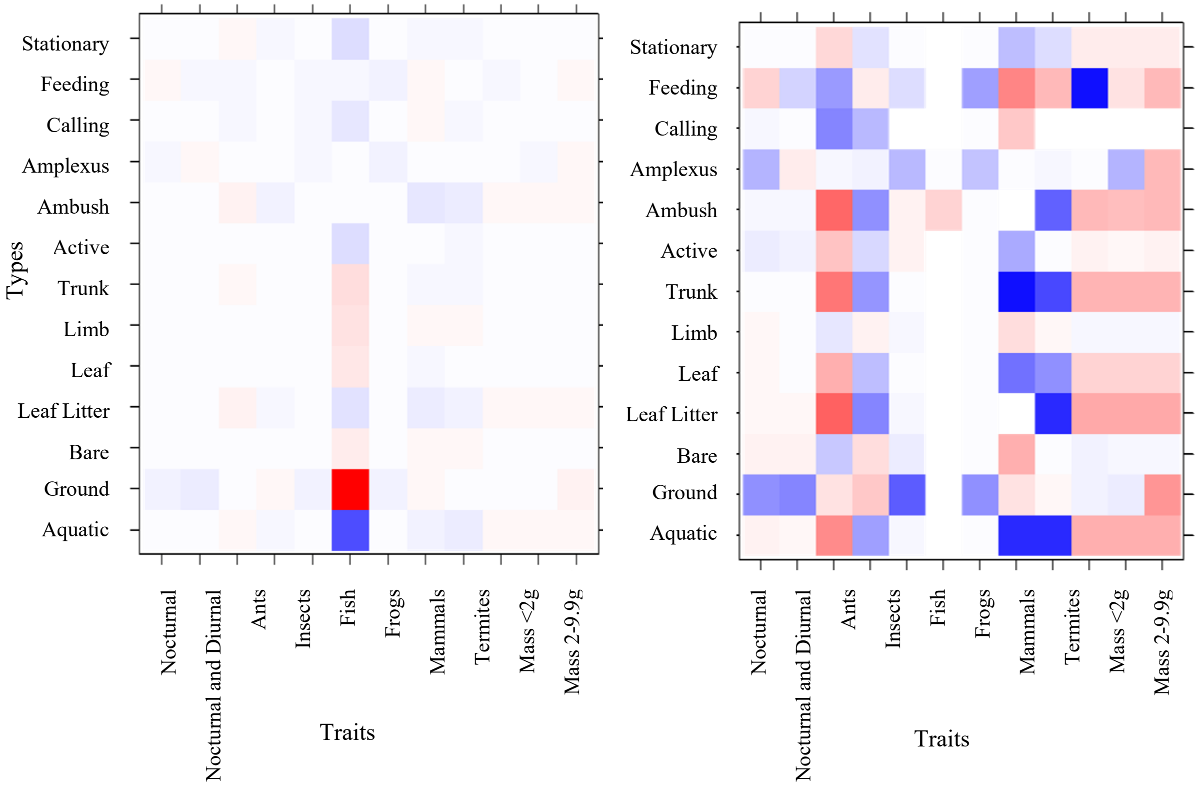


Figure 5.3: Lattice plots of natural history traits in relation to microhabitat and behavioural observation in the amphibian assemblage of Laguna del Tigre National Park. The left plot shows relationships with coefficient values up to 4000, the right shows the relationships with sensitivity reduced to 200. Red squares indicate significant positive relationships, blue squares indicate significant negative relationships. The stronger the colour, the stronger the signal.

residual plots and Q-Q plots confirmed that the latent variable GLM, and latent variable Trait GLM's did not suffer from overdispersion. Correlation plots for both models indicated that while there was correlation within the model, it occurred within acceptable levels.

The lattice plot produced for the trait model showed slight positive signals between Ants and Leaf Litter, and Termites and Bare Ground (Figure 5.3). Coupled with the negative signal of Termites and Leaf Litter, this could indicate different hunting strategies in Guild 1 (Table 5.3). For example, *H. variolosus* was frequently encountered feeding on termites on bare ground, whereas the other members of the guild were more commonly encountered in leaf litter. Species that feed on frogs show a strong association with aquatic microhabitats. Two microhabitats were shown to be particularly important for amphibians, aquatic margins and microhabitats associated with arboreality. This suggests that the amphibian assemblage

LTNP can be broadly described in two major groupings, terrestrial species that congregate at the water's edge, and arboreal species. Rescaling of the lattice plots revealed further relationships between the observed environmental variables and the natural history traits of amphibians (Figure 5.3). Most notably between amphibian species that feed on ants and aquatic and leaf litter microhabitats, and ambush and stationary behaviours. This is consistent with observations of *H. variolosus*.

Coefficient plots of the latent variable trait model revealed significant associations with all microhabitat categories and behaviours, with the exception of Feeding behaviour (Figure 5.4). Most amphibian species found in Disturbed habitat (MH1) tended to use bare ground or leaf litter. Of the species occurring in disturbed habitat only the treefrog *A. callidryas* showed significant associations with microhabitats related to arboreality. Only two species, *A. callidryas* and *B. mexicanus,* were significantly associated with behaviours (Ambush, Calling, and Stationary) in disturbed habitat. In Forest (MH2) and Edge (MH3) habitat amphibians fell into three categories of microhabitat usage (Figure 5.4), those that utilized aquatic microhabitats, those that prefer drier terrestrial microhabitats such as bare groundand leaf litter, and those that utilize arboreal microhabitats. Most amphibians in forest habitat tended to be active hunters (nine species), although two species were also associated with ambush habitat (MH1) tended to use bare ground or leaf litter. Of the species occurring in disturbed habitat only the treefrog *A. callidryas* showed significant associations with microhabitats related to arboreality. Only two species, *A. callidryas* and *B. mexicanus,* were significantly associated with behaviours (Ambush, Calling, and Stationary) in disturbed habitat. In Forest (MH2) and Edge (MH3) habitat amphibians fell into three categories of microhabitat usage (Figure 5.4), those that utilized aquatic microhabitats, those that prefer drier terrestrial microhabitats such as bare ground and leaf litter, and those that utilize arboreal microhabitats. Most amphibians in forest habitat tended to be active hunters (nine species), although two species were also associated with ambush strategies. In both Forest and Edge habitat amphibians also exhibited behaviours related to breeding (Calling and Amplexus) presumably due to the presence of water bodies in these habitats. Amphibians were often Stationary when encountered in all three habitats.

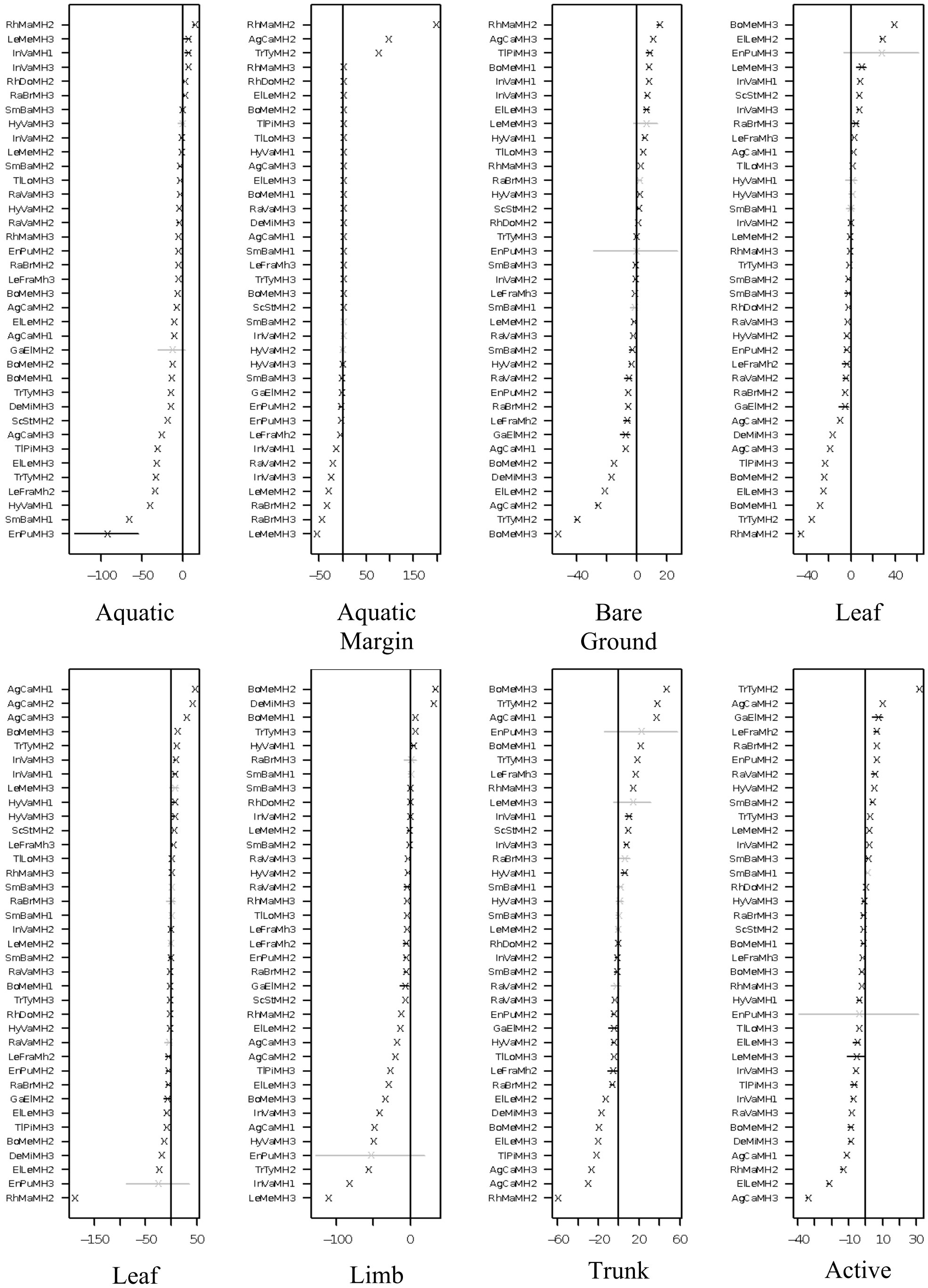
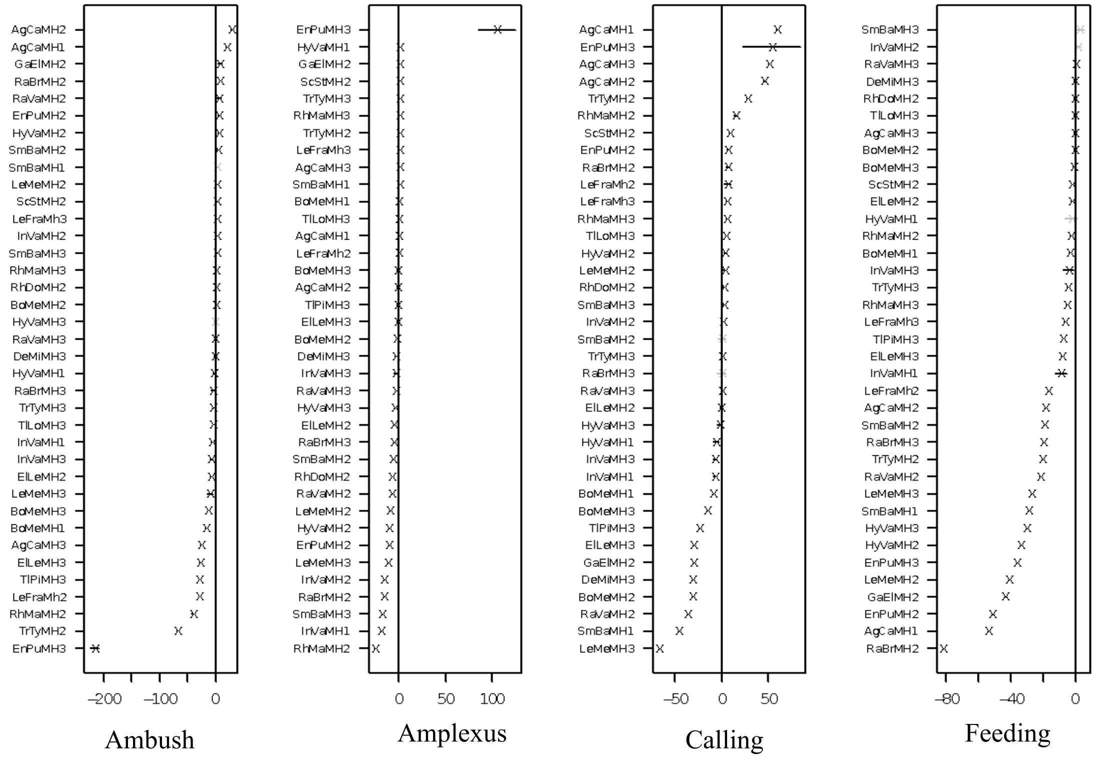
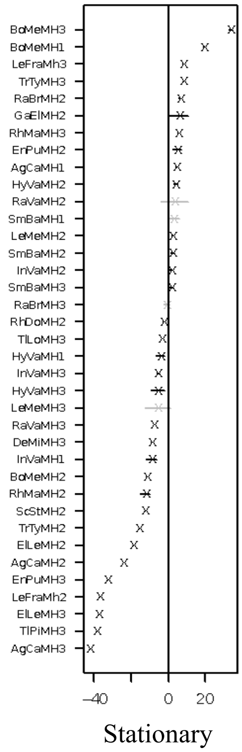


Figure 5.4: Latent variable coefficient plots with confidence intervals (horizontal lines) showing associations between amphibian species and microhabitats and behaviours. Significant coefficients are indicated in bold, and their confidence intervals do not cross zero. Coefficients that cross zero, and are therefore not significant, are indicated in grey. Habitat codes: MH1 = Disturbed habitat; MH2 = Forest habitat; MH3 = Edge habitat. See next page for species codes.





Species codes;

AgCa = *Agalychnis callidryas*
BoMe = *Bolitoglossa mexicanus*
DeMi = *Dendropsophus microcephalus*
ElLe = *Eleutherodactylus leprus*
EnPu = *Engystomops pustulosus*
GaEl = *Gastrophyryne elegans*
HyVa = *Hypopachus variolosus*
InVa = *Incilius valliceps*
LeFra = *Leptodactylus fragilis*
LeMe = *Leptodactylus melanonotus*

RaBr = *Rana brownorum*
RaVa = *Rana vaillanti*
RhDo = *Rhinophrynus dorsalis*
RhMa = *Rhinella marina*
ScSt = *Scinax staufferi*
SmBa = *Smilisca baudinii*
TlLo = *Tlalocohyla loquax*
TlPi = *Tlalocohyla picta*
TrPe = *Triprion petasatus*
TrTy = *Trachycephalus typhonius*

Figure 5.4 continued.

Table 5.4: Snake guilds in Laguna del Tigre National Park, Guatemala.

Guild Number	Guild Description	Species	Family
1	Diurnal arboreal feeding on lizards and amphibians	*Leptophis ahaetulla*	Colubridae
		Leptophis mexicanus	Colubridae
		Oxybelis aeneus	Colubridae
2	Diurnal terrestrial feeding on amphibians and lizards	*Drymobius margaritiferus*	Colubridae
		Mastigodryas melanolomus	Colubridae
		Xenodon rabdocephalus	Colubridae
3	Large diurnal feeding on endotherms and ectotherms	*Coluber mentovarius*	Colubridae
		Spilotes pullatus	Colubridae
4	Nocturnal arboreal feeding on lizards and amphibians	*Imantodes cenchoa*	Colubridae
		Leptodeira septentrionalis	Colubridae
5	Nocturnal arboreal feeding on birds and mammals	*Pseudelaphe flavirufa*	Colubridae
6	Nocturnal arboreal feeding on gastropods	*Sibon dimidiata*	Colubridae
		Sibon nebulatus	Colubridae
7	Nocturnal terrestrial feeding on lizards and snakes	*Clelia scytalina*	Colubridae
		Micrurus diastema	Elapidae
		Oxyrhopus petolarius	Colubridae
8	Nocturnal terrestrial feeding on amphibians	*Coniophanes imperialis*	Colubridae
		Coniphanes schmidti	Colubridae
		Pliocercus elapoides	Colubridae
9	Nocturnal terrestrial feeding on earthworms and gastropods	*Adelphicos quadrivirgattus*	Colubridae
		Ninia diademata	Colubridae
		Ninia sebae	Colubridae
		Tropidodipsas sartorii	Colubridae
10	Nocturnal terrestrial feeding on mammals and birds	*Bothrops asper*	Viperidae
		Boa imperator	Boidae
		Lampropeltis abnorma	Colubridae
11	Nocturnal terrestrial feeding on invertebrates	*Tantilla moesta*	Colubridae
12	Nocturnal aquatic feeding on fish	*Coniophanes bipunctatus*	Colubridae

5.4.2 Snake Assemblage

The snake assemblage was categorized into 12 guilds using published data contained in Lee (1996) (Table 5.4): 1. Diurnal arboreal feeding on lizards and amphibians (3 species); 2. Diurnal terrestrial feeding on amphibians and lizards (3 species); 3. Large diurnal feeding on endotherms and ectotherms (2 species); 4. Nocturnal arboreal feeding on lizards and amphibians (2 species); 5. Nocturnal arboreal feeding on birds and mammals (1 species); 6. Nocturnal arboreal feeding on gastropods (2 species); 7. Nocturnal terrestrial feeding on lizards and snakes (3 species); 8. Nocturnal terrestrial feeding on amphibians (3 species); 9. Nocturnal terrestrial feeding on earthworms and gastropods (4 species); 10. Nocturnal terrestrial feeding on mammals and birds (3 species); 11. Nocturnal terrestrial feeding on invertebrates (1 species); and 12. Nocturnal aquatic feeding on fish (1 species).

Based on BIC values, two latent variables were selected for the modelling process (Appendix I). Dunn-Smyth residual plots and Q-Q plots confirmed that the latent variable GLM, and latent variable Trait GLM's did not suffer from overdispersion. Correlation plots for both models indicated that while there was correlation within the model, it occurred within acceptable levels.

