THE IMPACT OF HABITAT STRUCTURE ON REPTILE OCCURRENCE IN A FRAGMENTED TROPICAL LANDSCAPE

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DECLARATION

I declare that this Dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

(Signature of candidate)

5th day of December 2018, Johannesburg.

ABSTRACT

Defining the spatial distributions of species with regards to habitat selection and landscape structure is an important part of biogeography, ecology and conservation research. I investigated reptile occurrence and community structure in two patches of dry forest in north western Madagascar using detection/non-detection data collected on repeated transect surveys for four years. A Bayesian hierarchical occupancy model and multispectral satellite imagery were used to assess the effects of vegetation structure, proximity to human development and edge proximity on the site presence of 37 squamate species in the context of taxonomic family and Threat Status. Mean species richness was highest at sites within a forest patch (23 (4, 30)). Sites with dense green vegetation promoted the highest levels of reptile occupancy among the Chamaeleonidae and Gekkoniidae families (with regression coefficient estimates up to 0.75 (0.12, 1.53)) and all species were more likely to occur at sites closer to the forest patch periphery. The Boidae had the widest 95% CRI for the regression coefficient estimates representing the effects of habitat variables on occupancy, indicating that they are highly variable in their habitat use. The regression coefficient estimates of mean reptile occupancy had 95% credible intervals (CRIs) including zero due to high variability between species. The proximity to roads did not have a statistically significant effect on any of the species, and *Uroplatus guentheri* was the only species which showed a significant preference for being further from a settlement (0.81 (0.05, 1.77)). The findings demonstrated the importance of using caution when assessing Threat Status at a regional level and suggest that the Red List's measure of Population Trend may be significantly influenced by imperfect detection.

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CHAPTER 1 – INTRODUCTION

The relationship between species distribution and landscape structure is fundamental to ecology, biogeography and conservation (Cowling et al., 1999; Guisan and Thuiller, 2005; Whittaker et al., 2005). Community composition can vary from one area to the next due to differential habitat-use of species, which occurs at the level of the individual organism but, because individuals within a species will tend to behave more similarly to one another than to other species, mean species habitat preferences can be reflected at landscape-level as species distributions. An animal's 'selection' of a habitat, or the probability of the species using a habitat when it is encountered (Lele et al., 2013), may be based either on its active searching for suitable habitat or the chance settling in an area if the conditions are suitable (Matthiopoulos et al., 2015). Multiple species can occur in the same area because they have adapted to prioritising resources differently, forming communities (Fischer et al., 2004). By studying the similarities and differences among species within a community and between communities, one can define which characteristics promote the occurrence of certain species, as well as species richness (Murphy et al., 2016). This is of great value to conservationists, because it is more resource-efficient to identify and conserve areas with characteristics which promote a high number of species than it is to focus on single species (Ferrier and Guisan, 2006; Rich et al., 2016).

1.1 Reptile landscape-use

Reptiles are of special interest with regards to studying species distributions in relation to landscape characteristics because their habitats are under high threat from anthropogenic land transformation and, in comparison to mammals and birds, there has not been sufficient research into the relationship between their distribution patterns and habitat-use, particularly in the southern hemisphere (Bonnet et al., 2002; Gardner et al., 2007; IUCN, 2018; Lewin et al., 2016; McCain, 2010). The conservation of reptiles is also highly relevant in the broader ecosystem context because in many habitats, reptiles are the highest-level predators in the trophic hierarchy and therefore play an important role in the population-management of other species (Dial and Roughgarden, 1995; Spiller and Schoener, 2009).

Additionally, reptiles are model organisms with which to study habitat selection because they are more directly dependent on their habitats than are most other animals, and thus clear patterns can be seen in their behaviour, success, and distributions in response to anthropogenic habitat transformation (Huey, 1991; Shine and Bonnet, 2000; Wasko and Sasa, 2012).

There is a great deal of evidence in the literature to suggest that terrestrial reptile presence is primarily associated with the habitat structure relating to vegetation and substrate (Bennett et al., 2006; Bruton et al., 2016; Lewin et al., 2016; Shah et al., 2004; Wanger et al., 2010) which is relevant to a reptile’s hunting (Tsairi and Bouskila, 2004; Wasko and Sasa, 2012), shelter (Beck and Jennings, 2003; Bruton et al., 2016; Masterson et al., 2008), and thermoregulation (Qian et al., 2007; Rodríguez et al., 2005) opportunities. Reptiles are also affected by proximity to human development such as roads and settlements (Böhm et al., 2016; Hódar et al., 2000; Shine et al., 2004). Species-specific characteristics such as lineage, foraging mode and morphology may also contribute to niche separation (Vitt, 1992) and thus spatial distribution. Such differential traits have resulted in species being specialised to differing degrees with regards to habitat (Botts et al., 2013), resulting in some species being more sensitive to, and thus threatened by, habitat transformation than others (Böhm et al., 2016; Murray et al., 2010). Being able to define reptile communities based on the structures of the landscapes in which they occur most frequently, and their resulting spatial distributions, aids in identifying and conserving areas that best promote the persistence of multiple reptile species.

1.2 Modelling the spatial distributions of species

The statistical methods used to define a species’ landscape-use range from hypothesis testing to species distribution modelling in programs such as Maxent (Phillips et al., 2018). Although useful, these approaches are limited in their ability to accurately and realistically define species distributions. When surveying species presence at a site, two processes are involved in the formulation of detection/non-detection data – the observation process and the ecological process. These processes involve 1) a species being present and recorded (true presence), 2) a species not being present and not recorded (true absence), and 3) a species being present but not recorded (pseudo-absence) (Dorazio and Royle, 2005; MacKenzie et al., 2006). Traditional species distribution models do not account for imperfect detection involved in the sampling protocol and thus fail to consider the third, unobserved process that results in pseudo-absences. Although detection probability may be calculated separately in some cases through distance sampling or mark-recapture, this is costly in time and effort (Royle and Nichols, 2003) and cannot be used for species with low recapture probabilities (Durso et al., 2011; Joseph et al., 2006; Pollock, 2006). The failure to take into account the 'present but unobserved state' may lead to inconsistent and biased population and community estimates, with negative implications for conservation management (Tobler et al., 2015; Wearn et al., 2017).

Occupancy models address the issues of pseudo-absence and imperfect detection by using data from repeated surveys and a regression for the detection process to calculate estimates of a species' probability of occurring at each site, even when it is not detected on a survey (MacKenzie et al., 2002). The basic occupancy model can be extended to a Bayesian multispecies, multi-season, hierarchical model with habitat covariates that assesses the effects of landscape structure on a site's ability to support species and communities of interest (Dorazio and Royle, 2005; MacKenzie et al., 2006; Rich et al., 2016). This approach is especially useful for rare or cryptic species (such as for many snake species (Durso et al., 2011; Luiselli, 2006)) where occurrence data can be 'borrowed' from other species in a community to calculate occupancy estimates of sparsely- recorded species (Zipkin et al., 2010).

1.3 Aims, objectives and dissertation structure

To investigate reptile landscape-use I sampled squamate occurrence in north western Madagascar, a species-rich country with a high number of endemic, habitat-specialist species under threat from anthropogenic land transformation. I assessed squamate community composition in a fragmented dry forest with the aim of understanding how the number and type of species found in an area is affected by habitat characteristics and species-specific traits. Using reptile detection/non-detection data collected over four years through Operation Wallacea and remotely sensed habitat data in a hierarchical Bayesian occupancy model, I explored and defined trends in habitat selection which may be globally applicable to the understanding of reptile community composition.

Chapter 2 of this dissertation focusses on the effects of site covariates (vegetation structure, proximity to human development and the location of a site in the context of a larger forest patch) on mean reptile occupancy and individual species occupancy probability. Based on these observations, I defined assemblages of species with certain land-use trends. This chapter investigates how sites (and their associated combinations of habitat/landscape covariates) are associated with species richness, species rarity, and species elusiveness. Chapter 3 builds on Chapter 2 by comparing groups of species (families and IUCN Red List Threat categories) in terms of occupancy probability, detection probability and mean group occupancy response to landscape structure. Chapters 2 and 3 are formatted as papers to facilitate future publication; consequently, there will be some necessary repetition in content. Chapter 4 draws conclusions on the landscape-use of squamate species by assessing how the trends in site preference defined in Chapter 2's species assemblages compare to the mean occupancy patterns of the species categories used in Chapter 3.

1.4 Literature cited

Beck, D.D., Jennings, R.D., 2003. Habitat use by Gila monsters: the importance of shelters. Herpetol. Monogr. 17, 111–129.

Bennett, A.F., Radford, J.Q., Haslem, A., 2006. Properties of land mosaics: implications for nature conservation in agricultural environments. Biol. Conserv. 133, 250–264.

Böhm, M., Williams, R., Bramhall, H.R., McMillan, K.M., Davidson, A.D., Garcia, A., Bland, L.M., Bielby, J., Collen, B., 2016. Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. Glob. Ecol. Biogeogr. 25, 391–405.

Bonnet, X., Shine, R., Lourdais, O., 2002. Taxonomic chauvinism. Trends Ecol. Evol. 17, 1–3. https://doi.org/10.1016/S0169-5347(01)02381-3

Botts, E.A., Erasmus, B.F., Alexander, G.J., 2013. Small range size and narrow niche breadth predict range contractions in S outh A frican frogs. Glob. Ecol. Biogeogr. 22, 567–576.