The lattice plot for the snake trait model (Figure 5.5) revealed that snakes that eat earthworms, mammals, and lizards had a strong preference for using logs as a microhabitat, as did venomous species. A strong relationship between eating mammals and being an active hunting species was also revealed. Medium to slight relationships were revealed between snail-eating species and microhabitat preferences that suggested arboreal tendencies. Additionally, a slight relationship was revealed between snail-eating species and terrestrial habits, and also between snakes that eat amphibians and arboreal habits. Larger snakes tended to be terrestrial, whereas smaller snakes tend to be arboreal. Rescaling of the lattice

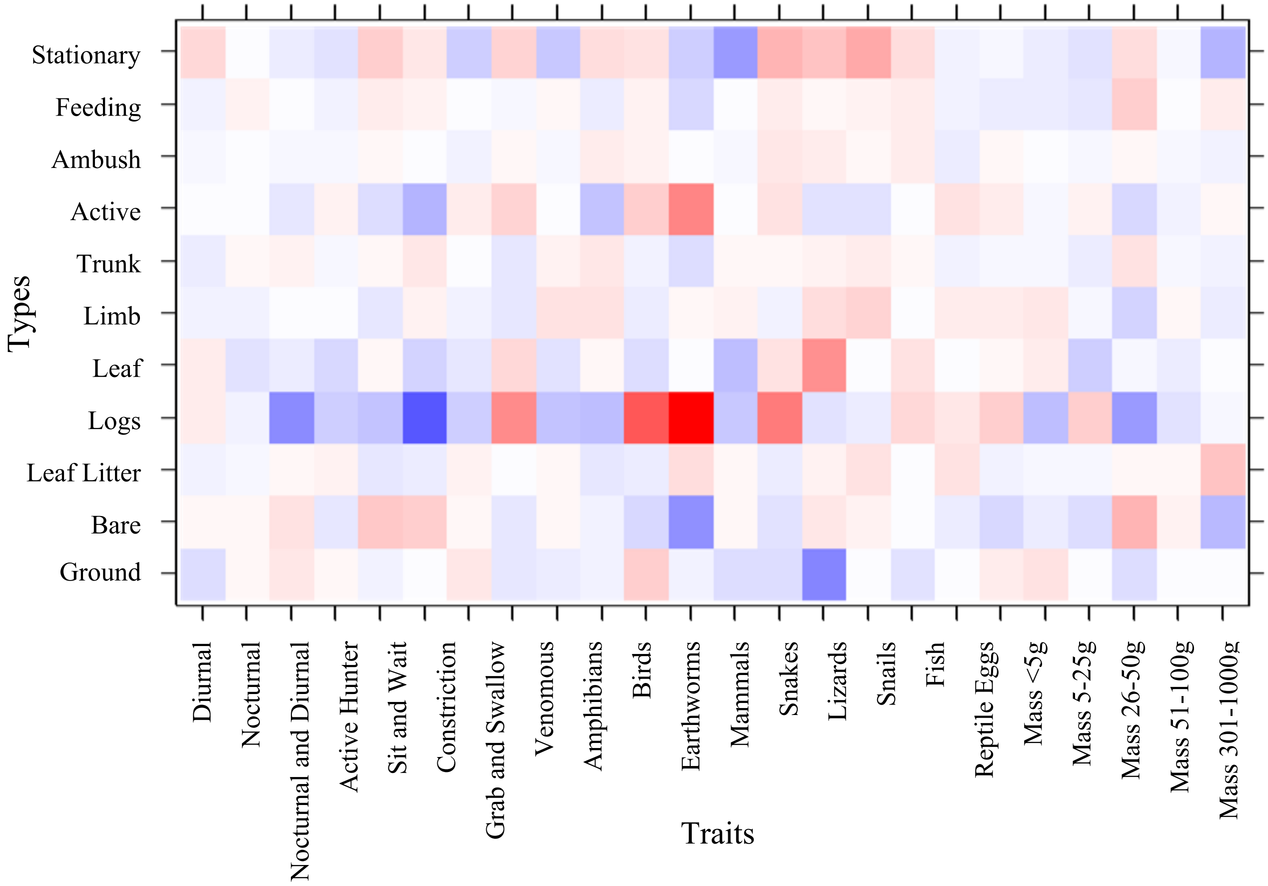
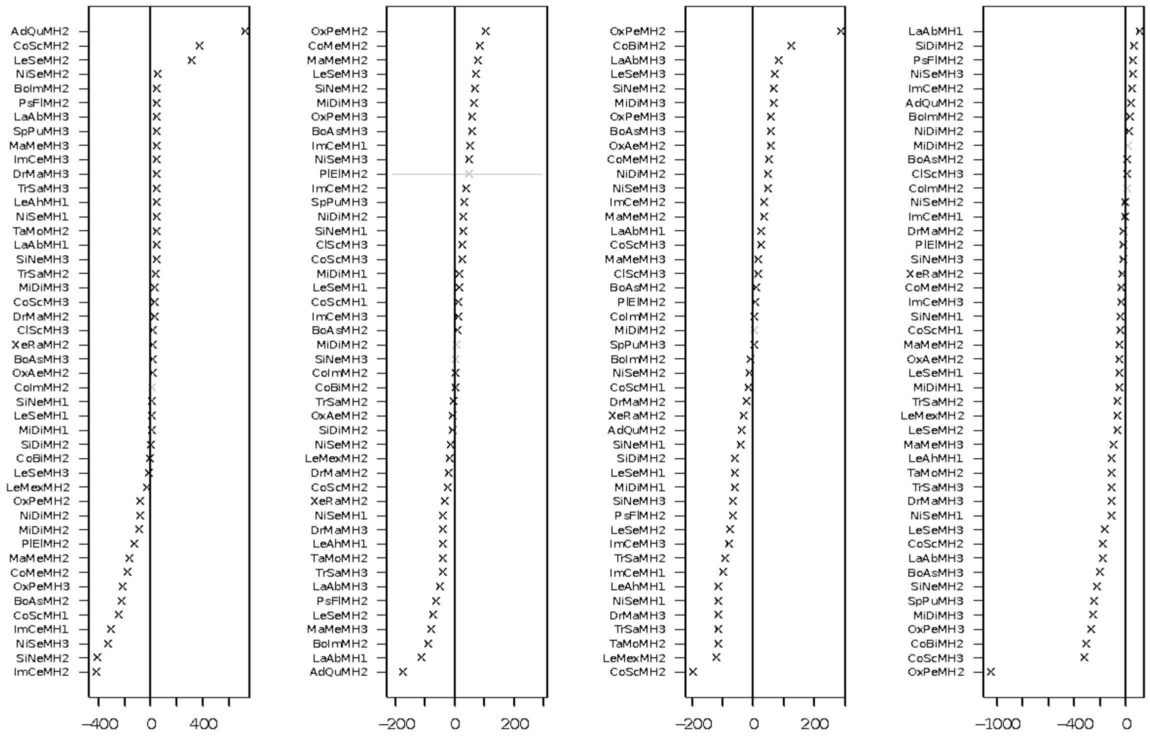


Figure 5.5: Lattice plot of natural history traits in relation to microhabitat and behavioural observation in the snake assemblage of Laguna del Tigre National Park. Red squares indicate significant positive relationships, blue squares indicate significant negative relationships. The stronger the colour, the stronger the signal.

trait plot did not reveal further relationships between observed microhabitat selection and behaviour, and natural history traits.

Latent variable coefficient plots (Figure 5.6) revealed significant associations with all forest habitat types. In general, a greater diversity of snake natural history traits were found in Forest habitat compared to Disturbed or Edge habitat. Snakes in Disturbed habitat (MH1) tended to be associated with terrestrial microhabitats (for example Bare Ground, Leaf Litter, and Logs), although the arboreal snake *I. cenchoa* was associated with Leaf and Limb. In Disturbed habitat snakes tended to be active and feeding when encountered. Significant

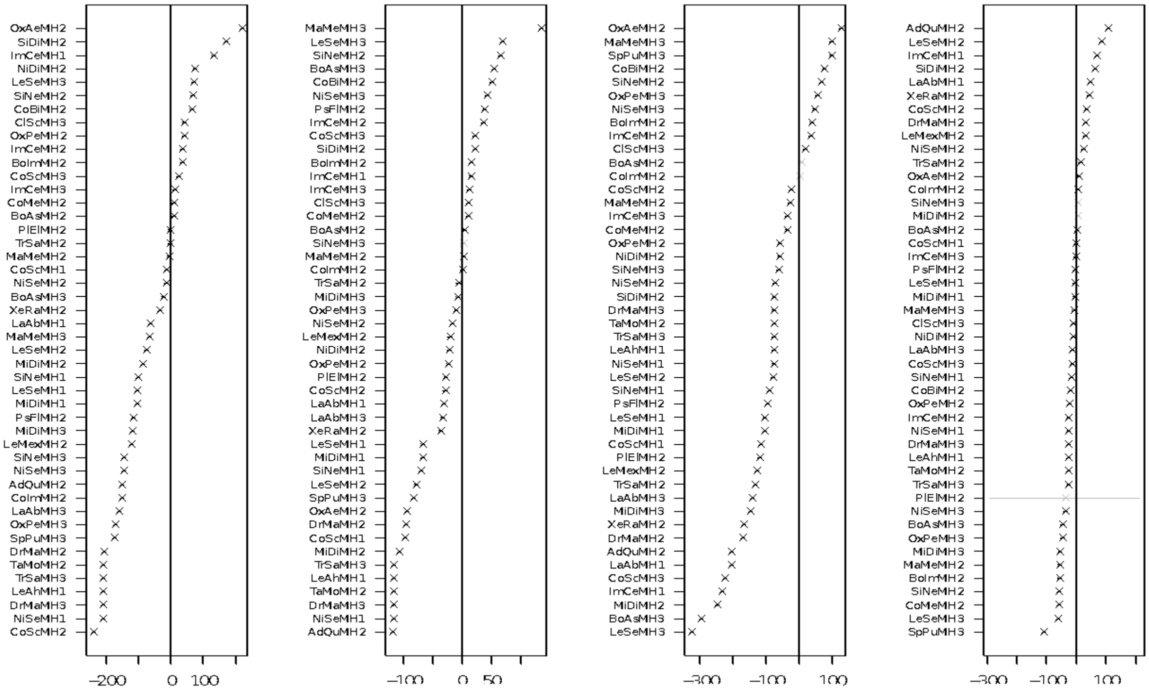


Aquatic

Bare Ground

Leaf Litter

Logs



Leaf

Limb

Trunk

Active

Figure 5.6: Latent variable coefficient plots with confidence intervals (horizontal lines) showing associations between snake species and microhabitats and behaviours. Significant coefficients are indicated in bold, and their confidence intervals do not cross zero. Coefficients that cross zero, and are therefore not significant, are indicated in grey. Habitat codes: MH1 = Disturbed habitat; MH2 = Forest habitat; MH3 = Edge habitat. See next page for species codes.

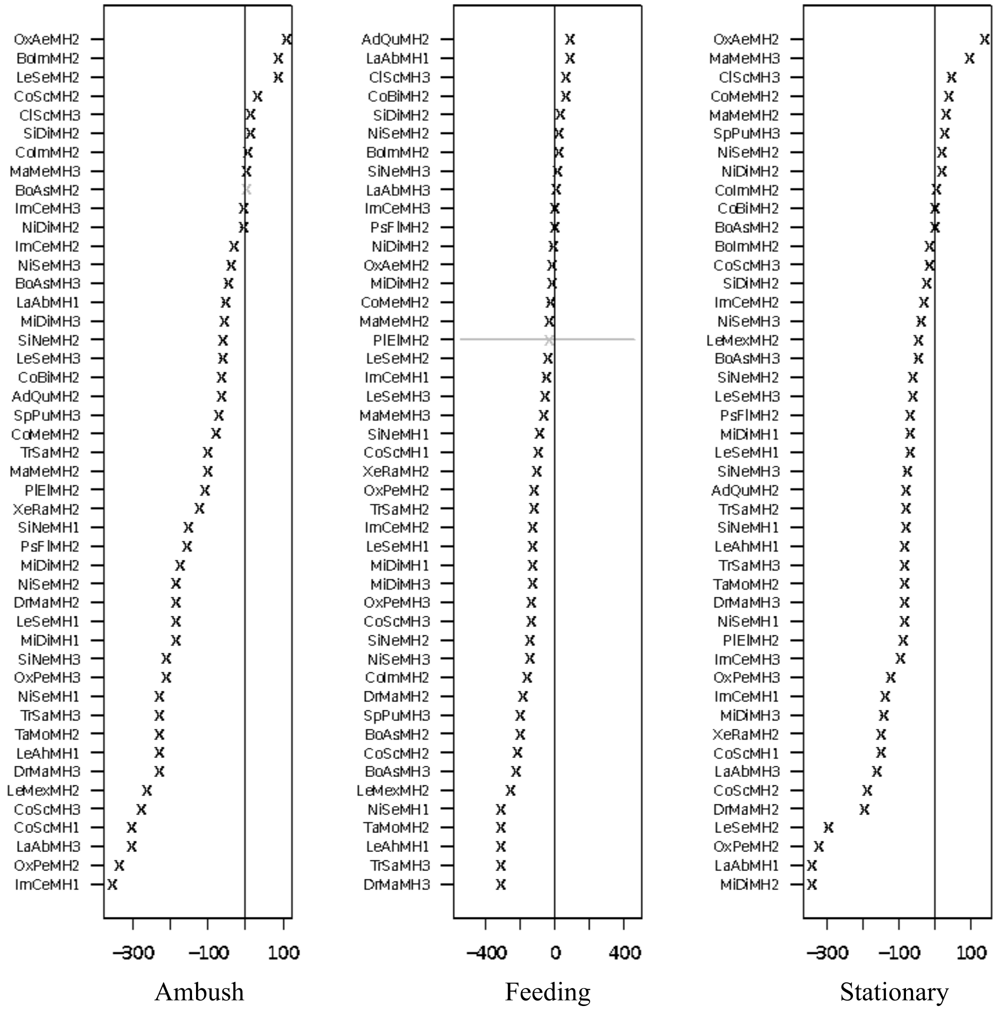


Figure 5.6 continued.

associations were found between seven microhabitat categories and snakes found in Forest habitat (MH2). Snakes in Forest habitat tended to use aquatic, terrestrial, and arboreal microhabitats. They tended to be either active or stationary/in ambush when encountered. Significant associations were found between snake species encountered in Edge habitat (MH3) and five microhabitat categories. Snakes in Edge habitat tended to be associated with terrestrial and arboreal microhabitats and were commonly encountered feeding and resting.

Table 5.5: Lizard guilds in Laguna del Tigre National Park, Guatemala.

Guild Number	Guild Description	Species	Family
1	Nocturnal arboreal large insects	*Corytophanes hernandezi*	Corytophanidae
		Thecadactylus rapicauda	Gekkonidae
2	Nocturnal small leaf litter arachnids	*Coleonyx elegans*	Eublepharidae
3	Diurnal large arboreal insects	*Basilicus vittatus*	Corytophanidae
		Corytophanes cristatus	Corytophanidae
4	Diurnal medium Arboreal insects	*Norops capito*	Dactyloidae
		Norops lemurinus	Dactyloidae
5	Diurnal bush small insects	*Norops rodriguezii*	Dactyloidae
6	Diurnal med to large terrestrial insects	*Holcosus festiva*	Teiidae
		Holcosus undulata	Teiidae
		Marisora undulata	Scincidae
		Mesoscincus schwartzei	Scincidae
		Sceloporus teapensis	Phrynosomatidae
7	Diurnal small leaf litter small insects	*Norops tropidonotus*	Dactyloidae
		Norops uniformis	Dactyloidae
		Sceloporus chrysostictus	Phrynosomatidae
		Sphaerodactylus glaucus	Gekkonidae
		Sphaerodactylus millepunctatus	Gekkonidae
		Sphenomorphus cherriei	Sincidae

5.4.4 Lizard Assemblage

Seven lizard guilds were identified using published data contained in Lee (1996) (Table 5.5): 1. Nocturnal arboreal lizards that feed on large insects (2 species); 2. Small nocturnal leaf litter lizards that feed on arachnids (1 species); 3. Large diurnal arboreal lizards that feed on insects (2 species); 4. Medium diurnal arboreal lizards that feed on insects (2 species); 5. Diurnal bush dwelling insects that feed on small insects (1 species); 6. Medium to large diurnal terrestrial lizards that feed on insects (5 species); and 7. Small diurnal leaf litter lizards the feed on small insects (6 species).

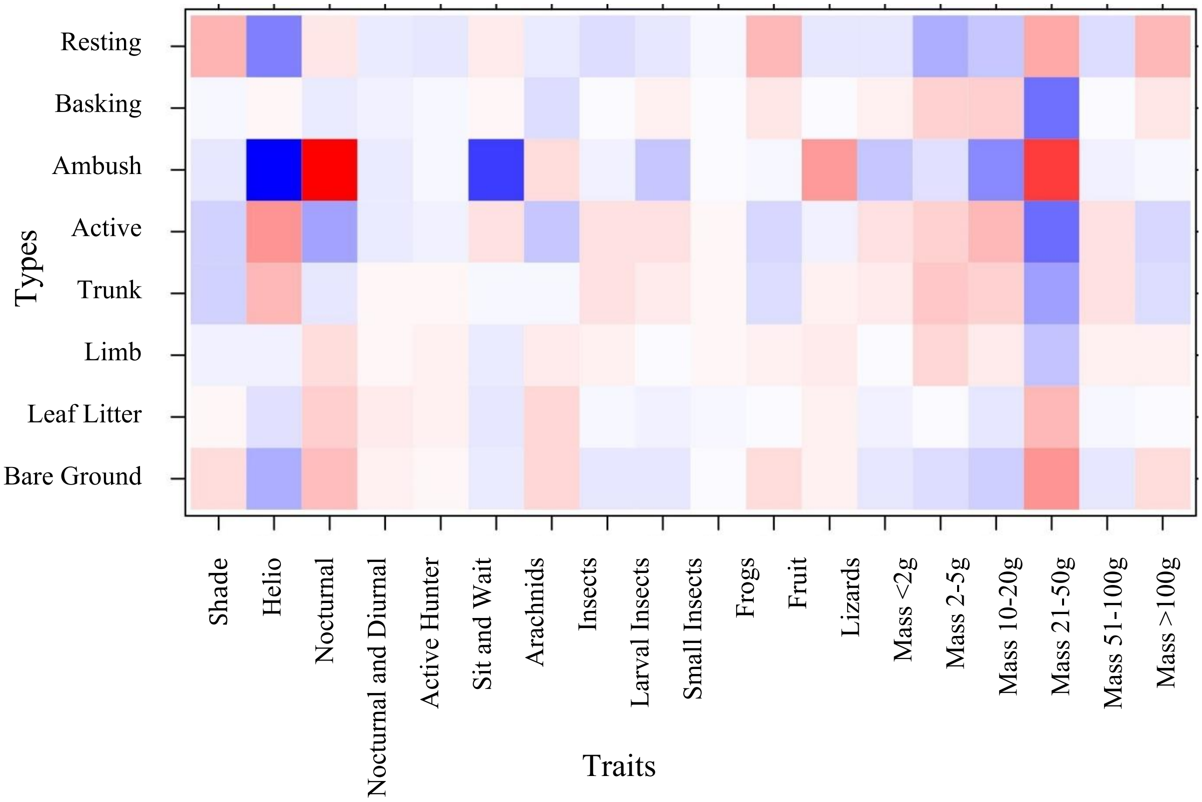


Figure 5.7: Lattice plot of natural history traits in relation to microhabitat and behavioural observation in the lizard assemblage of Laguna del Tigre National Park. Red squares indicate significant positive relationships, blue squares indicate significant negative relationships. The stronger the colour, the stronger the signal.

Based on BIC values, two latent variables were selected for the modelling process. Dunn-Smyth residual plots and Q-Q plots confirmed that the latent variable GLM, and latent variable Trait GLM's did not suffer from overdispersion. Correlation plots for both models indicated that while there was correlation within the model, it occurred within acceptable levels.

The lattice plot produced for the trait model (Figure 5.7) showed a strong signal between lizard-eating species and ambush behaviour. Moderate signals were found between shade-loving species and resting behaviour, and between sun-loving species and both trunk microhabitat and active behaviour. Finally, slight signals were found between sun-loving species and basking behaviour; active hunters and leaf litter; ambush predators (sit and wait) and microhabitats associated with arboreality (limb and trunk); and species that specialize on eating arachnids and active behaviour. Rescaling of the lattice trait plot did not

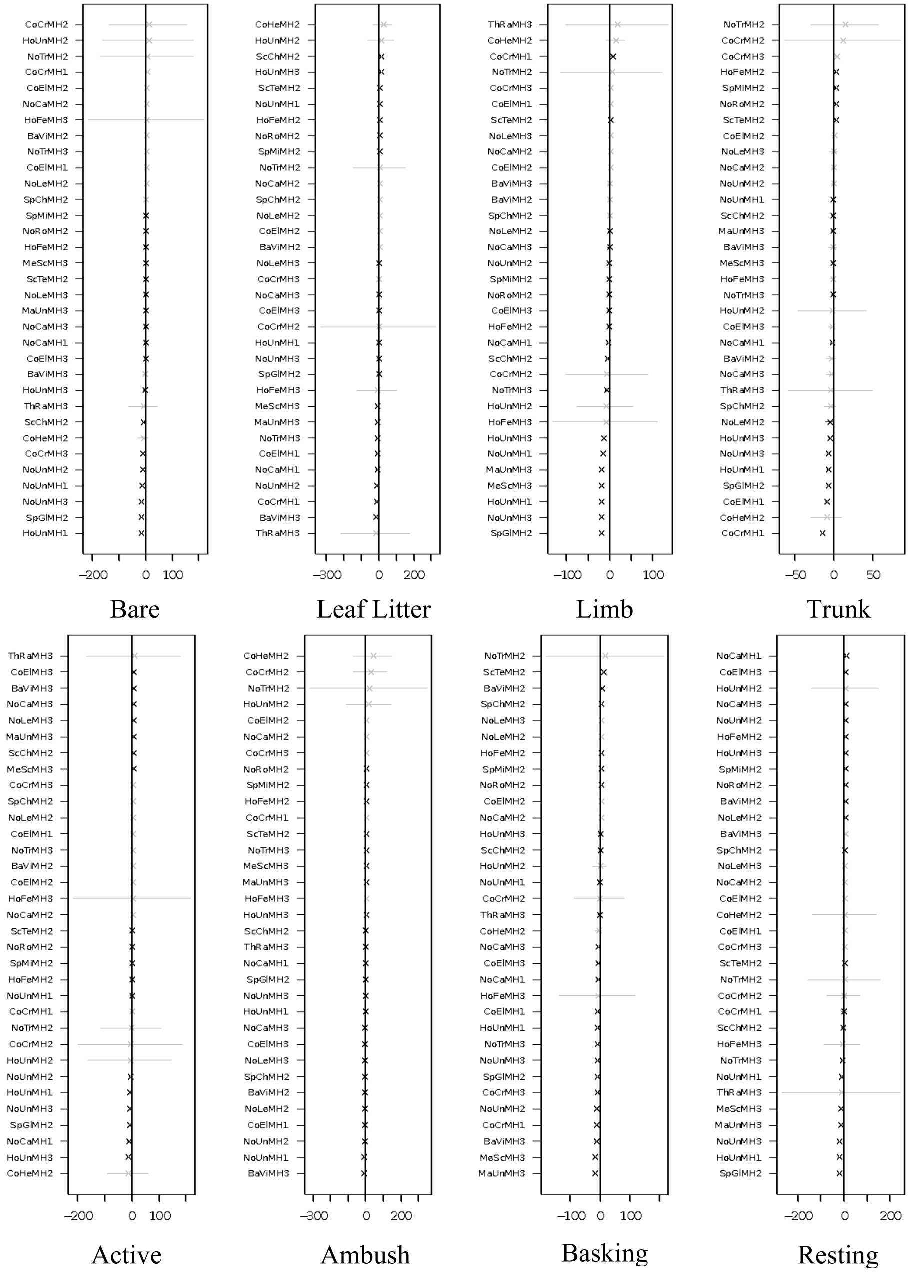


Figure 5.8: Latent variable coefficient plots with confidence intervals (horizontal lines) showing associations between snake species and microhabitats and behaviours. Significant coefficients are indicated in bold, and their confidence intervals do not cross zero. Coefficients that cross zero, and are therefore not significant, are indicated in grey. Species codes; BaVi = *Basiliscus vittatus*, CoCr = *Corytophanes cristatus*, CoEl = *Coleonyx elegans,* CoHe = *Corytophanes hernandezii*, HoFe = *Holcosus festiva*, HoUn = *Holcosus undulata*, MaUn = Marisora unimarginata, MeSc = *Mesoscincus schwartzei*, NoCa = *Norops capito*, NoLe = *Norops lemurinus*, NoRo = *Norops rodriguezii*, NoSe = *Norops sericeus*, NoTr = *Norops tropidonotus*, NoUn = *Norops uniformis*, ScCh = *Sceloporus chrysostictus*, ScTe = *Sceloporus teapensis*, SpCh = *Sphenomorphus cherriei*, SpGl = *Sphaerodactylus glaucus*, SpMi = *Sphaerodactylus millepunctatus*, ThRa = *Thecadactylus rapicauda*. Habitat codes: MH1 = Disturbed habitat; MH2 = Forest habitat; MH3 = Edge habitat.

reveal further relationships between observed microhabitat selection and behaviour, and natural history traits. Coefficient plots from the latent variable GLM failed to find any associations between microhabitats, behaviours, and species in any forest habitat (Figure 5.8).

5.5 Discussion

Overall, this study identified a greater diversity of ecological traits in Forest and Edge habitats compared to the Disturbed habitat at the edge of the forest close to the agricultural activities of the Paso Caballos community. This is consistent with other studies of the effects of forest edges and trait diversity (Vallen et al. 2004; Hirshfeld and Rödel 2017). Species encountered in Disturbed habitat tend to be associated with more terrestrial traits. For example, amphibians are primarily terrestrial and associated with bare ground, and snakes are primarily terrestrial.

Amphibian species that have significant or near significant associations with Bare Ground and / or Leaf Litter in one or more forest habitats are more likely to be found in Disturbed habitat where the vegetation is less dense in the other two habitat types. Amphibian species in Disturbed habitat are represented by three guilds (Nocturnal Terrestrial ant specialists, Nocturnal Terrestrial insect generalists, and Nocturnal arboreal insect generalists). Terrestrial amphibians seem to group into those that associate with water and those that associate with bare ground/leaf litter. This could explain why *Leptodactylus* species show significant association with Leaf Litter but are absent from Disturbed habitat where water bodies are also absent. Several *Leptodactylus* species have been shown to associate strongly with aquatic habitats in natural and agricultural habitats (Lee 1996; Souza et al. 2014). This suggests that the presence, or absence, of water plays an important role in the amphibian assemblage, as does the ability to tolerate open, drier habitats.

Lattice plots revealed separation within amphibian Guild 1 (Nocturnal, terrestrial, ant/termite eaters). Feeding on ants associates with leaf litter, whereas feeding on termites associates with bare ground. *Hypopachus variolosus* associates with bare ground and termites, whereas *Gastrophryne elegans* associates with ants. This distinction, centred around association with bare ground, may explain why *H. variolosus* is found in disturbed habitat and *G. elegans* is absent. Dietary partitioning has been reported in Australian microhylids where geographically restricted species expand their diet and thus increase their chance of survival, compared to widespread species that exhibit highly specialized diets often restricted to ants (Williams et al. 2006). The third member of amphibian guild 1, *Rhinophrynus dorsalis* has very different life history and spends most of the year buried underground and only comes to the surface to breed, this explains why this species does not cluster with other members of the guild in the ordinations.

The assemblage of amphibians and reptiles present in the disturbed habitat is dominated by five 'winning' species: two amphibians, *Hypopachus variolosus* and *Incilius valliceps*; one snake, *Coniophanes schmidti*; and two lizards, *Corytophanes cristatus* and *Norops capito* (Chapter 4, this thesis). Although no discernable pattern could be found in the two lizard species, a pattern did emerge with the amphibians and snakes when viewed in concert. Both *H. variolosus* and *I. valliceps* associated strongly with bare ground and leaf litter in multiple habitats. *Coniophanes schmidti* is a member of snake guild 8 (nocturnally active frog feeding snakes) and has been observed preying upon *I. valliceps* (Griffin In Press), and interestingly is the only member of the guild to show an association with bare ground. Certainly, in amphibians and snakes the association with bare ground is what allows a species to win in the disturbed habitat. Further work is needed to reveal why *C. cristatus* and *N. capito* are such a major component of the amphibian and reptile assemblage in disturbed habitat. There were several clusters in the ordination plots that made little ecological sense, these were likely due to mean variance effects within the data.

Homogenization can occur through 'invasions' of native species that would not normally be able to colonize forest habitats (McKinney and Lockwood 1999). For example, multiple vertebrate species that are not encountered in contiguous forest have been able to colonize remaining forest fragments from a mixed habitat matrix of forest and disturbed habitat (Gascon et al. 1999). Homogenization has been observed in amphibians in response to human-altered habitats and in most cases, generalists win at the expense of losing specialist species (Vallen et al. 2004; Hirshfeld and Rödel 2017). Metadata studies into patterns of global homogenization in amphibians identified that species/clades that are often most at risk are those with direct-developing tadpoles, for example, salamanders of the genus *Bolitoglossa*, and frogs of the genera *Pristimantis* and *Craugastor* (Nowakowski et al. 2018). Species that tend to do well as a result of homogenization are those that reproduce in standing pools of water (often associated with livestock water holes in an agricultural landscape), such as certain hylid frog groups. These amphibian groups tend to be older in evolutionary state and seem better adapted to changing environments, presumably because they are an older lineage that has adapted and survived throughout history (Nowakowski et al. 2008).

This study identified that an association with bare ground, and therefore a tolerance of drier habitats enables a small number of amphibian and snake species to utilize the disturbed forest close to agricultural land in LTNP. This is broadly in line with other studies which have identified that a reduced diversity of microhabitats, in particular reduction of leaf litter, bromeliads, and water bodies, influence tropical amphibian and reptile assemblage structure (Vallan et al. 2004; Gallmetzer and Schultze 2015; Hernandez-Ordoñez et al. 2015; Hirschfeld et al. 2017; Nowakowski et al. 2018). Of major conservation concern, this suggests that continued forest fragmentation in LTNP and the wider Mayan Biosphere Reserve will result in increased edge effects, a greater proportion of remaining forest kept in an early successional state, and with a highly reduced, and homogenized, amphibian and reptile assemblage of Northern Guatemala. The homogenization of species assemblages is not restricted to amphibians and reptiles and has been reported across a wide variety of taxa (McKinney and Lockwood 1999; Newbold et al. 2008). With rates of deforestation and fragmentation increasing across the tropics, there is a global threat of homogenization where generalist species win in favour of ‘losing’ specialist species (Tabarelli et al. 2012; Dang et al. 2019; Vargas Zeppetello et al. 2020). As such there is an urgent need to reduce the rate of habitat loss and fragmentation in the tropics in order to halt the continued homogenization of tropical faunal assemblages.

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Chapter 6 - Patterns of Amphibian and Reptile Diversity in the Mayan Biosphere Reserve, Petén, Northern Guatemala.

Central American boa constrictor– *Boa imperator*

6.1 Abstract

With global biodiversity declining at unprecedented rates, the focus of many biodiversity studies leans towards investigating rare species in need of conservation action. Rare species are often range-restricted due to reliance on limited habitat or resource availability and as such occasionally occur at a single location. Biological communities usually consist of many rare species and few common ones; as such more information about the diversity of assemblages can be gained from common species than rarer ones. the majority of information about a given assemblage is held by between the 20% and 35% most common species. Although this approach of 'Common to Rare' has been used successfully on multiple taxa, it is yet to be used for reptiles or complete amphibian assemblages, many species of which are cryptic in nature and/or occur in low numbers and are therefore difficult to detect. By combining presence/absence data from the amphibian and reptile assemblage of Laguna de Tigre National Park with historical records from multiple other sites within the Mayan Biosphere Reserve (MBR) this is the first attempt to assess the usefulness of using common amphibian and reptile species to investigate patterns of diversity on a wide geographic scale. In both cases common amphibian and reptile species contributed more information about the assemblage than did rare ones, however the difference was not as pronounced as found in other taxa. This may be due in part to the cryptic nature of amphibians and reptiles. Ordinations of Bayesian latent variable models identified associations between locations in the Mayan Biosphere Reserve and amphibian and reptile species. The combined results show that the presence of common, widespread amphibian and reptile species are useful in describing the overall species diversity at locations within the MBR, and that it is also possible to predict which species might be present at a location based on presence of known species at that location. In cases where studies are time-limited and rare species are difficult to detect, the presence of common widespread species provides important and usable information about the overall diversity at location, landscape, and regional scales and can be used to predict patterns of diversity and inform conservation management and policy.

6.2 Introduction

With global biodiversity declining at unprecedented rates, the focus of many biodiversity studies leans towards investigating rare species in need of conservation action. The majority of attention, historically, has been on understanding the distribution of rare species (Poiani et al. 2000). Rare species are often range-restricted due to reliance on limited habitat or resource availability and as such occasionally occur at a single location (Jetz and Rahbek 2002). The resulting information has been used to define conservation priorities set on geographic areas that hold large numbers of rare species (Asaad et al. 2017). This strategy has been necessary due to the higher risk of extinction faced by rare species (Lindenmayer et al. 2011). However, only a small proportion of global diversity has so far been protected through the creation of conservation areas (Pollock et al. 2017). Common species are also susceptible to declines (Lindenmayer et al. 2011), and a global increase of just 5% in the total area of protected land would increase the amount of protected biodiversity from ca. 10% to ca. 30% (Pollock et al. 2017). Biological communities usually consist of many rare species and few common ones (McGill et al. 2007; Matthews and Whittaker 2015). Rare species are often patchily distributed throughout the landscape, occur in low numbers, and are often difficult to detect. As a consequence, it can be costly both in terms of time and resources to conduct a study into rare species that garners sufficient data to be successful. Rare species contribute very little information about the overall species assemblage compared to common species which are widespread throughout the landscape, occur in high numbers and are easily detected (Mazaris et al. 2008).

Although rare species can reveal specific information about a location, they contribute relatively little to the understanding of the wider region (Mazaris et al. 2013). Conversely, common species occur at many locations throughout the landscape, they can reveal relationships between locations across a wide landscape (Lennon et al. 2004). Recent studies have shown that the majority of information about a given assemblage is held by between the 20% and 35% most common species (Lennon et al. 2004). In order to gain the same amount of information using rare species, it is necessary to sample a greater percentage of the assemblage (Lennon et al. 2011; Mazaris et al. 2013). This pattern has been described across multiple taxa including plants (Mazaris et al. 2013; Bispo et al. 2017), terrestrial and aquatic invertebrates (Schalkwyk et al. 2019), frogs (Oldekop et al. 2012), birds (Jetz et al. 2004), and mammals (Vázquez and Gaston 2004). Many biodiversity studies are necessarily conducted over short periods of time, they are therefore more likely to be biased towards detection of common, widespread species at the expense of rarer and more difficult to detect species (McCarthy et al. 2013). These studies might also be limited in their geographical scope and given the patchy distribution of many rare species it is reasonable to assume that these species may not be detected due to coverage of the study. Therefore, the presence of common species is a useful metric in diversity studies that are often conducted over short timeframes and with limited geographic reach (Mazaris et al. 2008). While this methodological approach has previously been applied to leaf litter frogs (Oldekop et al. 2012), it is yet to be used for reptiles or complete amphibian assemblages, many species of which are cryptic in nature and/or occur in low numbers and are therefore difficult to detect (Hutchens and DePerno 2009). The effective use of this methodology could allow useful inferences about the diversity of amphibian and reptile assemblages without the need for long-term monitoring in order to detect rarer, or cryptic, species.

The Mayan Biosphere Reserve (MBR), in Northern Guatemala was created in 1990, covers 1.6 million hectares, and is one of the largest areas of protected land in Central America (Bestelmeyer 2000; Hearne and Santos 2005). It consists of a buffer zone, multi-use zones, and a core zone (Hearne and Santos 2005). The core zone, which contains four National Parks and three Biotopes, accounts for 34% of the total area of the MBR (Radachowsky et al. 2012). Geographically, and biologically it forms the southern region of the wider Yucatán Peninsula (Bestelmeyer 2000). The multi-use zone comprises 40% of the MBR and within this area concessions have been granted for the extraction of timber and other non-timber forest products by communities legally existing in the MBR (Radachowsky et al. 2012). Despite being well protected under Guatemalan legislation widespread deforestation within the MBR continues (Tolisano and López 2010; Sesnie et al. 2017), the highest rates of which are found within the largest of the core protected areas, Laguna del Tigre National Park (Tolisano and López 2010; WCS 2016; Devine et al. 2020).

Although many research and conservation programmes exist within the MBR very few concern amphibians and reptiles and our understanding of the assemblage is limited and patchy (Bestelmeyer and Alonso 2000; Novak et al. 2005; Garcia-Anleu et al. 2007; Britt et al. 2014; Lepe-Lopez et al. 2018). Given the current rates of habitat loss, understanding the distribution and patterns of diversity of amphibians and reptiles is critical to building successful conservation policies within the MBR. Historical records exist from within the MBR although many of these records are incidental in nature. The most comprehensive dataset from within the MBR is from Laguna del Tigre National Park (LTNP), the largest park in the MBR, and is the subject of this thesis. By combining presence/absence data from the amphibian and reptile assemblage of LTNP with historical records from multiple other sites within the MBR this is the first attempt to assess the usefulness of using common amphibian and reptile species to investigate patterns of diversity on a wide geographic scale.

This chapter aims to investigate the patterns of diversity throughout the MBR and answer the following questions: (1) Do fewer common amphibian and reptile species contribute more to the understanding of patterns in biodiversity in the MBR than do rare species? (2) Does presence/absence data from locations within the MBR reveal patterns in species distributions and locations from throughout the MBR?

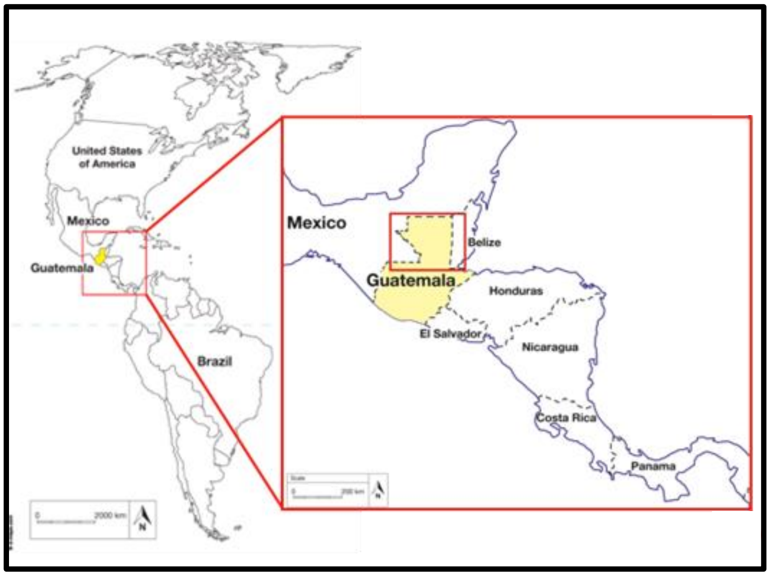

Figure 6.1: Map of the Americas, showing the location of Petén within Guatemala. Red box indicates area shown in Figure 6.2. Due to the curvature of the map the scale shown is representative of the scale at the equator. Map adapted from D-Maps.com

6.3 Methods

The Mayan Biosphere Reserve (MBR) is located in northern Petén, Guatemala (Figure 6.1). It consists of core protected areas, multiple-use zones, and a buffer zone, which together cover approximately 1.6 million hectares of lowland tropical humid forest. The location records of amphibians and reptiles were collected from 17 locations within all three zones of the MBR (Figure 6.2). Historical location data from the MBR was received from collections held at Universidad del Valle de Guatemala (UVG), University of Texas Arlington (UTA), and Global Biodiversity Information Facility (GBIF). Due to differences in collection methods all data was converted to presence/absence records. Sampling locations are shown in Figure 6.2.