Bruton, M.J., Maron, M., Franklin, C.E., McAlpine, C.A., 2016. The relative importance of habitat quality and landscape context for reptiles in regenerating landscapes. Biol. Conserv. 193, 37–47.

Cowling, R., Pressey, R., Lombard, A., Desmet, P., Ellis, A., 1999. From representation to persistence: requirements for a sustainable system of conservation areas in the species- rich mediterranean- climate desert of southern Africa. Divers. Distrib. 5, 51–71.

Dial, R., Roughgarden, J., 1995. Experimental Removal of Insectivores from Rain Forest Canopy: Direct and Indirect Effects. Ecology 76, 1821–1834. https://doi.org/10.2307/1940714

Dorazio, R.M., Royle, J.A., 2005. Estimating size and composition of biological communities by modeling the occurrence of species. J. Am. Stat. Assoc. 100, 389–398.

Durso, A.M., Willson, J.D., Winne, C.T., 2011. Needles in haystacks: estimating detection probability and occupancy of rare and cryptic snakes. Biol. Conserv. 144, 1508–1515.

Ferrier, S., Guisan, A., 2006. Spatial modelling of biodiversity at the community level. J. Appl. Ecol. 43, 393–404.

Fischer, J., Lindenmayer, D.B., Cowling, A., 2004. The challenge of managing multiple species at multiple scales: reptiles in an Australian grazing landscape. J. Appl. Ecol. 41, 32–44. https://doi.org/10.1111/j.1365-2664.2004.00869.x

Gardner, T.A., Barlow, J., Peres, C.A., 2007. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. Biol. Conserv. 138, 166–179.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009.

Hódar, J.A., Pleguezuelos, J.M., Poveda, J.C., 2000. Habitat selection of the common chameleon (Chamaeleo chamaeleon)(L.) in an area under development in southern Spain: implications for conservation. Biol. Conserv. 94, 63–68.

Huey, R.B., 1991. Physiological Consequences of Habitat Selection. Am. Nat. 137, S91–S115.

IUCN, 2016. The IUCN Red List of Threatened Species [WWW Document]. URL http://www.iucnredlist.org/search

Joseph, L.N., Field, S.A., Wilcox, C., Possingham, H.P., 2006. Presence–absence versus abundance data for monitoring threatened species. Conserv. Biol. 20, 1679–1687.

Lele, S.R., Merrill, E.H., Keim, J., Boyce, M.S., 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. J. Anim. Ecol. 82, 1183–1191. https://doi.org/10.1111/1365-2656.12141

Lewin, A., Feldman, A., Bauer, A.M., Belmaker, J., Broadley, D.G., Chirio, L., Itescu, Y., LeBreton, M., Maza, E., Meirte, D., 2016a. Patterns of species richness, endemism and environmental gradients of African reptiles. J. Biogeogr. 43, 2380–2390.

Lewin, A., Feldman, A., Bauer, A.M., Belmaker, J., Broadley, D.G., Chirio, L., Itescu, Y., LeBreton, M., Maza, E., Meirte, D., 2016b. Patterns of species richness, endemism and environmental gradients of African reptiles. J. Biogeogr. 43, 2380–2390.

Luiselli, L., 2006. Site occupancy and density of sympatric Gaboon viper (Bitis gabonica) and nose-horned viper (Bitis nasicornis). J. Trop. Ecol. 22, 555–564.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248–2255.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L., Hines, J.E., 2006. Occupancy in Community-Level Studies, in: Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press, pp. 249–266.

Masterson, G.P., Maritz, B., Alexander, G.J., 2008. Effect of fire history and vegetation structure on herpetofauna in a South African grassland. Appl. Herpetol. 5, 129–143.

Matthiopoulos, J., Fieberg, J., Aarts, G., Beyer, H.L., Morales, J.M., Haydon, D.T., 2015. Establishing the link between habitat selection and animal population dynamics. Ecol. Monogr. 85, 413–436.

McCain, C.M., 2010. Global analysis of reptile elevational diversity. Glob. Ecol. Biogeogr. 19, 541–553.

Murphy, A.J., Goodman, S.M., Farris, Z.J., Karpanty, S.M., Andrianjakarivelo, V., Kelly, M.J., 2016. Landscape trends in small mammal occupancy in the Makira–Masoala protected areas, northeastern Madagascar. J. Mammal. gyw168.

Murray, K.A., Rosauer, D., McCallum, H., Skerratt, L.F., 2010. Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. Proc. R. Soc. Lond. B Biol. Sci. rspb20101872.

Phillips, S.J., Dudík, M., Schapire, R.E., 2018. Maxent software for modeling species niches and distributions.