Data was collected in Laguna del Tigre National Park where visual encounter surveys were conducted along three 100 m transects in each of four forest habitats, Agricultural Edge, High

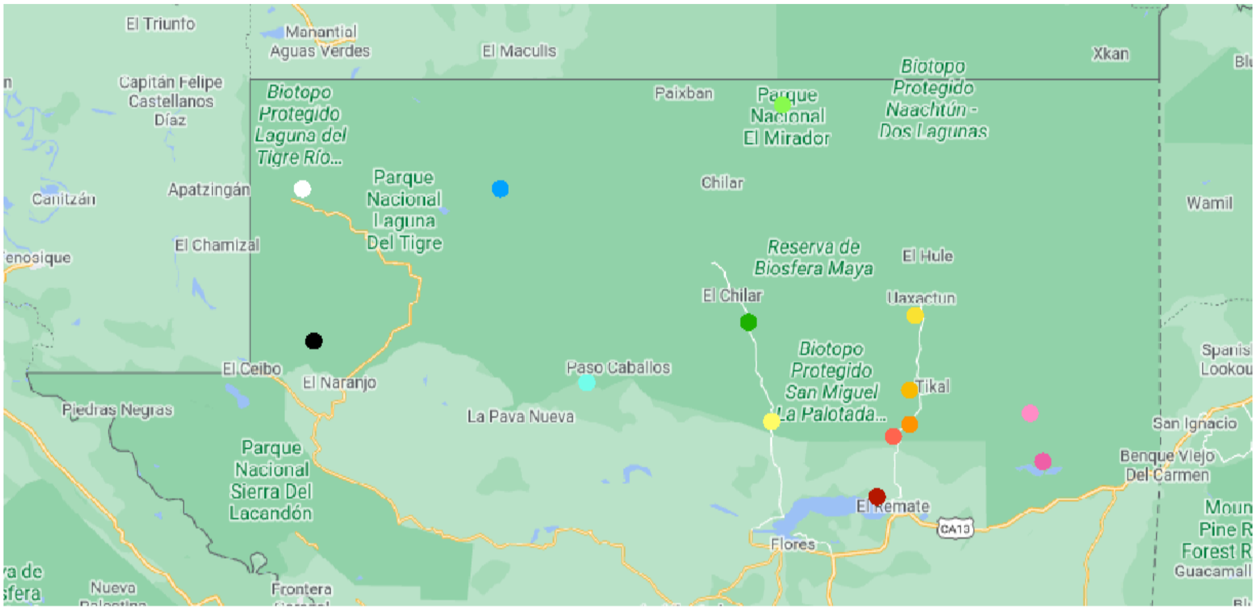

Figure 6.2: Map showing the sampling locations in the Mayan Biosphere Reserve and its buffer zone, Petén, Northern Guatemala. Locations are indicated by coloured dots. From left to right the locations are: White = Rio Escondido; Black = Rio Chocop; Dark Blue = Laguna Flor de Luna; Light Blue = four locations at Estación Biológica las Guacamayas, see text for further details; Dark Green = Road to Carmelita; Yellow = Cruce dos Aguadas; Light Green = El Mirador; Dark Red = Cerro Cahui; Light Red = El Remate A; Dark Orange = El Remate B; Light Orange Tikal; Dark Yellow = Uaxactún; Light Pink = Nakum; Dark Pink = Yaxhá. Solid blacklines indicate the position of international borders, the dotted black line indicates the position of the currently contested border between Guatemala and Belize.

Forest, Low Forest and Natural Edge. Due to the resolution needed to indicate all locations in the MBR all locations at EBG are represented by a single marker (Figure 6.2). In addition to historical records Visual Encounter Surveys were conducted in the following seven fieldwork periods: May-June 2013; November-December 2013; June 2014; October 2014; June 2015; December 2015; and June-July 2016. Each transect was surveyed three times in each survey period with a total of 120 surveys conducted over the life of the project. Any amphibian or reptile encountered during a survey was identified to species level and its GPS location recorded using a handheld GPS machine (Garmin GPSMap62s). See previous chapters for detailed methodology.

6.3.1 Statistical Analysis

Statistical analyses were carried out on the amphibian and reptile assemblages separately. Assessment of how much information is contained within the common species compared to rare species was carried out using the following protocol. The data from MBR was used to create sub-assemblages from most common species to most rare species (CtoR) and from most rare to most common (RtoC) (Lennon et al. 2004). To do this each species was ranked by the number of sampling locations (shown in Figure 6.2) it occurred at within MBR, so that in the CtoR sequence the first species was the species that occurred at the highest number of locations, and the last was the species that occurred at the fewest (Mazaris et al. 2008). This ranking was then reversed to create the RtoC sequence. The first sub-assemblage included only the first species in the sequence, the second sub-assemblage included the first and second species, and so on until all species had been included in the final sub-assemblage (Jetz and Rahbek 2002). The number of species that occurred at each location in each sub-assemblage was then correlated with the total number of species that occurred at each location in the final sub-assemblage sequentially until the final sub-assemblage had been included (Mazaris et al. 2008). This was conducted on both the CtoR and RtoC sub-assemblage sequences.

To investigate relationships between common and rare species, and locations, Bayesian unconstrained ordinations were performed on a latent variable model (LVM) using package Boral (Hui et al. 2015; Hui 2016). The resulting biplots were used to show associations between 17 locations within the MBR and species presence. Due to the size of the dataset and to facilitate interpretation of the ordinations, models were performed on the amphibian, snake, and lizard/turtle assemblages separately. Bayesian LVM's are useful at explaining multivariate composition while accounting for residual correlation. They are superior to non-metric multidimensional scaling (NMDS) because they make provision for possible mean-variance relationships in data without confounding location with dispersion (Warton et al. 2012; Hui et al. 2015).

For Boral models, estimation was performed using Bayesian Markov Chain Monte Carlo (MCMC) methods via software JAGS (Plummer 2003). The model comprised two latent variables, used a binomial family, ran 40000 iterations with 10000 discarded for burn-in, and was thinned by 30. Priors were set using Boral's modest automated uniform normal distribution detected and set through JAGS (priors = ~ dnorm (0,0.1)). Convergence was assessed using inspection of Geweke convergence diagnostic (Geweke 1992), a test which is similar to the Gelman statistic potential scale reduction factor (PSRF) (Gelman et al. 2013), but applicable given Boral operates with only a single MCMC chain (Hui 2016). Model assumptions of mean-variance and log-linearity were examined using Dunn-Smyth residuals vs. fit plots and normal quantile plots (Dunn and Smyth 1996). Correlation and residual correlation were checked by plotting a residual covariance matrix of latent variable regression coefficients using function get.residual.cor in Boral and package Corrplot. A strong residual covariance/correlation between factor variables can be interpreted as xevidence of autocorrelation in a model, however, acceptable levels have been recognized as indicative of an interaction/association (Pollock et al. 2014).

All analyses were carried out in the program R version 4.0.0 (R Core Team 2020). JAGS version 4.3.0 was utilized for performing Bayesian routines.

6.4 Results

The amphibian assemblage of MBR is represented by 23 species across the 17 sampling locations. The frequency of distributions for the amphibian assemblage was slightly right skewed with 21.7% of species occurring at up to 3 locations, only a single species occurred at the maximum number of locations. Although correlation coefficients for the Common to

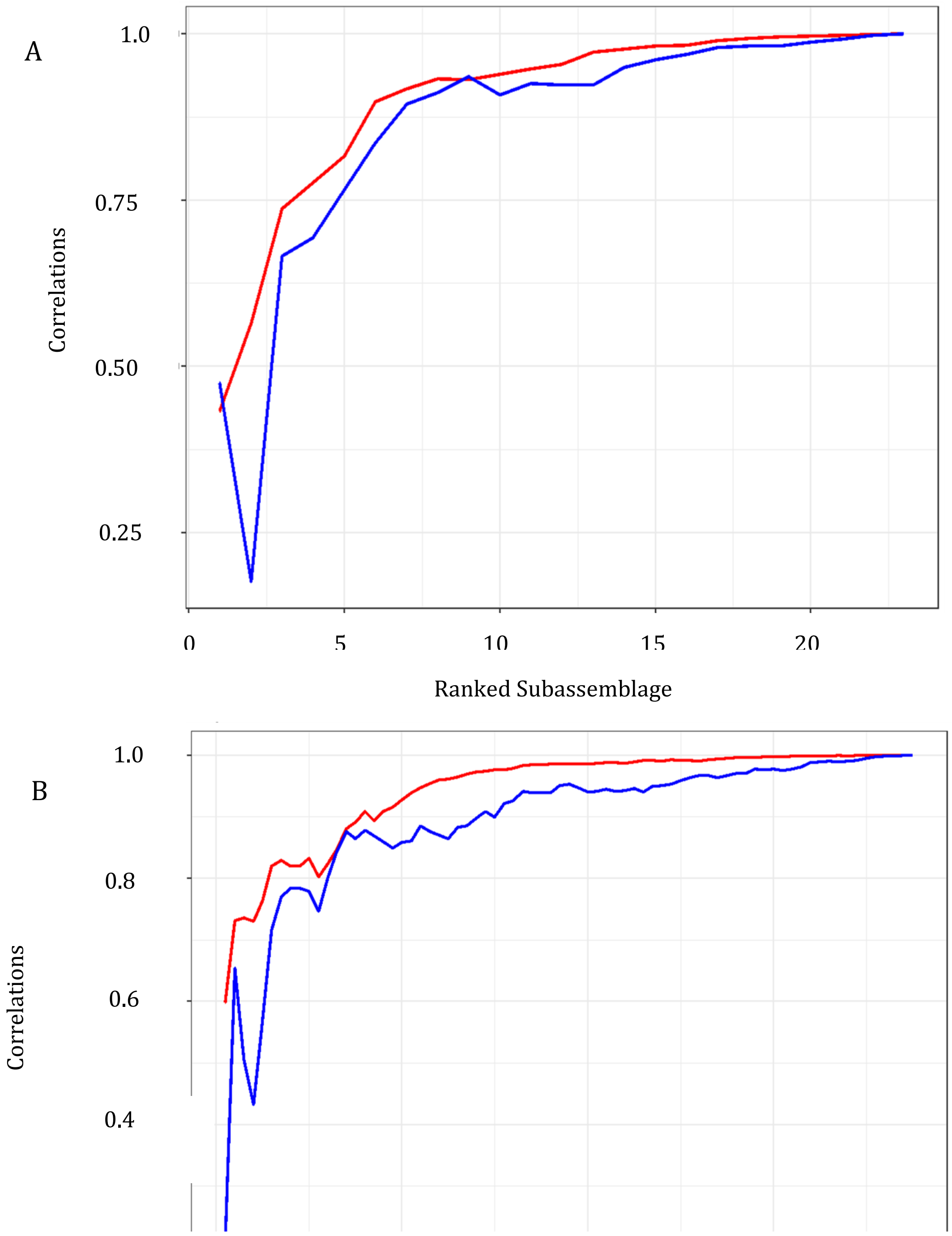

Figure 6.3: Ranked correlations of the 'common to rare' (red line) and 'rare to common' (blue line) amphibian (A) and reptile (B) subassemblages in the Mayan Biosphere Reserve.

Rare (CtoR) and Rare to Common (RtoC) sub-assemblage sequences increased in a similar manner, the CtoR sequence produced a more consistent and smoother curve (Fig. 6.3a). Using the CtoR sequence from LTNP, correlation with overall diversity needed a sample of the 20% of the most common species to reach a correlation coefficient 0.8 (p-value = 0.001) and 30% of the most common species to reach a correlation coefficient of 0.9 (p-value = 0.001) (Figure 6.3a). To reach similar levels using the RtoC sequence 26% and 34% of the rarest species needed to be sampled (Figure 6.3a).

The reptile assemblage of MBR is represented by 75 species across the 17 sampling locations. The frequency of distributions for the reptile assemblage was heavily right skewed with 34.6% of species occurring at a single location, only 2.6% of species occurred at the maximum number of locations. Although correlation coefficients for the CtoR and RtoC sub-assemblage sequences increased in a similar manner, the CtoR sequence produced a more consistent and smoother curve (Figure 6.3b). Using the CtoR sequence from LTNP, correlation with overall diversity needed a sample of the 8% of the most common species to reach a correlation coefficient 0.8 (p-value < 0.001 and 24% of the most common species to reach a correlation coefficient of 0.9 (p-value<0.001) (Figure 6.3b). To reach similar levels using the RtoC sequence 16% and 39% of the rarest species needed to be sampled (Figure 6.3b).

All three LVMs successfully converged with all Geweke *Z*-score p- values exceeding 0.05. Geweke scores of <0.05 are approximately equivalent to a PSRF of 1.96 which would indicate poor convergence. Residual plots of the models fit showed good distribution of linear predictors indicating minimal overdispersion in all cases. The residual correlation plot of the amphibian model revealed significant positive relationships between some species. The residual correlation plots of the snake and lizard/turtle models indicated positive and negative relationships between some species. In all cases the amount of correlation in the models was within acceptable levels (Pollock et al. 2014). Ordinations of the LVMs revealed multiple groupings of species and locations (Figures 6.4, 6.5. and 6.6).

The ordination of the amphibian LMV successfully identified relationships between location and amphibians (Figure 6.4). For example, the locations LF-LTNP, NE-LTNP, and Tikal

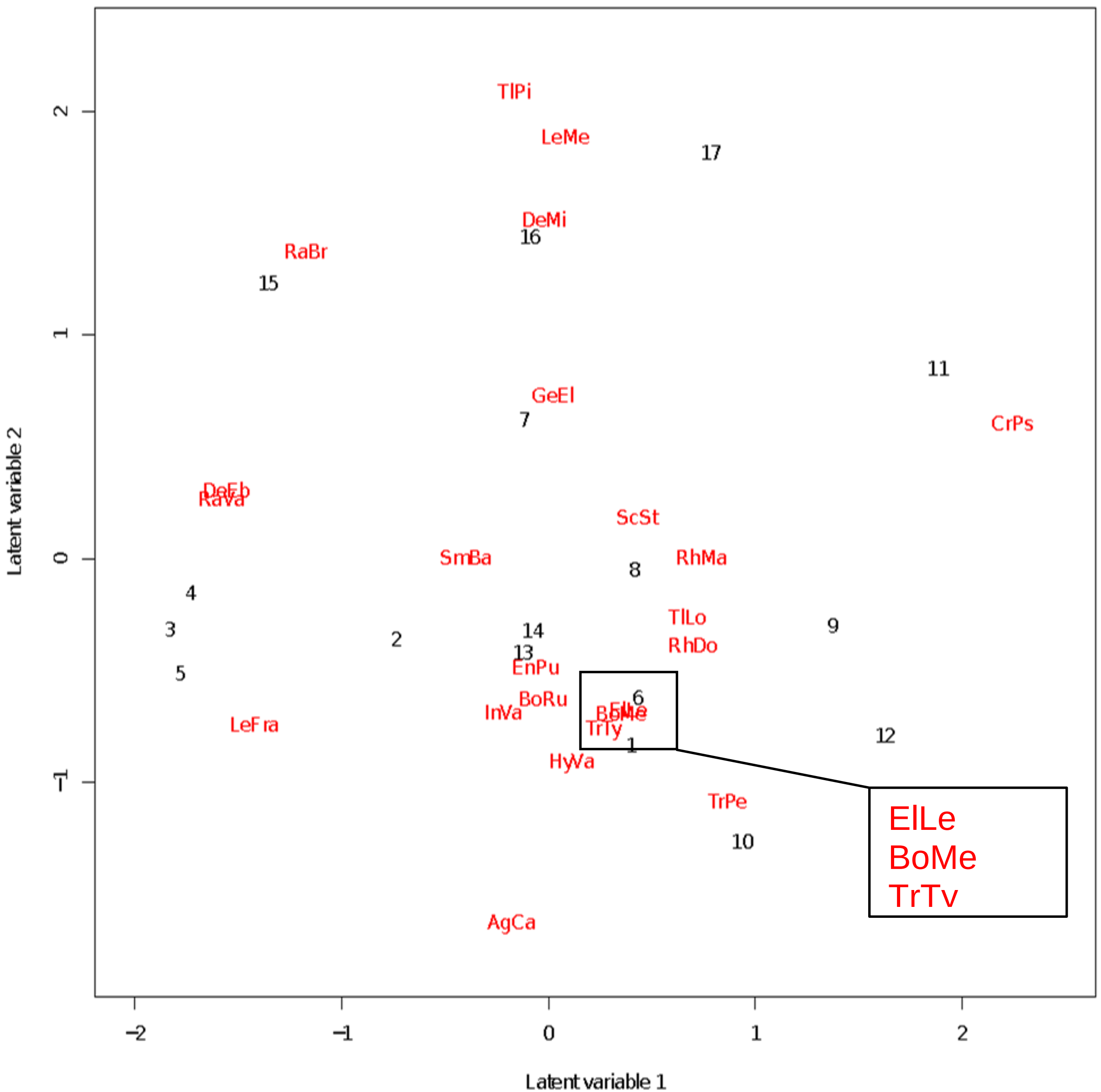

Figure 6.4: Unconstrained ordination biplot of latent variable posterior medians from the amphibian LVM. Species are stated, numbers are positions of latent variables for locations within the MBR. Species codes: AgCa = *Agalychnis callidryas;* BoMe = *Bolitoglossa mexicanus;* BoRu = *Bolitoglossa rufescens;* CrPs = *Craugastor psephosypharus;* DeEb = *Dendropsophus ebracctus;* DeMi = *Dendropsophus microcephalus;* ElLe = *Eleutherodactylus leprus;* EnPu = *Engystomops pustulosus;* GaEl = *Gastrophyryne elegans;* HyVa = *Hypopachus variolosus;* InVa = *Incilius valliceps;* LeFra = *Leptodactylus fragilis;* LeMe = *Leptodactylus melanonotus;* RaBr = *Rana brownorum;* RaVa = *Rana vaillanti;* RhDo = *Rhinophrynus dorsalis;* RhMa = *Rhinella marina;* ScSt = *Scinax staufferi; SmBa = Smilisca baudinii;* TlLo = *Tlalocohyla loquax;* TlPi = *Tlalocohyla picta;* TrPe = *Triprion petasatus;* TrTy = *Trachycephalus typhonius.* Sample locations are indicated by the following numbers: 1= AE-LTNP; 2 = HF-LTNP; 3 = LF-LTNP; 4 = NE-LTNP; 5 = Tikal; 6 = Uaxactún; 7 = Carmelita; 8 = Yaxhá; 9 = Nakum; 10 = Mirador; 11 = Cruce Dos Aguadas; 12 = Cerro Cahui; 13 = El Remate A; 14 = El Remate B; 15 = Rio Chocop; 16 = Rio Escondido; 17 = Laguna Flor de Luna.

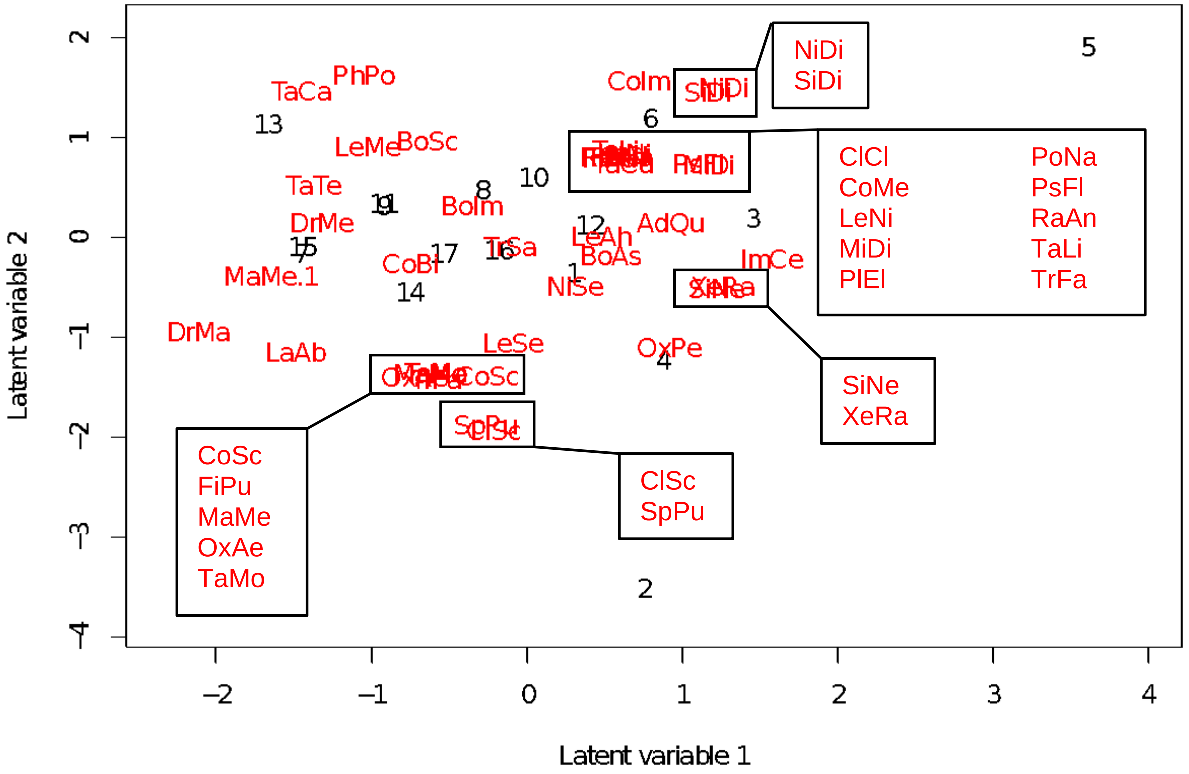

Figure 6.5: Unconstrained ordination biplot of latent variable posterior medians from the snake LVM. Species are stated, numbers are positions of latent variables for locations within the MBR. Species codes; AdQu = *Adelphicos quadrivigattus*, BoAs = *Bothrops asper,* BoSc = *Bothriechis schlegelii,* BoIm = *Boa imperator*, ClCl = Clelia clelia, ClSc = *Clelia scytalina*, CoBi = *Coniophanes bipunctatus*, CoIm = *Coniophanes imperialis*, CoMe = *Coluber mentovarius*, CoSc = *Coniophanes schmidti*, DrMa = *Drymobius margaritiferus*, FiPu = *Ficimia publia,* ImCe = *Imantodoes cenchoa*, LaAb = *Lampropeltis abnorma*, LeAh = *Leptophis ahaetulla*, LeMex = *Leptophis mexicanus*, LeNi = *Leptodeira nigrofasciata,* LeSe = *Leptodiera septentrionalis*, MaMe = *Mastigodryas melanonomus*, MiDi = *Micrurus diastema*, NiDi = *Ninia diademata*, NiSe = *Ninia sebae*, OxAe = *Oxybelis aeneus*, OxPe = *Oxyrhopus petolarius*, PhPo = *Phrynonax poecilionotus,* PlEl = *Pliocercus elapoides*, PoNa = *Porthidium nasutum,* PsFl = *Psuedelaphe flavirufa*, RaAn = Rhadinea decorata, SiDi = *Sibon dimidiata*, SiNe = *Sibon nebulata*, SpPu = *Spilotes pullatus*, TaCa = *Tantillita canula,* TaLi = *Tantilla lintoni,* TaMo = *Tantilla moesta*, TaTe = *Tantilla tenuis, TrFa = Tropidodipsas fasciatus,* TrSa = *Tropidodipsas sartorii*, XeRa = *Xenodon rabdocephalus*. Sample locations are indicated by the following numbers: 1= AE-LTNP; 2 = HF-LTNP; 3 = LF-LTNP; 4 = NE-LTNP; 5 = Tikal; 6 = Uaxactún; 7 = Carmelita; 8 = Yaxhá; 9 = Nakum; 10 = Mirador; 11 = Cruce Dos Aguadas; 12 = Cerro Cahui; 13 = El Remate A; 14 = El Remate B; 15 = Rio Chocop; 16 = Rio Escondido; 17 = Laguna Flor de Luna.

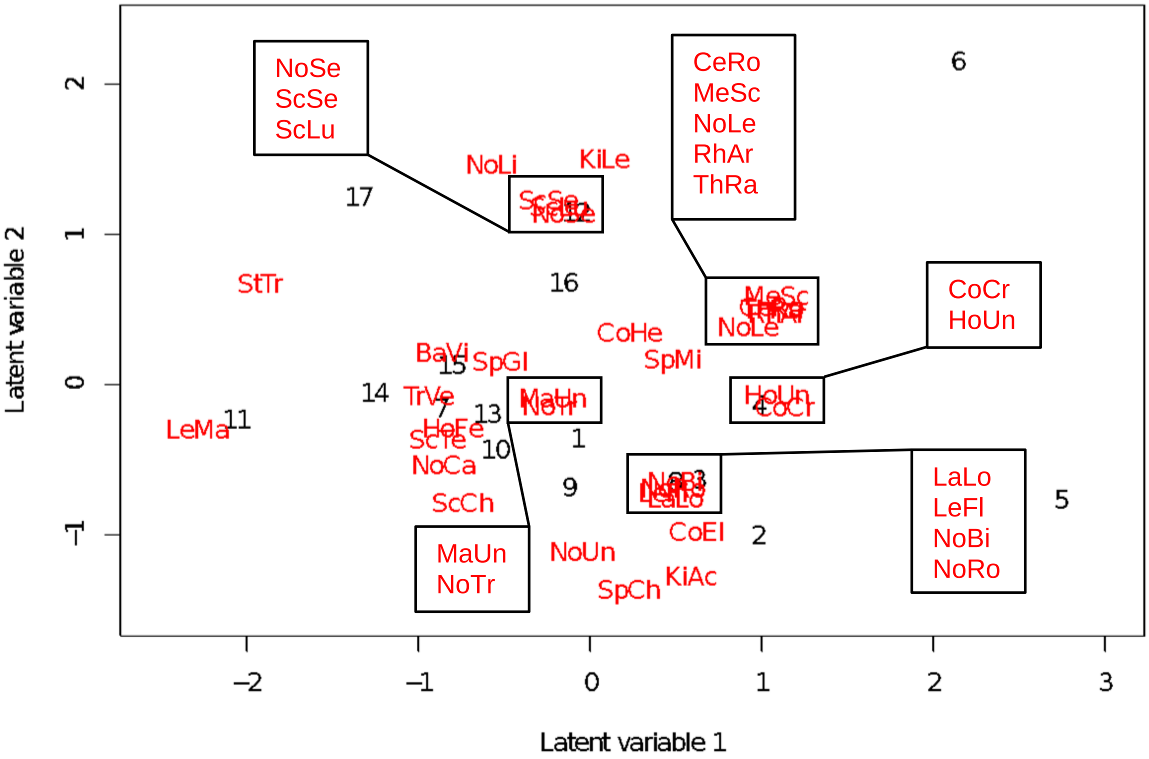

Figure 6.6: Unconstrained ordination biplot of latent variable posterior medians from the lizard/turtle LVM. Species are stated, numbers are positions of latent variables for locations within the MBR. Species codes; BaVi = *Basiliscus vittatus*, CeRo = *Celestus rozalae,* CoCr = *Corytophanes cristatus*, CoEl = *Coleonyx elegans,* CoHe = *Corytophanes hernandezii*, HoFe = *Holcosus festiva*, HoUn = Ho*lcosus undulata*, KiAc = *Kinosternon acutum*, KiLe = *Kinosternon leucostomum*, LaLo = *Laemanctus longipes,* LeFl = *Lepidophyma flavimaculatum,* LeMa = *Lepidophyma mayae,* MaUn = Marisora unimarginata*,* MeSc = *Mesoscincus schwartzei*, NoBi = *Norops biporcatus,* NoCa = *Norops capito*, NoLe = *Norops lemurinus*, NoLi = *Norops limifrons,* NoRo = *Norops rodriguezii*, NoSe = *Norops unilobatus*, NoTr = *Norops tropidonotus*, NoUn = *Norops uniformis*, RhAr = *Rhinoclemmys areolata*. ScCh = *Sceloporus chrysostictus*, ScLu = *Sceloporus lundelli,* ScSe = *Sceloporus serrifer,* ScTe = *Sceloporus teapensis*, SpCh = *Sphenomorphus cherriei*, SpGl = *Sphaerodactylus glaucus*, SpMi = *Sphaerodactylus millepunctatus*, StTr = *Staurotypus triporcatus,* ThRa = *Thecadactylus rapicauda,* TrVe = *Trachemys venusta*. Sample locations are indicated by the following numbers: 1= AE-LTNP; 2 = HF-LTNP; 3 = LF-LTNP; 4 = NE-LTNP; 5 = Tikal; 6 = Uaxactún; 7 = Carmelita; 8 = Yaxhá; 9 = Nakum; 10 = Mirador; 11 = Cruce Dos Aguadas; 12 = Cerro Cahui; 13 = El Remate A; 14 = El Remate B; 15 = Rio Chocop; 16 = Rio Escondido; 17 = Laguna Flor de Luna.

(represented on the biplot by the numbers 3, 4, and 5 respectively) are all locations that are characterized by having abundant water sources. Three species of anurans, *Dendropsophus ebreccatus, Leptodactylus fragilis,* and *Rana vailantii,* are associated with this group of locations*.* The latter two species exhibit ecologies that are strongly tied to water sources. A cluster between sampling locations 15, 16, and 17 (Rio Chocop, Rio Escondido, and Flor de Luna respectively) and the anurans *Dendropsophus microcephalus, Leptodactylus melanonotus, Rana brownorum,* and *Tlalocohyla picta* was also identified in the ordination, again this cluster is characterized by the availability of water, in this case large water bodies including rivers and a lake. Further clusters included four species that are associated with Yaxhá (location 8) and two species that are both associated with a single location; *Triprion petasatus*, a dry forest adapted hylid, is associated with the highly seasonally dry forest of Mirador (location 10 on the biplot) and *Gastrophryne elegans*, a microhylid, is associated with Carmelita (location 7 on the biplot).

The largest cluster was between four locations and seven species and is an association between the locations AE-LTNP, Uaxactún, El Remate A, and El Remate B (represented on the biplot by numbers 1, 6, 13, and 14 respectively). This cluster identifies three widespread and commonly occurring species (*Incilius valliceps*, *Hypopachus variolosus*, and *Trachycephalus typhonius*) that account for the six most common sub-assemblages (26% of the total assemblage) and four species that occur rarely within the MBR (*Engystomops pustulosus*, *Eleutherodactylus leprus, Bolitoglossa mexicanus* and *B. rufescens*) that account for the eight most rare sub-assemblages (35% of the total assemblage)*.*

Ordination of the snake LVM revealed several clusters, the largest of which was between three locations (AE-LTNP, LF-LTNP, and Cerro Cahui) and seven species that included three of the eight most commonly occurring species (*Ninia sebae, Bothrops asper,* and *Imantodes cenchoa*) (Fig 6.5). A further grouping consisted of four locations (Carmelita, Nakum, Cruce Dos Aguadas, and Rio Chocop) and included three species of snakes (*Drymarchon melanurus, Mastigodryas melanolomus*, and *Tantilla tenuis*). Two species, *Tantillita canula* and *Phrynonax poecilionotus*, were associated with El Remate A, and *Oxyrhopus petolarius* was associated with NE-LTNP. Several clusters of locations and species were revealed in the ordination of the lizard and turtle LVM (Figure 6.6). Nine species, including three species from the ten most common species (*Basiliscus vittatus, Marisora unimarginata,* and *Norops tropidonotus*) showed associations with five locations (Carmelita, Mirador, El Remate A, El Remate B, and Rio Chocop) across the MBR. Four species (*Norops biporcatus, N. rodriguezi, Laemanctus longipes,* and *Lepidophyma flavimaculatum*) were associated with LF-LTNP and Yaxhá. A further three clusters involved a single location and between one and five species. Five species (*N. unilobatus, Sceloporus serrifer, S. lundelli,* and *Kinosternon leucostomum*) clustered with Cerro Cahui. *Holcosus undulata* and *Corytophanes cristatus* clustered with NE-LTNP, and *Lepidophyma mayae* clustered with Cruce Dos Aguadas.

6.5 Discussion

The analysis of CtoR and RtoC sub-assemblages showed that both for the amphibian and reptile assemblages of the MBR the presence of common species was more useful in predicting the overall diversity of the complete assemblage than were the rare species. At a regional scale, studies across multiple taxa have found that in general this pattern holds true (Jetz et al. 2004; Lennon et al 2004; Mazaris et al. 2010; Oldekop et al. 2012). The most widespread 25% of bird species have been shown to account for 62-75% of variation in diversity (Lennon et al. 2004). Although the CtoR analysis showed that common species of amphibians and reptiles may describe the overall diversity of the MBR more than rare ones, the difference in prediction between C2R and R2C subassemblages was small in comparison to previous studies on other taxa (Mazaris et al. 2008; Lennon et al. 2011). Studies of multiple taxa in Ecuador also revealed a difference in the ability of common species to predict overall diversity compared to rare ones, in particular cryptic leaf-litter frogs (Oldekop et al. 2012). It is possible that the cryptic nature of many amphibian and reptile species confounds the use of C2R methodologies to successfully reveal information about overall diversity of the assemblage.

Because we know more about the ecology of common species it is therefore possible to infer characteristics of the habitat they occur in. Changes in climate and land-use are likely to show their affects through changing patterns in the species richness through changes detected in the abundance and dominance of common species rather than rare ones (Lennon et al.

2004). Human disturbance has been found to affect the relative contribution of common or rare species to the overall species diversity of a given area, in that common, widespread species dominate the assemblage at disturbed locations and so contribute more to the understanding of diversity in those locations, whereas rare species contribute more information in undisturbed locations (Oldekop et al. 2012). High levels of dominance of both amphibians and reptiles have been reported in disturbed habitats in LTNP (see Chapter 4 of this thesis), and so this effect should be taken into consideration in the wider MBR region. Net productivity and habitat heterogeneity have been implicated as predictors of patterns of diversity (Jetz and Rahbek 2002). In the MBR, areas with a mosaic of natural habitats can be expected to have higher diversity of species, this might be especially true for amphibians as shown by higher diversity of amphibians and reptiles in low lying forest in LTNP (see Chapter 2 of this thesis). Predicting patterns of diversity using the presence of common species is more accurate when using large datasets that are at a finer geographical resolution (Mazaris et al. 2008). The larger reptile dataset was more effective at predicting larger numbers of species than the smaller amphibian dataset, with a correlation of 0.8 reached with 8% of the most common reptile species, compared to 20% of the most common amphibian species. Although widely spread throughout the MBR, the sampling locations in this study are quite patchy, so increased sampling will likely increase the accuracy of our understanding of the patterns of amphibian retile diversity in the MBR.

Ordinations of the three LVM's were successful in not only revealing relationships between locations in the MBR, and between species, but also between locations and species. The relationships between locations were different in each model highlighting the need to consider differences in the relationships between different taxa and locations. This is to be expected given the wide diversity in resource requirements found between taxa. Studies of bird assemblages in sub-Saharan Africa used GIS mapping techniques to predict the location of regions with high levels of endemism, this required a comprehensive knowledge of the distribution of birds on wide geographical scale (Jetz et al. 2004). In the current study, similar predictions of species distributions were made possible with a smaller, and less comprehensive dataset using Bayesian latent variable ordinations to elucidate relationships between species and locations across a smaller regional scale.

The combined results show that the presence of common, widespread amphibian and reptile species are useful in describing the overall species diversity at locations within the MBR, and that also it is possible to predict which species might be present at a location based on certain characteristics. In particular the presence of small and large water bodies might be useful in predicting the presence of certain species. The ordinations showed associations between species and locations where they had not yet been recorded based on their presence at locations in the same cluster. This might be suggestive of actual presence at locations in those clusters. This is particularly useful given the pressing need to quickly understand the diversity of amphibian and reptiles in the MBR with growing pressure from forest loss and other pressures within the reserve (Radachowsky et al. 2012; Sesnie et al. 2017; Devine et al. 2020). Rapid field assessments at as yet unsampled locations within the MBR combined with a similar methodology as employed in the current study will be useful in identifying distributional patterns of amphibian and reptile species in order to inform appropriate and effective forest management techniques and conservation policy at a regional scale in the MBR. Studies have also shown that this approach is appropriate for a wide range of taxa and could be deployed by other studies in the MBR to bolster conservation efforts (Jetz et al. 2004; Lennon et al. 2004; Mazaris et al. 2008; Oldekop et al. 2012; Bispo et al. 2017).

Understanding species distribution is critical to halting the global decline of biodiversity. To the best of our knowledge this is the first time the CtoR approach has been applied to a full amphibian and reptile assemblage. The results presented in this study confirm that this approach is effective for understanding patterns of amphibian and reptile diversity in the MBR. In cases where studies are time-limited and rare species are difficult to detect, the presence of common widespread species provides important and usable information about the overall diversity at location, landscape, and regional scales and can be used to predict patterns of diversity and inform conservation management and policy.

6.6 References

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Chapter 7 - General Discussion

False fer de lance – *Xenodon rabdocephalus*

7.1 General Discussion

The herpetofauna of Laguna del Tigre National Park (LTNP) is highly diverse and as currently understood contains 93 native species and 2 introduced species of gekkonid lizards and represents 24% of the country's native amphibian and reptile diversity (Chapter 2). The number of species known from LTNP is likely to rise with more survey effort, especially in respect to snakes (Chapter 3). Significant changes in both assemblage diversity and structure were detected in response to changes in land-use within the national park (Chapters 3 and 4). Analysis of natural history traits found within the amphibian and reptile assemblages identified that the ecology of a given species strongly influenced the presence or absence of that species in respect to proximity to forest edges. Trait analysis was also successful in identifying traits in amphibians and snakes that allowed certain species to successfully colonise disturbed habitats and, in some cases, dominate the assemblages of those habitats (Chapter 5). The presence of easily detected, widespread and commonly occurring species was useful in predicting levels of diversity at a given location within LTNP and by using Bayesian ordinations, it was possible to identify and use associations between diversity levels and location within the Mayan Biosphere Reserve (MBR) to predict patterns of diversity over large geographical scales.

Global biodiversity levels are declining at a rapidly increasing rate and while there are many factors contributing to those declines the most significant factor is consistently habitat loss and change in land-use (Mantyka-Pringle et al. 2011). Habitat loss and change in land-use are currently at their highest levels within the tropical regions and Central America is no exception. Within Central America, deforestation rates are highest in Guatemala which are being driven by a rapidly increasing human population, a consequence of which is that many forested areas are being converted to agriculture and cattle ranching (Tolisano and López 2010; Ceballos et al. 2015). The highest rates of deforestation in Guatemala have been documented in LTNP and MBR and have been reported to be driven by narcotics trafficking (Sesnie et al. 2017).