Pollock, J.F., 2006. Detecting population declines over large areas with presence- absence, time- to-encounter, and count survey methods. Conserv. Biol. 20, 882–892.

Qian, H., Wang, X., Wang, S., Li, Y., 2007. Environmental determinants of amphibian and reptile species richness in China. Ecography 30, 471–482.

Rich, L.N., Miller, D.A., Robinson, H.S., McNutt, J.W., Kelly, M.J., 2016. Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. J. Appl. Ecol. 53, 1225–1235.

Rodríguez, M.Á., Belmontes, J.A., Hawkins, B.A., 2005. Energy, water and large-scale patterns of reptile and amphibian species richness in Europe. Acta Oecologica 28, 65–70.

Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence–absence data or point counts. Ecology 84, 777–790.

Shah, B., Shine, R., Hudson, S., Kearney, M., 2004. Experimental analysis of retreat-site selection by thick-tailed geckosNephrurus milii. Austral Ecol. 29, 547–552. https://doi.org/10.1111/j.1442-9993.2004.01388.x

Shine, R., Bonnet, X., 2000. Snakes: a new ‘model organism’ in ecological research? Trends Ecol. Evol. 15, 221–222. https://doi.org/10.1016/S0169-5347(00)01853-X

Shine, R., Lemaster, M., Wall, M., Langkilde, T., Mason, R., 2004. Why Did the Snake Cross the Road? Effects of Roads on Movement and Location of Mates by Garter Snakes (*Thamnophis sirtalis parietalis*). Ecol. Soc. 9. https://doi.org/10.5751/ES-00624-090109

Spiller, D., Schoener, T., 2009. Species–area relationship. Encycl. Isl. Univ. Calif. Press Berkeley 857–861.

Tobler, M.W., Zúñiga Hartley, A., Carrillo- Percastegui, S.E., Powell, G.V., 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. J. Appl. Ecol. 52, 413–421.

Tsairi, H., Bouskila, A., 2004. Ambush Site Selection of a Desert Snake (Echis coloratus) at an Oasis. Herpetologica 60, 13–23.

Vitt, L.J., 1992. Diversity of Reproductive Strategies Among Brazilian Lizards and Snakes: The Significance of Lineage and Adaptation, in: Reproductive Biology of South American Vertebrates. Springer, New York, NY, pp. 135–149. https://doi.org/10.1007/978-1-4612-2866-0_10

Wanger, T.C., Iskandar, D.T., Motzke, I., Brook, B.W., Sodhi, N.S., Clough, Y., Tscharntke, T., 2010. Effects of Land-Use Change on Community Composition of Tropical Amphibians and Reptiles in Sulawesi, Indonesia. Conserv. Biol. 24, 795–802. https://doi.org/10.1111/j.1523-1739.2009.01434.x

Wasko, D.K., Sasa, M., 2012. Food resources influence spatial ecology, habitat selection, and foraging behavior in an ambush-hunting snake (Viperidae: Bothrops asper): an experimental study. Zoology 115, 179–187. https://doi.org/10.1016/j.zool.2011.10.001

Wearn, O.R., Rowcliffe, J.M., Carbone, C., Pfeifer, M., Bernard, H., Ewers, R.M., 2017. Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling approach. Biol. Conserv. 212, 162–171.

Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E., Willis, K.J., 2005. Conservation biogeography: assessment and prospect. Divers. Distrib. 11, 3–23.

Zipkin, E.F., Royle, J.A., Dawson, D.K., Bates, S., 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. Biol. Conserv. 143, 479–484.

CHAPTER TWO – LANDSCAPE STRUCTURE AND SQUAMATE SPECIES OCCUPANCY IN MAHAMAVO, MADAGASCAR

2.1 Abstract

Landscape structure has a substantial influence on reptile habitat selection, resulting in species distributions being strongly linked to the availability of shelter, basking sites and hunting opportunities. When assessing the distributions of reptiles, the diverse habits and morphologies of species can result in occurrence estimates being biased in favour of species that are more easily detected. Using Bayesian hierarchical occupancy modelling and remote sensing, I investigated the effects of vegetation structure and anthropogenic development on reptile species in a dry forest in Madagascar, while accounting for imperfect detection. Species richness was highest at sites with within a forest patch (23 (4, 30)) but the high variability among species meant that estimates suggesting significant responses to habitat variables could not be calculated for mean reptile occupancy, and species-specific estimates therefore were more useful to explore. The occupancy estimates of some species (such as *Lygodactylus tolampyae* and *Furcifer angeli*) demonstrated strong responses to habitat variables (regression coefficient estimates), particularly for sites located within a forest patch ((6.71 (2.76, 8.07) and (6.61 (2.97, 10.44) respectively). All species indicated a preference for sites closer to the edge of a forest patch. The proximity of anthropogenic development did not have a statistically significant effect on occurrence, except for *Uroplatus guentheri* which showed a preference for sites far from settlements (0.81 (0.05, 1.77)). Investigations such as these illuminate distribution patterns that are useful in land management involving the conservation of reptile species.

2.2 Introduction

The effect of landscape structure on the distribution of species is a central concept in ecology and biogeography (Cowling et al., 1999; Guisan and Thuiller, 2005; Whittaker et al., 2005). As well as being necessary for our understanding of why species occur where they do, defining the relative importance of habitat characteristics to different species can be used to predict changes in species occurrence in response to habitat transformation, which is critical to conservation management (Murphy et al., 2016). Considering that habitat change is a primary threat to present and future biodiversity loss (Lötter, 2010; Sala et al., 2000; Tilman et al., 2001), this topic is especially relevant to current conservation science.

Reptiles are in need of particular attention with regards to conservation research because a higher percentage of reptile species face extinction than do birds and mammals (IUCN, 2018) and have received relatively little attention in comparison to other vertebrates, especially in the southern hemisphere (Bonnet et al., 2002; Gardner et al., 2007; Lewin et al., 2016; McCain, 2010). Squamates (snakes, amphisbaenids and other lizards) are model organisms with which to study habitat selection because their geographic distributions are more directly dependant on feeding and thermoregulation opportunities in comparison to other animals (Huey, 1991; Shine and Bonnet, 2000; Wasko and Sasa, 2012). This means that, by defining the thermoregulation and feeding opportunities in an area, we can predict squamate distributions and identify areas that promote presence with a fair degree of confidence.

The term ‘habitat’ is a broad description of the environment in which an organism occurs, and is used vaguely and inconsistently in the literature (Hall et al., 1997; Morrison, 2001). In some studies, habitat refers only to the physical resources available to an organism, while in other studies it includes species interactions. In the context of this study, habitat is the combination of physical factors contributing to the environment in which an individual occurs, which tends to be more similar among individuals within a species than between species. ‘Habitat selection’ is an organism’s probability of using a habitat when encountered (Lele et al., 2013), with their ‘selection’ based either on active searching for suitable habitat or the chance/passive settling in an area if the conditions are suitable (Matthiopoulos et al., 2015). Squamates ‘select’ habitat (actively or passively) based on the opportunities that an area offers for predator-avoidance, thermoregulation, feeding and social interaction (Butler et al., 2000; Downes and Shine, 1998). Habitat is selected at an individual level, and is therefore limited to the individual’s sensory range at a scale of centimetres to a few meters. The mean habitat ‘choice’ of individuals of a species can be reflected at the scale of species distributions in relation to landscape structure. Therefore, by studying and defining the structure of the landscape occupied, one can assess how these ecological aspects are prioritized to different degrees by species (Adolph, 1990; Butler et al., 2000; Hartmann and Marques, 2005).

An important component of a reptile’s habitat is vegetation and a number of studies that have concluded that vegetation cover and vegetation health are the most important predictors of terrestrial reptile occurrence and species richness patterns (Bennett et al., 2006; Bruton et al., 2016; Lewin et al., 2016; Wanger et al., 2010). Vegetation provides reptiles with shelter (Beck and Jennings, 2003; Bruton et al., 2016; Masterson et al., 2008) which is critical for thermoregulation (Qian et al., 2007; Rodríguez et al., 2005), protection from predators (Downes, 2001) and avoiding dehydration (Lagarde et al., 2012). Vegetation creates a hunting environment for squamates because their prey, such as small mammals and insects, also tend to rely on (and thus occur near) vegetation (Tsairi and Bouskila, 2004; Wasko and Sasa, 2012). Many ambush predator reptiles rely on the complex microhabitats that ground vegetation and fallen vegetation debris offer, and these habitats are particularly prone to anthropogenic transformation (Reed and Shine, 2002; Wasko and Sasa, 2009).

The basking opportunities available in an area are also important to consider with regards to squamate habitat selection because reptile physiological performance is strongly dependent on body temperature (Huey, 1991). Thick-tailed geckos (*Nephrurus milii*) favour rock surfaces that enhance heat gain during basking (Shah et al., 2004) and black rat snakes (*Elaphe obsoleta obsolete*) actively seek out forest edges after feeding, which offer the best basking sites in forests (Blouin- Demers and Weatherhead, 2001). Similarly, ornate tree lizards (*Urosaurus ornatus*) favour sparsely-vegetated areas that offer better basking sites over woodland areas (Paterson and Blouin- Demers, 2018). As with vegetation structure, individual habitat choices for areas with certain thermoregulatory properties are reflected at a landscape level by species distributions – squamate occurrence has been considered by a number of studies to coincide primarily with optimal ambient temperature ranges that an area provides for thermoregulation (Blouin- Demers and Weatherhead, 2001; Hawkins et al., 2003; Reinert, 1993). Thus, although the presence of vegetation can be beneficial in a reptile's habitat, the availability of open basking areas, or areas with less dense canopy, is also an important factor that influences reptile species distributions.