Guatemala is a mega-diverse country (Sales et al. 2016), and current estimates indicate that Guatemala holds 10,364 species of plants, 1,033 fish, 735 birds, 244 mammals, 143 amphibians, and 246 reptiles (Köhler 2008; Acevedo et al. 2010; Tolisano and López 2010; Köhler 2011). Much of Guatemala's biodiversity is found in the mountainous regions that form much of the central and southern part of the country (Tolisano and López 2010). This is especially the case for amphibians and reptiles, where all but one of Guatemalan endemics are restricted to the highlands (Acevedo et al. 2010). Endemic species account for 27% of amphibians and 9.8% of reptiles in Guatemala (Acevedo et al. 2010). With the exception of the endangered Central American river turtle (Anleu et al. 2007), very little conservation focus is currently given to the herpetofauna of LTNP, the MBR, or northern Guatemala. However, many of the species that occur in this region have distributions that are restricted to the wider Yucatán Peninsula and are found at the southern-most part of their ranges in northern Guatemala and in terms of the country's herpetofaunal diversity only occur in this region (Lee 1996; González-Sánchez et al. 2017). Although current assessments at both global and national levels do not consider the majority amphibians and reptiles found in LTNP to be of conservation concern, they represent a significant proportion of Guatemala's diversity (16% of amphibians and 30% of reptiles). The MBR, of which LTNP is the largest core protected area, protects a significant portion of northern Guatemala and with much of the land outside of the reserve converted to agriculture it represents an important stronghold for the amphibians and reptiles of northern Guatemala. With this consideration, the herpetofauna of the MBR and its national parks may be of greater conservation concern than currently realised.

Chapter 2 increased knowledge of the herpetofauna of LTNP and increased the species list from 36 to 95 species. It also assessed species conservation priorities using Environmental Vulnerability Scores (EVS) at a local scale for the first time. The results of the EVS analysis showed that a higher proportion of the herpetofaunal assemblage of LTNP deserves to be considered of conservation concern than shown by either global IUCN Red List or national endangered species assessments. Endemism is a commonly used factor in assessing national conservation status, and although only 9.1% of amphibian and 25.2% reptile species present in LTNP were found to be range restricted or regionally endemic, EVS assessment revealed that 18% of amphibians and 49.3% of reptiles are of local conservation concern.

Chapters 3 and 4 showed that change in land-use affects both diversity and structure of amphibian and reptile assemblages in LTNP, with effects of being felt up to seven kilometres from forest edges. While diversity of both amphibians and reptiles was lower in forest edge habitat close to agriculture than in undisturbed forest the drivers for those differences was different for each group. Low diversity in reptiles at the forest edge was driven by disturbance from agriculture, whereas for amphibians, diversity was higher in undisturbed forest because environmental conditions were more suitable (Chapter 3). Analysis of the assemblage structure showed that not only was diversity lower closer to agriculture but that the assemblages were dominated by just a few successful species, additionally the presence and abundance of the majority of amphibian and lizard species responded negatively to forest edges regardless of their nature (i.e., natural or anthropogenically created), whereas the majority of snake species were more sensitive to the presence of agriculture (Chapter 4).

Chapter 5 showed that life history traits are a major influence on the ability of a given species to utilise disturbed habitats. Amphibians that can tolerate drier conditions or those that eat ants seem to colonise disturbed areas more successfully than those that do not, as do those snake species that specialize on feeding on nocturnal and terrestrial anurans. Chapters 4 and 5 showed that fragmentation has a significant affect further into the forest of LTNP and that this significantly affects the amphibian and reptile assemblages. Chapter 6 showed that it is possible to use the presence of common widespread species to assess overall diversity of amphibians and reptiles at a given location. This approach could be particularly useful because many amphibian and reptile species are cryptic and/or occur at low densities and are therefore difficult to detect. Combining knowledge of the distribution of common species with ordination techniques it was possible to identify similarities in the diversity of different locations in the MBR without the need for intensive survey effort (Chapter 6).

Laguna del Tigre National Park by its definition of being the largest core protected area within the MBR is an effort by the Guatemalan authorities to spare land for the conservation of biodiversity. Interestingly, the current situation in LTNP also fits the land sharing approach with legal agricultural concessions issued to two Mayan communities. As such it offers a unique insight into how the theoretical approaches of land sparing and land sharing function in a real-life situation. This thesis shows that the effects of habitat loss and change in land-use could have a more significant impact on amphibians and reptiles than realised with edge effects being felt at significant distances into the forest. In this example the implementation of land sharing in LTNP has significant effects on the amphibian and reptile assemblages in LTNP. As a result of this and combined with high rates of illegal deforestation in other parts of LTNP, change in land use is having a significant negative effect on the diversity and abundance of amphibians and reptiles in the park. The EVS approach is useful for assessing conservation priorities on a local level (it may be possible for this approach to be extended to other taxa). The presence of common species and relationships between the diversity of assemblages at different locations can be used to target conservation efforts. With increasing rates of habitat loss and resulting fragmentation of forest cover in Petén, including the MBR and LTNP, the amphibian and reptile assemblages of northern Guatemala are likely to be severely impacted and reduced to just a handful of species dominating the remaining assemblages even if relatively large fragments of forest remain. As such the conservation policy for amphibians and reptiles within the MBR should take their local conservation status into consideration in addition to national and global assessments.

Biodiversity loss is continuing at unprecedented rates, and is driven primarily by habitat loss through habitat destruction and change in land use. This is particularly prevalent in the tropical regions where human population growth and biodiversity are at their highest. This thesis shows that while overall diversity declines in disturbed habitats there are fine scale effects on the faunal assemblage that are more nuanced and often driven by the ability to adapt to the new environmental conditions. Winning species in these areas tend to dominate the assemblage, leading to widespread homoginisation and marginalization of losing species. This effect is unrelated to conservation status, and continued reliance on international designations, such as IUCN redlist status, for setting regional conservation priorities may lead to continued declines in populations of ‘low’ priority species to the point of local extirpations and extinctions.

7.2 References

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Appendix I - Tables of Bayesian GLM models for the amphibian and reptile assemblages of LTNP in response to distance to agriculture and forest edge

Table I.1: Bayesian GLM results showing response of amphibian species in AE to the presence of agriculture.

Species	**Present/ Absent**	**Lower95**	**Upper95**	**Mean**	**SD**	**SSeff**	**psrf**
DeMi	A	**-1981.7**	**-2.403**	**-804.31**	608.437	49046	1.000059
ElLe	A	**-1944.6**	**-3.31**	**-794.01**	597.632	47867	1.000039
EnPu	A	**-1953.5**	**-2.756**	**-798.11**	599.185	50271	0.999994
GaEl	A	**-1964.2**	**-2.929**	**-800.65**	603.039	48783	1.000034
LeFra	A	**-1966.4**	**-1.961**	**-800.63**	603.548	49267	1.000036
LeMe	A	**-1964.6**	**-2.064**	**-801.73**	603.774	48440	1.000081
RaBr	A	**-1949**	**-2.208**	**-794.42**	597.416	51802	1.000013
RaVa	A	**-1972.6**	**-2.839**	**-803.57**	605.53	46374	1.000014
RhDo	A	**-1967.5**	**-3.208**	**-803.01**	604.363	50122	1.000112
RhMa	A	**-1951**	**-3.199**	**-799.43**	598.879	49154	1.000043
ScSt	A	**-1963.1**	**-2.61**	**-798.3**	601.867	48378	1.000117
TlLo	A	**-1957.4**	**-2.405**	**-798.58**	600.564	49559	0.999997
TlPi	A	**-1978.1**	**-2.938**	**-808.26**	604.761	47988	1.000033
TrPe	A	**-1955.3**	**-2.16**	**-804.66**	600.954	49432	1.000013
TrTy	A	**-1960.7**	**-2.214**	**-801.66**	603.612	47593	1.000031

Species codes; DeMi = *Dendropsophus microcephalus,* ElLe = *Eleutherodactylus leprus,* EnPu = *Engystomops pustulosus,* GaEl = *Gastrophyryne elegans,* LeFra = *Leptodactylus fragilis,* LeMe = *Leptodactylus melanonotus,* RaBr = *Rana brownorum,* RaVa = *Rana vailantii,* RhDo = *Rhinophrynus dorsalis,* RhMa = *Rhinella marina,* ScSt = *Scinax staufferi,* TlLo = *Tlalocohyla loquax,* TlPi = *Tlalocohyla picta,* TrPe = *Triprion petasatus,* TrTy = *Trachycephalus typhonius.* Significant results highlighted in bold.

Table I.2: Bayesian GLM results showing response of amphibian species in HF to the presence of agriculture.

Species	**Present / Absent**	**Lower95**	**Upper95**	**Mean**	**SD**	**SSeff**	**psrf**
BoMe	A	**-1960**	**-3.143**	**-800.2**	601.875	48167	0.999985
DeMi	A	**-1955**	**-3.265**	**-801.6**	602.091	48628	1.000126
RaVa	A	**-1976.6**	**-2.79**	**-802.76**	606.684	47733	1.000045
RhDo	A	**-1954.1**	**-3.648**	**-800.15**	599.584	49408	1.000063
RhMa	A	**-1961.4**	**-3.143**	**-803.81**	603.49	48760	1.000032
ScSt	A	**-1968.3**	**-3.485**	**-803.63**	604.195	49679	1.000093
TrPe	A	**-1956.8**	**-3.714**	**-796.53**	598.207	48906	1.000006

Species codes; BoMe = *Bolitoglossa mexicanus,* DeMi = *Dendropsophus microcephalus,* RaVa = *Rana vailantii,* RhDo = *Rhinophrynus dorsalis,* RhMa = *Rhinella marina,* ScSt = *Scinax staufferi,* TrPe = *Triprion petasatus.* Significant effects indicated in bold.

Table I.3: Bayesian GLM results showing response of amphibian species in LF to the presence of agriculture.

Species	Present/ Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
DeMi	A	**-1958.053**	**-2.970**	**-801.250**	603.906	49435	1.0000511
ElLu	A	**-1968.517**	**-2.617**	**-804.804**	605.820	49004	1.0000943
TlLo	A	**-1959.081**	**-3.818**	**-799.294**	600.400	48729	1.0000205
TlPi	A	**-1959.018**	**-3.556**	**-801.225**	600.823	48850	0.9999878

Species codes; DeMi = *Dendropsophus microcephalus,* ElLe = *Eleutherodactylus leprus,* TlLo = *Tlalocohyla loquax,* TlPi = *Tlalocohyla picta.* Significant effects indicated in bold.

Table I.4: Bayesian GLM results showing response of amphibian species in NE to the presence of agriculture.

Species	Present/ Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
GaEl	A	**-1962.9**	**-3.499**	**-800.71**	603.32	48320	1.000119
RhDo	A	**-1949.1**	**-3.977**	**-799.76**	598.543	49042	1.000064
ScSt	A	**-1963**	**-3.059**	**-802.59**	602.335	49801	0.99998
TlLo	A	**-1965.6**	**-3.44**	**-802.04**	602.844	48806	1.000084
TlPi	A	**-1961**	**-3.456**	**-800.89**	601.018	50291	1.000119
TrPe	A	**-1960.3**	**-3.829**	**-798.85**	603.628	48487	1.000092

Species codes; GaEl = *Gastrophyryne elegans,* RhDo = *Rhinophrynus dorsalis,* ScSt = *Scinax staufferi,* TlLo = *Tlalocohyla loquax,* TlPi = *Tlalocohyla picta,* TrPe = *Triprion petasatus.* Significant effects indicated in bold.

Table I.5: Bayesian GLM results showing response of amphibian species in AE to the presence of forest edge.

Species	Present/ Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
DeMi	A	**-1967**	**-2.82**	**-803.75**	603.198	49643	1.000077
ElLu	A	**-1966.8**	**-3.138**	**-798.39**	602.434	48754	1.000049
EnPu	A	**-1953.7**	**-2.866**	**-798.31**	599.357	50859	0.999989
GaEl	A	**-1961**	**-1.979**	**-798.29**	603.568	50026	1.00001
LeFra	A	**-1970.9**	**-2.632**	**-801.58**	603.641	49056	1.000039
LeMe	A	**-1981.5**	**-2.577**	**-807.76**	609.017	49841	1.000006
RaBr	A	**-1954.1**	**-2.191**	**-798.53**	598.306	50843	1.000118
RaVa	A	**-1960.7**	**-2.228**	**-801.86**	602.985	48562	1.000045
RhDo	A	**-1967.2**	**-2.822**	**-801.89**	605.726	47596	0.999998
RhMa	A	**-1976.7**	**-2.491**	**-802.53**	604.772	48598	1.000305
ScSt	A	**-1959.9**	**-2.366**	**-795.4**	600.005	48764	1.000035
TlLo	A	**-1974.4**	**-2.638**	**-805.3**	607.588	47237	1
TlPi	A	**-1974.4**	**-2.216**	**-802.64**	606.06	47974	1.000027
TrPe	A	**-1956.6**	**-2.789**	**-797.7**	600.096	49021	1.000086
TrTy	A	**-1948.8**	**-2.751**	**-797.37**	598.749	48362	1.000059

Species codes; DeMi = *Dendropsophus microcephalus,* ElLe = *Eleutherodactylus leprus, EnPu = Engystomops pustulosus,* GaEl = *Gastrophyryne elegans,* LeFra = *Leptodactylus fragilis,* LeMe = *Leptodactylus melanonotus,* RaBr = *Rana brownorum,* RaVa = *Rana vailantii,* RhDo = *Rhinophrynus dorsalis,* RhMa = *Rhinella marina,* ScSt = *Scinax staufferi,* TlLo = *Tlalocohyla loquax,* TlPi = *Tlalocohyla picta,* TrPe = *Triprion petasatus,* TrTy = *Trachycephalus typhonius.* Significant effects indicated in bold.

Table I.6: Bayesian GLM results showing response of amphibian species in HF to the presence of forest edge.

Species	Present/ Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
BoMe	A	**-1969.387**	**-3.899**	**-804.588**	603.146	49163	1.000096
DeMe	A	**-1956.600**	**-3.702**	**-800.900**	601.774	48781	1.0000262
RaVa	A	**-1961.243**	**-3.706**	**-800.419**	601.316	48509	1.0000413
RhDo	A	**-1959.460**	**-3.325**	**-798.275**	600.298	48843	1.0000942
RhMa	A	**-1972.381**	**-3.517**	**-802.618**	603.647	48793	1.0001255
ScSt	A	**-1955.566**	**-3.738**	**-800.361**	599.642	49334	1.0000051
TrPe	A	**-1959.699**	**-3.846**	**-799.832**	600.064	49743	1.0000699

Species codes; BoMe = *Bolitoglossa mexicanus,* DeMi = *Dendropsophus microcephalus,* RaVa = *Rana vailantii,* RhDo = *Rhinophrynus dorsalis,* RhMa = *Rhinella marina,* ScSt = *Scinax staufferi,* TrPe = *Triprion petasatus.* Significant effects indicated in bold.

Table I.7: Bayesian GLM results showing response of amphibian species in LF to the presence of forest edge.

Species	Present/ Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
DeMi	A	**-1966.493**	**-3.740**	**-805.832**	604.675	48876	1.0000664
ElLu	A	**-1959.187**	**-3.586**	**-799.598**	600.591	49526	1.0000524
TlLo	A	**-1948.920**	**-3.960**	**-797.534**	598.875	51297	1.0000123
TlPi	A	**-1961.739**	**-4.133**	**-806.981**	602.695	49254	1.0000693

Species codes; DeMi = *Dendropsophus microcephalus,* ElLe = *Eleutherodactylus leprus,* TlLo = *Tlalocohyla loquax,* TlPi = *Tlalocohyla picta.* Significant effects indicated in bold.

Table I.8: Bayesian GLM results showing response of amphibian species in NE to the presence of forest edge.

Species	Present/ Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
GaEl	A	**-1968.517**	**-3.710**	**-803.789**	603.875	48864	0.9999988
RhDo	A	**-1947.776**	**-3.642**	**-794.907**	597.457	48610	1.0000205
ScSt	A	**-1974.973**	**-3.634**	**-804.506**	603.926	50523	1.0000044
TlLo	A	**-1980.669**	**-3.252**	**-807.686**	608.251	48865	1.0000358
TlPi	A	**-1973.685**	**-2.846**	**-803.862**	603.991	48816	1.0000276
TrPe	A	**-1971.323**	**-3.526**	**-803.342**	606.523	48420	1.0000189

Species codes; GaEl = *Gastrophyryne elegans,* RhDo = *Rhinophrynus dorsalis,* ScSt = *Scinax staufferi,* TlLo = *Tlalocohyla loquax,* TlPi = *Tlalocohyla picta,* TrPe = *Triprion petasatus.* Significant effects indicated in bold.

Table I.9: Bayesian GLM results showing response of snake species in AE to the presence of agriculture.

Species	Present / Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
AdQu	A	-1968.407	0.909	-799.206	603.831	24466	1.000042
BoAs	A	-1950.603	0.991	-798.922	601.799	24515	1.0002955
BoIm	A	-1967.667	0.902	-803.693	606.119	25102	0.9999849
ClSc	A	**-1958.24**	**-0.594**	**-797.942**	601.214	24592	1.0000228
CoBi	A	***-1985.2***	***0.111***	***-803.364***	607.635	24696	1.000018
CoIm	A	**-1965.85**	**-0.31**	**-796.299**	602.617	24151	1.0001059
CoMe	A	-1942.838	1.126	-799.195	598.745	25240	1.0000016
CoSc	P	-1.122	3.184	0.912	1.097	233	1.0199963
DrMa	A	-1956.619	0.929	-795.435	601.02	24812	1.0002043
ImCe	P	-4.194	2.177	-0.922	1.61	530	1.0081949
LaAb	A	***-1941.18***	***0.48***	***-791.608***	599.211	23886	1.0001801
LeAh	P	-4.153	2.165	-0.915	1.605	547	1.0085069
LeMex	A	-1981.95	0.549	-805.677	606.771	23807	1.0000017
LeSe	P	0	0	0	0	NA	NA
MaMe	A	***-1965.15***	***0.458***	***-802.064***	606.089	24529	0.999999
MiDi	P	-4.202	2.121	-0.92	1.596	545	1.0076201
NiDi	A	-1989.671	0.743	-804.016	609.928	23691	0.9999861
NiSe	P	-4.23	2.101	-0.929	1.602	597	1.0080683
OxAe	A	**-1968.3**	**-0.004**	**-806.26**	606.683	24749	1.0004243
OxPe	A	***-1960.97***	***0.048***	***-798.675***	603.28	24101	1.0000244
PlEl	A	***-1978.96***	***0.484***	***-800.554***	609.741	23391	1.0000664
PsFl	A	-1953.657	0.757	-799.98	604.334	25394	1.000266
SiDi	A	-1968.319	0.632	-801.87	605.169	24090	1.0000907
SiNe	A	-1956.065	1.337	-798.216	603.265	24538	1.0002809
SpPu	A	***-1964.6***	***0.089***	***-801.888***	603.482	24242	0.9999878
TaMo	A	-1991.524	0.54	-802.796	611.231	24017	1.0000594
TrSa	P	-4.141	2.206	-0.92	1.607	612	1.0078458
XeRa	A	***-1969.06***	***0.356***	***-802.72***	604.022	24356	0.999989

Species codes; AdQu = *Adelphicos quadrivigattus*, BoAs = *Bothrops asper,* BoIm = *Boa imperator*, ClSc = *Clelia scytalina*, CoBi = *Coniophanes bipunctatus*, CoIm = *Coniophanes imperialis*, CoMe = *Coluber mentovarius*, CoSc = *Coniophanes schmidtii*, DrMa = *Drymobius margaritiferus*, ImCe = *Imantodoes cenchoa*, LaAb = *Lampropeltis abnorma*, LeAh = *Leptophis ahaetulla*, LeMex = *Leptophis mexicanus*, LeSe = *Leptodiera septentrionalis*, MaMe = *Mastigodryas melanonomus*, MiDi = *Micrurus diastema*, NiDi = *Ninia diademata*, NiSe = *Ninia sebae*, OxAe = *Oxybelis aeneus*, OxPe = *Oxyrhopus petolarius*, PlEl = *Pliocercus elapoides*, PsFl = *Psuedelaphe flavirufa*, SiDi = *Sibon dimidiata*, SiNe = *Sibon nebulata*, SpPu = *Spilotes pullatus*, TaMo = *Tantilla moesta*, TrSa = *Tropidodipsas sartorii*, XeRa = *Xenodon rabdocephalus*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.10: Bayesian GLM results showing response of snake species in HF to the presence of agriculture.