Animals can be affected by proximity to human development such as roads and settlements (Forman and Alexander, 1998; Laurance et al., 2009) where they are most likely to come into contact with humans. Some reptile species are negatively affected by direct human contact or when they live in areas that are highly accessible (Böhm et al., 2016), either when snakes are seen as a threat, such as occurs with Australian elapids (Whitaker and Shine, 2000), when reptiles are captured for use in traditional medicines or the pet trade (Alves et al., 2008; Whiting et al., 2013) or due to the increased chance of exposure to toxic household chemicals (Tilbury, 2018). Snakes and amphibians are at particular risk with regards to road mortalities (Jochimsen et al., 2014; Rytwinski and Fahrig, 2012) and the presence of roads has been observed to disrupt mate-searching of garter snakes (Shine et al., 2004). Some species may avoid some roads but not others, such as eastern hognose snakes which avoid crossing busy paved roads, but not unpaved roads (Robson and Blouin-Demers, 2013). These negative impacts can cause reptile distributions to be positively associated with habitats that are further away from areas that are easily accessible to humans.

However, not all impacts of human development on reptiles are negative, and transformed habitats may favour certain species under some conditions, such as the common chameleon (*Chamaeleo chamaeleon*) which frequents roadsides in Spain (Hódar et al., 2000) and juvenile skinks in Australian regrowth woodlands (Bruton et al., 2013). Low-level habitat disturbance and forest-clearing can promote habitat heterogeneity and thus increase the availability of shelters (Bruton et al., 2013; Pike et al., 2011) and basking sites (Shine et al., 2002). Additionally, some snakes and geckos (such as the *Lamprophis* house snakes and *Hemidactylus* geckos) favour human dwellings for the increased prey availability they offer (Alexander and Marais, 2007). Therefore, depending on the priorities and inherent traits of the species, anthropogenic influences may promote or deter a reptile's selection of a habitat and ultimately affect species distributions.

Another characteristic which may affect species occurrence at a site is the site's proximity to the edge of the habitat patch in which it occurs. The concept of 'edge effects' is a key aspect of reserve design and its relation to island biogeography (Diamond, 1975), although there is little consensus on its influence within the literature (Murcia, 1995). Sites on the edges of forests are more susceptible to physical changes from the surrounding ecosystem, and are therefore traditionally considered to be lower-quality habitats and negatively associated with species presence than interior sites (Murcia, 1995) although, due to the species that may arise under such selection pressures, habitat patch edges are often valued for their high levels of biodiversity (Harris, 1988). With regard to reptiles, the reports of edge effects is varied in the literature, although there is a trend for more often negative impacts than positive. Reptile occurrence can be lower at edges than interiors due to inconsistent temperatures and humidity and the increased risk of habitat disturbance (Lehtinen et al., 2003; Schneider-Maunoury et al., 2016; Semlitsch and Bodie, 2003), or higher due to an increased number of open basking sites and suboptimal conditions for parasites (Blouin- Demers and Weatherhead, 2001; Schlaepfer and Gavin, 2001).

Defining how landscape attributes determine where species occur is one approach to conserving biodiversity in disturbed or threatened environments. Any one environmental factor (vegetation, topography, and human proximity) or a combination of a few (sometimes called its ecological niche (Raxworthy et al., 2003)) may influence the occurrence of squamate species. A model that describes the combination of landscape characteristics that supports a species can be used to predict where species will most likely occur, and may be more useful in land management, more relevant to decision makers and more cost-effective in protecting multiple species than are species-specific studies (Ferrier and Guisan, 2006; Rich et al., 2016). This is especially useful in situations where funding for conservation is severely lacking, where limited resources must be used efficiently to conserve areas with the greatest number of threatened species, such as in developing countries (Brooks et al., 2006; Myers et al., 2000; Sutherland et al., 2004).

Popular analyses used to investigate landscape use include generalised linear models, principal component analysis, and species distribution modelling (Liu et al., 2005) in programs such as Maxent. These methods focus on the ecological processes involved in determining a species' presence in an area, but often do not consider the underlying observational process that contributes to creating a dataset, and therefore do not account for imperfect detection (Dorazio and Royle, 2005; MacKenzie et al., 2006). An elusive species (able to camouflage or hide) or rare species (low abundance or small spatial range) may not be recorded in a land type, which will affect how the species' habitat selection and distribution is defined (Durso et al., 2011; Joseph et al., 2006; Pollock, 2006). Community-level Bayesian hierarchical occupancy modelling addresses pseudo-absence and imperfect detection by estimating the probability of detecting a species if it is present and incorporating this into an ecological model that estimates the probability that a species will occur at a site (Dorazio and Royle, 2005; MacKenzie et al., 2002; MacKenzie et al., 2006).

Using conservation prioritisation modelling, Kremen et al. (2008) concluded that Madagascar, an ecological hotspot (Myers et al., 2000; Harper et al., 2007), requires community-level research to adequately conserve its biodiversity. The exceptional endemism in Madagascar (more than 90% for reptiles and 92% for terrestrial vertebrates (Goodman and Benstead, 2005; Vences et al., 2009)) is likely due to the island's ancient isolation from the African mainland (~165 Ma) and from India (~80 Ma), as well as its complex topography and ocean currents which created multiple climates from sub-arid to humid (Irwin et al., 2010; Vences et al., 2009). The strong selection pressure created by these conditions led to species divergence through adaptation to local conditions, sometimes within very small geographic ranges. Madagascar is considered to be a model area in which to research patterns of species richness, because of the island's abundance of micro-endemics (species with ranges restricted to small parts of the island) (Kremen et al., 2008; Vences et al., 2009). Due to the fine resolution of its species richness patterns (Brooks et al., 2006), local rather than country-wide studies are more relevant when studying Madagascan biodiversity. Organism response to anthropogenic land-change in

Madagascar is not adequately researched, especially in broad taxonomic groups such as the reptiles (Irwin et al., 2010).

In light of this dearth of information, I investigated the associations between landscape structure and squamate occurrence in the Mahamavo region of Madagascar. Detection/non-detection data and satellite imagery collected annually at the site since 2014 were used in a community-level hierarchical occupancy model. The results were used to define squamate landscape use in the region, and shed light on how vegetation and anthropogenic proximity contribute to reptile occurrence and community structure. In light of the findings of other studies, I hypothesise that reptile presence will be greatest in sheltered areas with high levels of green vegetation that are furthest from human development and the periphery of the forest edge, although I expect that there will be some species that favour areas which offer open basking sites.

2.3 Methodology

2.3.1 Study area

Data were collected in the two main forest patches in the Mahamavo watershed, a mosaic of dry forest and wetland patches resulting from both natural land configuration and human interference (Long et al., 2013; Willis et al., 2015). Each forest patch was between 4 km and 6 km in diameter, and irregularly-shaped, with the entire study area being within 15x8 km^2 (Figure 2.1). The Mariarano village (-15.478821, 46.695887) and associated roads were located between these patches, and there were two small settlements on the outskirts of the larger eastern forest patch (Figure 2.1). During the winter months in which the surveys took place, the conditions were hot (~30°C) and dry and the climate was relatively homogenous over the study area.

2.3.2 Study species

Mahamavo is a transition zone between northern and western reptile species assemblages (Long et al., 2013). A biodiversity survey in 2013 found 46 squamate species (the majority of which are endemic to the island) from eight families (Long et al., 2013). As reptiles, all of the species are ectothermic and predatory. Predators of the small and moderately-sized squamates are mainly birds, while the large snakes such as the boids and hognose snakes are top consumers in the area (Glaw and Vences, 2007).