Species	Present/Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
AdQu	A	**-1958.32**	**-1.165**	**-802.555**	604.679	24554	0.9999803
BoAs	P	-1.615	2.613	0.442	1.082	247	1.0218778
BoIm	P	-0.681	3.235	1.2	1.011	205	1.0258719
ClSc	A	**-1972.08**	**-0.673**	**-802.966**	604.622	25015	1.0000734
CoBi	A	-1972.943	0.617	-807.754	608.298	24338	1.000008
CoIm	A	**-1955.81**	**-0.94**	**-794.876**	598.882	24909	1.0001221
CoMe	P	-4.551	1.798	-1.392	1.601	534	1.0084234
CoSc	P	-2.099	2.393	0.102	1.14	266	1.0180849
DrMa	P	-2.837	2.053	-0.393	1.231	300	1.0155936
ImCe	P	-1.042	2.983	0.885	1.035	219	1.0242773
LaAb	A	**-1962.61**	**-0.033**	**-797.094**	603.763	24208	1.0000271
LeAh	A	**-1980.76**	**-0.578**	**-801.783**	606.995	24669	0.9999905
LeMex	P	-4.584	1.599	-1.382	1.578	554	1.0082787
LeSe	P	-0.65	3.302	1.199	1.013	219	1.0249115
MaMe	P	-4.684	1.635	-1.401	1.598	635	1.0087486
MiDi	P	-2.809	2.103	-0.397	1.242	296	1.0151473
NiDi	A	**-1955.44**	**-0.008**	**-797.068**	598.679	25702	1.0000007
NiSe	P	-0.826	3.164	1.055	1.025	204	1.0240368
OxAe	P	-4.634	1.625	-1.385	1.589	503	1.0109382
OxPe	P	-2.125	2.36	0.105	1.135	252	1.0196434
PlEl	P	-4.646	1.687	-1.392	1.604	554	1.0102755
PsFl	A	**-1961.94**	**-0.259**	**-795.87**	604.145	24459	0.9999822
SiDi	A	**-1979.57**	**-0.468**	**-803.817**	604.204	25544	1.0001106
SiNe	P	-2.034	2.425	0.113	1.134	250	1.0171423
SpPu	A	***-1955***	***0.275***	***-799.945***	603.769	24803	1.0000396
TaMo	P	-4.528	1.739	-1.402	1.58	578	1.0087679
TrSa	P	-2.072	2.394	0.111	1.137	258	1.0196006
XeRa	A	**-1954.02**	**-0.596**	**-794.252**	600.886	24896	1.0001526

Species codes; AdQu = *Adelphicos quadrivigattus*, BoAs = *Bothrops asper,* BoIm = *Boa imperator*, ClSc = *Clelia scytalina*, CoBi = *Coniophanes bipunctatus*, CoIm = *Coniophanes imperialis*, CoMe = *Coluber mentovarius*, CoSc = *Coniophanes schmidtii*, DrMa = *Drymobius margaritiferus*, ImCe = *Imantodoes cenchoa*, LaAb = *Lampropeltis abnorma*, LeAh = *Leptophis ahaetulla*, LeMex = *Leptophis mexicanus*, LeSe = *Leptodiera septentrionalis*, MaMe = *Mastigodryas melanonomus*, MiDi = *Micrurus diastema*, NiDi = *Ninia diademata*, NiSe = *Ninia sebae*, OxAe = *Oxybelis aeneus*, OxPe = *Oxyrhopus petolarius*, PlEl = *Pliocercus elapoides*, PsFl = *Psuedelaphe flavirufa*, SiDi = *Sibon dimidiata*, SiNe = *Sibon nebulata*, SpPu = *Spilotes pullatus*, TaMo = *Tantilla moesta*, TrSa = *Tropidodipsas sartorii*, XeRa = *Xenodon rabdocephalus*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.11: Bayesian GLM results showing response of snake species in LF to the presence of agriculture.

Species	Present / Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
BoIm	A	-1969.04	0.883	-804.103	603.347	24917	0.9999821
ClSc	A	***-1969.01***	***-0.827***	***-799.255***	602.456	24738	1.0000667
CoMe	A	-1958.331	1.177	-798.483	601.485	24905	1.0000358
LaAb	A	-1945.444	0.761	-791.318	598.622	26106	1.0002371
LeAh	A	-1953.812	1.058	-795.98	602.373	24371	1.0000661
LeMex	A	-1985.414	0.521	-807.578	611.447	24497	1.0001707
MaMe	A	**-1952.08**	**0.41**	**-794.244**	601.535	24421	1.0000928
OxAe	A	**-1948.89**	**0.461**	**-794.377**	599.373	24233	1.0005537
OxPe	A	-1958.083	0.869	-796.887	601.446	24458	1.0002739
PlEl	A	**-1952.72**	**-0.072**	**-796.726**	601.188	25201	1.0001487
SpPu	A	***-1955.67***	***-0.521***	***-795.381***	601.821	25152	1.0001009
TaMo	A	-1954.164	0.511	-799.955	603.391	24969	0.9999949

Species codes; BoIm = *Boa imperator*, ClSc = *Clelia scytalina*, CoMe = *Coluber mentovarius*, LaAb = *Lampropeltis abnorma*, LeAh = *Leptophis ahaetulla*, LeMex = *Leptophis mexicanus*, MaMe = *Mastigodryas melanonomus*, OxAe = *Oxybelis aeneus*, OxPe = *Oxyrhopus petolarius*, PlEl = *Pliocercus elapoides*, SpPu = *Spilotes pullatus*, TaMo = *Tantilla moesta*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.12: Bayesian GLM results showing response of snake species in NE to the presence of agriculture.

Species	**Present /Absent**	**Lower95**	**Upper95**	**Mean**	**SD**	**SSeff**	**psrf**
AdQu	A	**-1960.22**	**-0.973**	**-801.813**	601.46	25410	1.0000011
BoIm	A	**-1957.11**	**-0.409**	**-802.744**	602.659	24268	0.9999936
CoBi	A	***-1957.13***	***0.381***	***-794.62***	604.421	24768	1.0001135
CoIm	A	***-1955.27***	***0.05***	***-795.992***	599.943	24965	1.0003003
CoMe	A	**-1977.53**	**-0.417**	**-804.477**	606.879	24143	1.000148
LeAh	A	***-1959.43***	***0.177***	***-799.812***	603.448	25227	0.9999879
LeMex	A	**-1957.12**	**-0.843**	**-793.629**	597.77	24910	1.000016
NiDi	A	**-1958.45**	**-0.616**	**-800.022**	607.22	24379	1.0001713
OxAe	A	**-1965.21**	**-1.19**	**-799.634**	601.848	25336	1.0000438
PlEl	A	**-1996.2**	**-0.214**	**-805.496**	612.5	23985	1.0002525
PsFl	A	**-1963.3**	**-0.593**	**-799.621**	603.189	24562	1.0005778
SiDi	A	**-1963.14**	**0.119**	**-799.638**	603.311	24910	1.0001169
TaMo	A	**-1977.66**	**0.402**	**-808.382**	608.738	22753	1.0002365
XeRa	A	**-1968.45**	**-1.074**	**-802.412**	602.701	25384	0.9999866

Species codes; AdQu = *Adelphicos quadrivigattus„* BoIm = *Boa imperator*, ClSc = *Clelia scytalina*, CoBi = *Coniophanes bipunctatus*, CoIm = *Coniophanes imperialis*, CoMe = *Coluber mentovarius*, LeAh = *Leptophis ahaetulla*, NiDi = *Ninia diademata*, OxAe = *Oxybelis aeneus*, PlEl = *Pliocercus elapoides*, PsFl = *Psuedelaphe flavirufa*, SiDi = *Sibon dimidiata*, TaMo = *Tantilla moesta*, XeRa = *Xenodon rabdocephalus*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.13: Bayesian GLM results showing response of snake species in AE to the presence of forest edge.

Species	Present/Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
AdQu	A	-1959.595	1.417	-795.32	599.592	50615	1.0001471
BoAs	A	-1968.323	0.686	-799.466	605.486	49184	1.0000558
BoIm	A	***-1966.39***	***0.344***	***-797.632***	602.059	51001	1.0000377
ClSc	A	***-1966.04***	***0.206***	***-798.668***	605.103	48191	1.0000345
CoBi	A	***-1948.47***	***0.374***	***-794.449***	598.47	49784	1.0000061
CoIm	A	-1959.728	0.813	-797.188	599.375	49469	1.0000145
CoMe	A	***-1975.91***	***0.351***	***-799.785***	606.178	48552	0.9999945
CoSc	P	-1.165	3.14	0.905	1.095	541	1.0085806
DrMa	A	**-1956.96**	**-0.072**	**-801.146**	600.481	49474	0.9999984
ImCe	P	-4.174	2.114	-0.925	1.6	1333	1.0032694
LaAb	A	***-1957.4***	***0.065***	***-796.756***	600.563	48663	1.0000832
LeAh	P	-4.156	2.186	-0.937	1.61	1422	1.0035477
LeMex	A	***-1961.45***	***0.105***	***-802.34***	605.155	48585	1.0000976
LeSe	P	0	0	0	0	NA	NA
MaMe	A	***-1953.43***	***0.445***	***-797.552***	601.245	49822	0.9999822
MiDi	P	-4.161	2.174	-0.935	1.6	1335	1.0030388
NiDi	A	***-1958.23***	***0.461***	***-796.447***	601.181	48293	1.0001403
NiSe	P	-4.191	2.124	-0.934	1.604	1295	1.0033528
OxAe	A	***-1962.53***	***0.267***	***-799.168***	602.838	49016	1.0001464
OxPe	A	***-1967.48***	***0.255***	***-806.062***	606.452	47813	1.0001635
PlEl	A	-1961.853	0.803	-801.585	603.571	51171	1.0000047
PsFl	A	***-1968.14***	***0.408***	***-802.988***	603.871	49025	1.0000487
SiDi	A	-1966.337	0.538	-798.262	601.774	49457	1.0002473
SiNe	A	***-1974.34***	***0.315***	***-799.07***	604.348	48741	1.0000718
SpPu	A	***-1959.14***	***0.168***	***-797.956***	602.877	50470	1.0000102
TaMo	A	***-1961.67***	***0.331***	***-799.122***	602.738	50335	1.000012
TrSa	P	-4.14	2.133	-0.936	1.593	1256	1.0029193
XeRa	A	***-1958.43***	***0.123***	***-799.44***	603.315	48245	1.0000772

Species codes; AdQu = *Adelphicos quadrivigattus*, BoAs = *Bothrops asper,* BoIm = *Boa imperator*, ClSc = *Clelia scytalina*, CoBi = *Coniophanes bipunctatus*, CoIm = *Coniophanes imperialis*, CoMe = *Coluber mentovarius*, CoSc = *Coniophanes schmidtii*, DrMa = *Drymobius margaritiferus*, ImCe = *Imantodoes cenchoa*, LaAb = *Lampropeltis abnorma*, LeAh = *Leptophis ahaetulla*, LeMex = *Leptophis mexicanus*, LeSe = *Leptodiera septentrionalis*, MaMe = *Mastigodryas melanonomus*, MiDi = *Micrurus diastema*, NiDi = *Ninia diademata*, NiSe = *Ninia sebae*, OxAe = *Oxybelis aeneus*, OxPe = *Oxyrhopus petolarius*, PlEl = *Pliocercus elapoides*, PsFl = *Psuedelaphe flavirufa*, SiDi = *Sibon dimidiata*, SiNe = *Sibon nebulata*, SpPu = *Spilotes pullatus*, TaMo = *Tantilla moesta*, TrSa = *Tropidodipsas sartorii*, XeRa = *Xenodon rabdocephalus*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.14: Bayesian GLM results showing response of snake species in HF to the presence of forest edge.

Species	Present /Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
AdQu	A	**-1954.77**	**-0.394**	**-798.548**	601.103	48440	1.0001972
BoAs	P	-1.009	2.915	0.831	1.003	435	1.0104457
BoIm	P	-1.981	2.27	0.079	1.077	500	1.0085143
ClSc	A	**-1970.86**	**-0.17**	**-801.491**	604.262	48984	1.0000265
CoBi	A	**-1966.3**	**-0.79**	**-798.62**	604.078	50090	1.0000546
CoIm	A	***-1963.17***	***0.376***	***-797.6***	603.037	49154	1.0002538
CoMe	P	-5.01	1.262	-1.761	1.599	1160	1.0039216
CoSc	P	-2.404	2.045	-0.256	1.121	565	1.0075798
DrMa	P	-3.137	1.735	-0.75	1.229	693	1.0054229
ImCe	P	-1.426	2.584	0.524	1.028	459	1.0087407
LaAb	A	**-1964.89**	**-0.436**	**-799.689**	605.349	47652	1.0000419
LeAh	A	**-1981.65**	**-0.319**	**-805.314**	608.35	48314	1.0000276
LeMex	P	-4.978	1.296	-1.765	1.593	1253	1.003415
LeSe	P	-1.06	2.862	0.839	1.001	432	1.0106069
MaMe	P	-4.967	1.303	-1.755	1.59	1266	1.0030436
MiDi	P	-3.138	1.75	-0.756	1.233	709	1.0060216
NiDi	A	**-1961.82**	**-0.341**	**-800.725**	602.363	48773	1.0000563
NiSe	P	-1.178	2.779	0.695	1.011	441	1.0090648
OxAe	P	-4.958	1.273	-1.751	1.58	1141	1.003378
OxPe	P	-2.388	2.03	-0.254	1.119	568	1.0075209
PlEl	P	-4.956	1.28	-1.766	1.586	1282	1.002557
PsFl	A	**-1953.2**	**-0.086**	**-795.085**	600.08	48704	1.000045
SiDi	A	**-1970.26**	**-0.481**	**-801.299**	604.379	49883	1.0000068
SiNe	P	-2.459	2.001	-0.255	1.128	569	1.0068504
SpPu	A	**-1960.34**	**-0.417**	**-800.8**	601.505	50266	1.0000545
TaMo	P	-4.999	1.273	-1.743	1.581	1349	1.0039716
TrSa	P	-2.426	2.005	-0.252	1.123	581	1.0071769
XeRa	A	***-1964.92***	***0.137***	***-801.388***	603.409	48850	1.0000435

Species codes; AdQu = *Adelphicos quadrivigattus*, BoAs = *Bothrops asper,* BoIm = *Boa imperator*, ClSc = *Clelia scytalina*, CoBi = *Coniophanes bipunctatus*, CoIm = *Coniophanes imperialis*, CoMe = *Coluber mentovarius*, CoSc = *Coniophanes schmidtii*, DrMa = *Drymobius margaritiferus*, ImCe = *Imantodoes cenchoa*, LaAb = *Lampropeltis abnorma*, LeAh = *Leptophis ahaetulla*, LeMex = *Leptophis mexicanus*, LeSe = *Leptodiera septentrionalis*, MaMe = *Mastigodryas melanonomus*, MiDi = *Micrurus diastema*, NiDi = *Ninia diademata*, NiSe = *Ninia sebae*, OxAe = *Oxybelis aeneus*, OxPe = *Oxyrhopus petolarius*, PlEl = *Pliocercus elapoides*, PsFl = *Psuedelaphe flavirufa*, SiDi = *Sibon dimidiata*, SiNe = *Sibon nebulata*, SpPu = *Spilotes pullatus*, TaMo = *Tantilla moesta*, TrSa = *Tropidodipsas sartorii*, XeRa = *Xenodon rabdocephalus*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.15: Bayesian GLM results showing response of snake species in LF to the presence of forest edge.

Species	Present /Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
AdQu	P	-3.262	1.673	-0.864	1.245	740	1.0057653
BoAs	P	-1.091	2.851	0.792	1.008	445	1.0097862
BoIm	A	-1950.178	0.723	-799.347	600.868	47927	1.0000053
ClSc	A	***-1954.24***	***0.12***	***-795.456***	602.171	49559	1.0000956
CoBi	P	-5.027	1.239	-1.809	1.585	1146	1.0033779
CoIm	P	-0.666	3.193	1.173	0.989	422	1.0105081
CoMe	A	***-1963.71***	***0.064***	***-799.414***	602.41	49987	1.000087
CoSc	P	-1.568	2.487	0.418	1.036	458	1.008859
DrMa	P	-3.258	1.643	-0.793	1.235	666	1.0050851
ImCe	P	-1.991	2.256	0.052	1.077	513	1.00801
LaAb	A	**-1958.14**	**-0.597**	**-798.362**	601.023	49940	1.0000177
LeAh	A	***-1967.57***	***0.303***	***-803.43***	605.877	46551	0.999994
LeMex	A	**-1964.39**	**-1.173**	**-801.095**	604.549	47199	1.0000141
LeSe	P	-1.279	2.703	0.6418	1.017581	445	1.0092496
MaMe	A	**-1961.57**	**-0.737**	**-802.181**	602.721	50171	1.0000071
MiDi	P	-4.967	1.28	-1.799	1.585	1225	1.0037443
NiDi	P	-5.035	1.243	-1.801	1.587	1247	1.0038779
NiSe	P	-0.775	3.119	1.036	0.993	417	1.0094103
OxAe	A	**-1956.24**	**-0.237**	**-793.411**	600.02	48575	1
OxPe	A	**-1947.37**	**-0.423**	**-796.788**	599.805	49204	1.0000379
PlEl	A	**-1957.52**	**-0.371**	**-798.628**	602.118	50188	1.0000578
PsFl	P	-5.075	1.247	-1.821	1.602	1240	1.003416
SiDi	P	-5.057	1.197	-1.797	1.589	1234	1.0033275
SiNe	P	-2.425	2.017	-0.287	1.126	613	1.0075874
SpPu	A	**-1971.5**	**-0.476**	**-800.908**	607.781	48879	1.0000551
TaMo	A	**-1948.67**	**-0.136**	**-797.382**	598.917	48600	1.0000546
TrSa	P	-5.069	1.166	-1.804	1.58	1283	1.0036904
XeRa	P	-2.095	2.159	0.051	1.081	489	1.0084742

Species codes; AdQu = *Adelphicos quadrivigattus*, BoAs = *Bothrops asper,* BoIm = *Boa imperator*, ClSc = *Clelia scytalina*, CoBi = *Coniophanes bipunctatus*, CoIm = *Coniophanes imperialis*, CoMe = *Coluber mentovarius*, CoSc = *Coniophanes schmidtii*, DrMa = *Drymobius margaritiferus*, ImCe = *Imantodoes cenchoa*, LaAb = *Lampropeltis abnorma*, LeAh = *Leptophis ahaetulla*, LeMex = *Leptophis mexicanus*, LeSe = *Leptodiera septentrionalis*, MaMe = *Mastigodryas melanonomus*, MiDi = *Micrurus diastema*, NiDi = *Ninia diademata*, NiSe = *Ninia sebae*, OxAe = *Oxybelis aeneus*, OxPe = *Oxyrhopus petolarius*, PlEl = *Pliocercus elapoides*, PsFl = *Psuedelaphe flavirufa*, SiDi = *Sibon dimidiata*, SiNe = *Sibon nebulata*, SpPu = *Spilotes pullatus*, TaMo = *Tantilla moesta*, TrSa = *Tropidodipsas sartorii*, XeRa = *Xenodon rabdocephalus*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.16: Bayesian GLM results showing response of snake species in NE to the presence of forest edge.

Species	**Present /Absent**	**Lower95**	**Upper95**	**Mean**	**SD**	**SSeff**	**psrf**
AdQu	A	**-1969.67**	**-0.393**	**-801.497**	604.57523	47800	1.0000203
BoIm	A	***-1967.11***	***0.182***	***-797.703***	604.76664	49000	1.0000786
CoBi	A	**-1964.69**	**-0.567**	**-801.989**	601.62937	49214	1.0000089
CoIm	A	**-1955.7**	**-0.157**	**-798.333**	599.78741	50395	1.0000215
CoMe	A	**-1964.07**	**-1.04**	**-799.686**	602.36059	49123	1.000087
LeAh	A	***-1955.25***	***0.225***	***-796.99***	602.38616	47861	1.0001057
LeMex	A	**-1955.15**	**-0.072**	**-795.053**	600.33919	49707	1.0000525
NiDi	A	**-1969.26**	**-1.097**	**-797.475**	604.89134	49752	1.0001141
OxAe	A	**-1974.71**	**-0.022**	**-802.813**	606.33332	49241	1.0000018
PlEl	A	**-1957.06**	**-0.756**	**-793.971**	599.98528	47801	1.0003573
PsFl	A	**-1951.05**	**-0.316**	**-797.26**	599.31531	48874	1.0000341
SiDi	A	**-1965.64**	**-0.266**	**-799.871**	603.88322	49224	0.9999908
TaMo	A	**-1956.64**	**-0.81**	**-794.747**	601.00344	49220	1.000024
XeRa	A	***-1963.27***	***0.159***	***-795.481***	601.70814	50013	1.0000066

Species codes; AdQu = *Adelphicos quadrivigattus*, BoIm = *Boa imperator*, CoBi = *Coniophanes bipunctatus*, CoIm = *Coniophanes imperialis*, CoMe = *Coluber mentovarius*, LeAh = *Leptophis ahaetulla*, LeMex = *Leptophis mexicanus*, LeSe = *Leptodiera septentrionalis*, MaMe = *Mastigodryas melanonomus*, MiDi = *Micrurus diastema*, NiDi = *Ninia diademata*, OxAe = *Oxybelis aeneus*, PlEl = *Pliocercus elapoides*, PsFl = *Psuedelaphe flavirufa*, SiDi = *Sibon dimidiata*,, TaMo = *Tantilla moesta*, XeRa = *Xenodon rabdocephalus*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.17: Bayesian GLM results showing response of lizard species in AE to the presence of agriculture.

Species	Present /Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
BaVi	A	-1958.07	0.563	-798.631	601.893	49514	1.0000093
CoEl	P	0	0	0	0	NA	NA
CoCr	P	-1.977	3.24	0.62	1.314	561	1.0051447
CoHe	A	***-1955.48***	***0.47***	***-797.647***	600.654	48021	1.0002344
HoFe	A	***-1967.88***	***0.343***	***-799.846***	605.992	48719	1.0000137
HoUn	P	-4.431	2.436	-0.856	1.735	1042	1.0028321
MaUn	A	***-1976.07***	***0.001***	***-805.068***	604.789	49321	1.0000323
MeSc	A	-1964.829	0.923	-799.635	605.918	48765	1.0000817
NoCa	P	-0.985	3.901	1.411	1.237	467	1.0058425
NoLe	A	-1950.541	0.628	-794.482	598.914	50664	1.0000261
NoRo	A	-1972.116	1.137	-800.556	605.423	47554	1.0000944
NoSe	A	***-1968.32***	***0.5***	***-801.877***	605.817	48760	1.0001597
NoTr	A	**-1957.9**	**-0.476**	**-795.604**	600.585	48966	1.0000457
NoUn	P	-2.641	2.923	0.137	1.406	641	1.004791
ScCh	A	-1956.59	0.524	-797.443	601.073	48645	1.000018
ScTe	A	-1957.1	0.823	-798.499	598.85	49720	0.999992
SpGl	A	-1960.65	1.079	-801.016	603.416	48489	1.000135
SpMi	A	-1960.77	0.712	-800.987	603.225	48101	1.000156
SpCh	A	-1953.6	0.621	-797.142	601.135	49474	1.000095
ThRa	A	-1964.79	0.827	-797.861	603.864	47924	1.000042

Species codes; BaVi = *Basiliscus vittatus*, CoEl = *Coleonyx elegans*, CoCr = *Corytophanes cristatus*, CoHe = *Corytophanes hernandezii*, HoFe = *Holcosus festiva*, HoUn = H*olcosus undulata*, MaUn = Marisora unimarginata, MeSc = *Mesoscincus schwartzei*, NoCa = *Norops capito*, NoLe = *Norops lemurinus*, NoRo = *Norops rodriguezii*, NoSe = *Norops sericeus*, NoTr = *Norops tropidonotus*, NoUn = *Norops uniformis*, ScCh = *Sceloporus chrysostictus*, ScTe = *Sceloporus teapensis*, SpCh = *Sphenomorphus cherriei*, SpGl = *Sphaerodactylus glaucus*, SpMi = *Spaerodactylus millepunctatus*, ThRa = *Thecadactylus rapicauda*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.18: Bayesian GLM results showing response of lizard species in HF to the presence of agriculture.

Species	Present /Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
HoFe	A	-1970.37	0.929	-801.933	604.786	50781	1.000072
MaUn	A	-1951.65	0.785	-796.14	602.326	50229	1.000034
MeSc	A	-1964.82	0.691	-802.347	603.894	49420	1.000149
NoRo	A	-1961.91	1.174	-795.83	602.067	49011	1.000272
NoSe	A	-1947.88	1.278	-795.663	600.144	49868	1.000032
ScTe	A	-1946.52	1.369	-791.722	597.732	49763	1.000097
SpMi	A	-1960.69	0.912	-798.935	603.719	49126	1.000028
ThRa	A	-1961.83	0.76	-800.672	602.51	47766	1.000028

Species codes; HoFe = *Holcosus festiva*, MaUn = Marisora unimarginata*,* MeSc = *Mesoscincus schwartzei*, NoRo = *Norops rodriguezii*, NoSe = *Norops sericeus*, ScTe = *Sceloporus teapensis*, SpMi = *Spaerodactylus millepunctatus*, ThRa = *Thecadactylus rapicauda*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.19: Bayesian GLM results showing response of lizard species in LF to the presence of agriculture.

Species	Present /Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
CoCr	A	-1958.88	2.046	-796.107	604.723	48070	1.000081
HoUn	A	-1967.68	1.448	-799.978	604.553	49478	0.999997
MaUn	A	-1964.38	1.766	-797.176	602.177	49879	1.000017
MeSc	A	-1944.33	1.962	-790.765	600.115	48176	1.000142
NoSe	A	-1970.48	2.501	-801.878	604.273	48715	1.000062
ScCh	A	-1954.07	1.618	-797.034	603.177	49619	1.000031
SpGl	A	-1958.33	1.519	-799.224	602.901	48751	1.00004
ThRa	A	-1969.56	2.052	-798.953	605.262	49120	1.00003

Species codes; CoCr = *Corytophanes cristatus*, HoUn = H*olcosus undulata*, MaUn = Marisora unimarginata*,* MeSc = *Mesoscincus schwartzei*, NoSe = *Norops sericeus*, ScCh = *Sceloporus chrysostictus*, SpGl = *Sphaerodactylus glaucus*, ThRa = *Thecadactylus rapicauda*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.20: Bayesian GLM results showing response of lizard species in NE to the presence of agriculture.

Species	Present /Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
CoHe	A	-1973.05	0.874	-798.824	605.223	48357	1.000042
NoRo	A	-1962.96	0.939	-798.281	602.888	49081	1.000062
ScCh	A	-1951.45	0.991	-791.54	598.983	48701	1.000064
ScTe	A	***-1954.56***	***0.131***	***-797.265***	600.187	49319	1
SpCh	A	***-1956.72***	***0.529***	***-799.346***	603.051	49313	1.00002
SpGl	A	***-1959.4***	***0.499***	***-798.172***	601.351	50295	0.999992
SpMi	A	***-1976.37***	***0.494***	***-803.885***	606.546	49370	1.00001

Species codes; CoHe = *Corytophanes hernandezii*, NoRo = *Norops rodriguezii*, ScCh = *Sceloporus chrysostictus*, ScTe = *Sceloporus teapensis*, SpCh = *Sphenomorphus cherriei*, SpGl = *Sphaerodactylus glaucus*, SpMi = *Spaerodactylus millepunctatus*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.21: Bayesian GLM results showing response of lizard species in AE to the presence of forest edge.

Species	Present /Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
BaVi	A	**-1965.1**	**-0.127**	**-801.27**	604.153	48165	1.000028
CoEl	P	0	0	0	0	NA	NA
CoCr	P	-2.063	3.133	0.514	1.313	635	1.001751
CoHe	A	-1950.38	0.177	-795.944	598.858	50607	1.0001
HoFe	A	-1967.09	1.17	-798.996	603.438	49731	1.000067
HoUn	P	-4.538	2.27	-0.982	1.729	1196	1.001652
MaUn	A	-1961.3	0.752	-798.812	602.562	49433	1.000013
MeSc	A	***-1965.73***	***0.195***	***-800.048***	604.153	49275	1.000143
NoCa	P	-1.115	3.75	1.298	1.227	542	1.002596
NoLe	A	-1954.35	1.062	-794.695	601.192	49468	1.000002
NoRo	A	-1970.47	0.592	-797.738	605.043	49042	1.000062
NoSe	A	***-1979.79***	***0.047***	***-803.992***	608.16	46562	1.000008
NoTr	A	-1977.31	0.688	-804.01	605.35	49258	1.000005
NoUn	P	-2.75	2.832	0.014	1.409	757	1.001567
ScCh	A	**-1946.3**	**-0.32**	**-795.32**	599.456	50384	1.000068
ScTe	A	-1964.03	0.73	-799.385	602.616	48385	1.000057
SpGl	A	-1965.48	0.959	-800.66	603.154	49380	0.999995
SpMi	A	-1954.03	1.79	-795.201	599.367	47557	1.000047
SpCh	A	-1970.23	1.381	-801.833	604.646	49978	1.000109
ThRa	A	-1959.6	1.131	-797.124	601.515	50059	1.000155

Species codes; BaVi = *Basiliscus vittatus*, CoEl = *Coleonyx elegans*, CoCr = *Corytophanes cristatus*, CoHe = *Corytophanes hernandezii*, HoFe = *Holcosus festiva*, HoUn = H*olcosus undulata*, MaUn = Marisora unimarginata*,* MeSc = *Mesoscincus schwartzei*, NoCa = *Norops capito*, NoLe = *Norops lemurinus*, NoRo = *Norops rodriguezii*, NoSe = *Norops sericeus*, NoTr = *Norops tropidonotus*, NoUn = *Norops uniformis*, ScCh = *Sceloporus chrysostictus*, ScTe = *Sceloporus teapensis*, SpCh = *Sphenomorphus cherriei*, SpGl = *Sphaerodactylus glaucus*, SpMi = *Spaerodactylus millepunctatus*, ThRa = *Thecadactylus rapicauda*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.22: Bayesian GLM results showing response of lizard species in HF to the presence of forest edge.

Species	Present /Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
BaVi	P	-3.379	1.948	-0.624	1.347	667	1.002035
CoEl	P	-0.72	3.728	1.483	1.121	414	1.003313
CoCr	P	-3.297	1.994	-0.638	1.342	633	1.002456
CoHe	P	-4.957	1.587	-1.621	1.667	1033	1.001793
HoFe	A	***-1942.17***	***0.134***	***-789.957***	597.173	50118	1.000061
HoUn	P	-3.277	2.028	-0.627	1.346	647	1.002206
MaUn	A	**-1970.6**	**-0.457**	**-799.96**	605.969	48395	1.000127
MeSc	A	**-1959.8**	**-0.314**	**-795.54**	600.755	49458	1.000156
NoCa	P	-0.565	3.841	1.626	1.112	427	1.004274
NoLe	P	-2.135	2.602	0.208	1.203	498	1.002493
NoRo	A	**-1964**	**-0.256**	**-799.22**	602.763	48928	1.000069
NoSe	A	***-1961.64***	***0.258***	***-800.782***	599.256	49423	1.000129
NoTr	P	-3.294	1.992	-0.632	1.338	654	1.002131
NoUn	P	-5.004	1.574	-1.632	1.675	1080	1.002008
ScCh	P	-5.111	1.459	-1.627	1.673	1155	1.002033
ScTe	A	**-1979.6**	**-0.051**	**-803.16**	606.322	49828	1.000054
SpGl	P	-5.015	1.572	-1.623	1.669	1073	1.001257
SpMi	A	**-1965.1**	**-0.362**	**-799.03**	603.711	48858	1.000013
SpCh	P	-2.132	2.607	0.211	1.201	534	1.003476
ThRa	A	***-1951.53***	***0.187***	***-796.177***	601.071	50135	1.000009

Species codes; BaVi = *Basiliscus vittatus*, CoEl = *Coleonyx elegans*, CoCr = *Corytophanes cristatus*, CoHe = *Corytophanes hernandezii*, HoFe = *Holcosus festiva*, HoUn = H*olcosus undulata*, MaUn = Marisora unimarginata*,* MeSc = *Mesoscincus schwartzei*, NoCa = *Norops capito*, NoLe = *Norops lemurinus*, NoRo = *Norops rodriguezii*, NoSe = *Norops sericeus*, NoTr = *Norops tropidonotus*, NoUn = *Norops uniformis*, ScCh = *Sceloporus chrysostictus*, ScTe = *Sceloporus teapensis*, SpCh = *Sphenomorphus cherriei*, SpGl = *Sphaerodactylus glaucus*, SpMi = *Spaerodactylus millepunctatus*, ThRa = *Thecadactylus rapicauda*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.23: Bayesian GLM results showing response of lizard species in LF to the presence of forest edge.

Species	Present /Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
BaVi	P	-2.56	2.375	-0.133	1.248	535	1.002267
CoEl	P	-1.592	2.968	0.64	1.156	481	1.003101
CoCr	A	***-1953.1***	***0.183***	***-796.428***	598.135	48874	1.000061
CoHe	P	-5.105	1.537	-1.636	1.681	1070	1.001626
HoFe	P	-2.173	2.538	0.187	1.196	500	1.002609
HoUn	A	**-1966.9**	**-0.592**	**-799**	603.438	50014	1.000007
MaUn	A	***-1965.2***	***0.111***	***-800.66***	603.022	49507	1.000005
MeSc	A	**-1969.5**	**-0.111**	**-802.44**	604.424	48229	0.999989
NoCa	P	-1.402	3.169	0.854	1.161	470	1.002881
NoLe	P	-0.818	3.595	1.369	1.12	446	1.003028
NoRo	P	-5.071	1.551	-1.64	1.682	1098	1.001477
NoSe	A	**-1948.1**	**-0.651**	**-799.01**	600.419	49064	1.000066
NoTr	P	-4.953	1.621	-1.65	1.673	1086	1.001068
NoUn	P	-5.019	1.592	-1.64	1.68	1199	1.001475
ScCh	A	**-1973.8**	**-0.236**	**-799.28**	605.68	48901	1
ScTe	P	-3.328	1.987	-0.638	1.342	660	1.001883
SpGl	A	**-1960.6**	**-0.107**	**-799.06**	601.81	50226	1.000096
SpMi	P	-5.031	1.551	-1.631	1.675	1154	1.001395
SpCh	P	-0.998	3.491	1.22	1.132	453	1.002973
ThRa	A	***-1965.08***	***0.117***	***-802.153***	599.618	48542	1.000129

Species codes; BaVi = *Basiliscus vittatus*, CoEl = *Coleonyx elegans*, CoCr = *Corytophanes cristatus*, CoHe = *Corytophanes hernandezii*, HoFe = *Holcosus festiva*, HoUn = H*olcosus undulata*, MaUn = Marisora unimarginata, MeSc = *Mesoscincus schwartzei*, NoCa = *Norops capito*, NoLe = *Norops lemurinus*, NoRo = *Norops rodriguezii*, NoSe = *Norops sericeus*, NoTr = *Norops tropidonotus*, NoUn = *Norops uniformis*, ScCh = *Sceloporus chrysostictus*, ScTe = *Sceloporus teapensis*, SpCh = *Sphenomorphus cherriei*, SpGl = *Sphaerodactylus glaucus*, SpMi = *Spaerodactylus millepunctatus*, ThRa = *Thecadactylus rapicauda*. Significant effects indicated in bold. Near significant effects indicated in bold italics

Table I.24: Bayesian GLM results showing response of lizard species in NE to the presence of forest edge.

Species	Present /Absent	Lower95	Upper95	Mean	SD	SSeff	psrf
BaVi	P	-2.831	2.035	-0.409	1.227	533	1.002453
CoEl	P	-0.635	3.637	1.475	1.08	396	1.003681
CoCr	P	-2.412	2.237	-0.075	1.18	472	1.002891
CoHe	A	***-1949.22***	***0.001***	***-794.178***	599.114	49241	1.000185
HoFe	P	-2.826	2.046	-0.413	1.229	560	1.002455
HoUn	P	-5.197	1.348	-1.905	1.662	1009	1.001544
MaUn	P	-5.216	1.3	-1.922	1.657	1094	1.00126
MeSc	P	-5.184	1.345	-1.89	1.654	1071	1.001602
NoCa	P	-1.856	2.634	0.377	1.137	435	1.003267
NoLe	P	-0.985	3.326	1.11	1.09	410	1.003224
NoRo	A	**-1959.7**	**-1.29**	**-795.93**	603.986	48685	1.000142
NoSe	P	-5.302	1.237	-1.911	1.662	1059	1.001185
NoTr	P	-5.283	1.268	-1.906	1.664	1129	1.001159
NoUn	P	-5.348	1.224	-1.914	1.669	1118	1.001597
ScCh	A	**-1968.1**	**-0.6**	**-797.26**	601.842	49979	1.000006
ScTe	A	**-1951.4**	**-0.043**	**-799.14**	600.981	49185	1.000099
SpGl	A	**-1969.9**	**-1.044**	**-798.16**	603.68	49502	1.000085
SpMi	A	**-1951.6**	**-0.246**	**-795.71**	600.435	48369	1.000002
SpCh	A	***-1960.88***	***0.12***	***-799.041***	603.665	49955	1.000007
ThRa	P	-3.572	1.681	-0.908	1.326	647	1.002568

Species codes; BaVi = *Basiliscus vittatus*, CoEl = *Coleonyx elegans*, CoCr = *Corytophanes cristatus*, CoHe = *Corytophanes hernandezii*, HoFe = *Holcosus festiva*, HoUn = H*olcosus undulata*, MaUn = Marisora unimarginata*,* MeSc = *Mesoscincus schwartzei*, NoCa = *Norops capito*, NoLe = *Norops lemurinus*, NoRo = *Norops rodriguezii*, NoSe = *Norops sericeus*, NoTr = *Norops tropidonotus*, NoUn = *Norops uniformis*, ScCh = *Sceloporus chrysostictus*, ScTe = *Sceloporus teapensis*, SpCh = *Sphenomorphus cherriei*, SpGl = *Sphaerodactylus glaucus*, SpMi = *Spaerodactylus millepunctatus*, ThRa = *Thecadactylus rapicauda*. Significant effects indicated in bold. Near significant effects indicated in bold italics