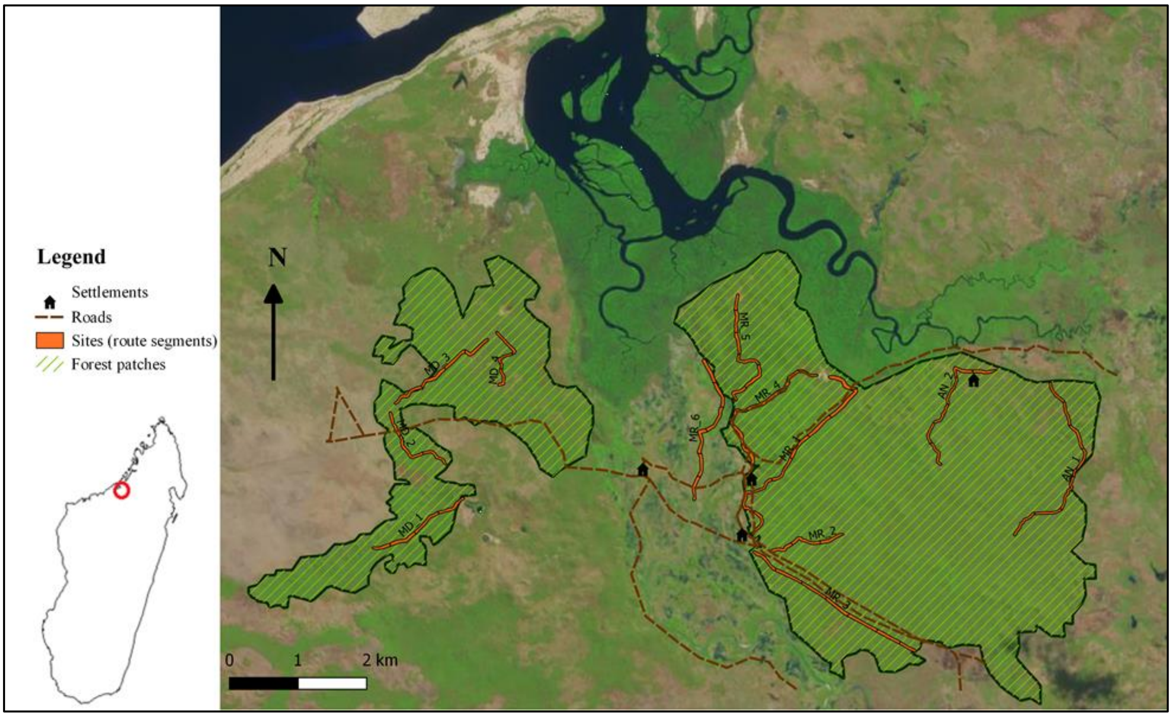


Figure 2.1. Map of the Mahamavo study area, showing sites (route segments) within survey routes sampled in the two main forest patches and nearby roads and settlements.

2.3.3 Experimental design and protocol

Reptile detection/non-detection *data*

Reptile detection/non-detection data from 2014-2017 were sourced from a database compiled by Operation Wallacea, created by surveys conducted in June and July (the dry season) by a team of ~6 surveyors. Eleven terrestrial routes, each between 2 and 4 km long, were sampled with visual encounters using line-transect sampling (Figure 2.1). A route was walked every morning and evening for 45 days; each route was sampled a minimum of six times per year. When a snake or lizard was detected, the species was identified and the GPS coordinates of its location recorded. Species were identified with the use of guide books and with the help of resident researchers on the survey team who are familiar with the reptiles in the area.

Defining site areas

Squamate detection/non-detection data were displayed in QGIS v2.18 and overlain with a map layer of the transect routes. The spatial distribution of a route's reptile community, or the area on and around a survey route that would be sampled during a survey occasion, was defined by creating a fixed buffer of 20 m (this distance estimated to be the maximum distance that an observer would be able to detect a reptile in the forest) around the line of the route. This buffer included all but a few outlying species locality records, which were removed from the analysis. Each route polygon was then divided into 500 m segments (Figure 2.1). Henceforth, 'sites' refer to these route segments (63 sites in total). This investigation is approached at a moderate resolution, focusing on species occupancy in a whole site, rather than to the microhabitat of individual squamates at point localities, but still limited to an area and its subset of species rather than to the entire patch or the whole island.

Proximity of sites to the closest road, settlement and edge of forest patch

Each site polygon was overlain with a map layer of the roads and settlements in the study area. I measured the straight-line distance from the midpoint of each site to the closest points of the closest road, village, and perimeter of the forest patch in which the squamate was present. For sites located outside of a forest patch, I multiplied the distance to the nearest point of the forest edge by -1 to differentiate these values from the distance values of sites within a forest patch.

Vegetation indices

Multispectral images recorded in 2014, 2015 and 2017 of the study area were acquired from the RapidEye satellite (5 m^2 spatial resolution; European Space Agency Observation Portal, https://earth.esa.int) and the remaining one image from the Sentinel II satellite (10 m^2 spatial resolution; European Space Agency Observation Portal, https://earth.esa.int) for 2016, because there were no cloudless RapidEye images for 2016. Pre-processing and calculations of the Sentinel II image were performed semi-automatically in QGIS (QGIS Development Team, 2015). Processing of the RapidEye images was done manually in ENVI v5.3. This involved radiometric calibration, which converts the digital numbers captured by the satellite into radiance values, and atmospheric correction using the FLAASH package (Adler-Golden et al., 1998), which removes atmospheric effects from the reflectance values (see http://www.harrisgeospatial.com/docs/FLAASH.html; http://www.harrisgeospatial.com/docs/CalibratingImagesTutorial.html).

Greenness and brightness indices were calculated for each site to investigate green vegetation density and soil reflectance using the Tasselled Cap Transformation developed by Kauth and Thomas, 1976. The Tasselled Cap Transformation is an effective measure of the landscape's vegetation and physical structure as it concentrates the information held by multiple bands into manageable indices that are directly correlated to the physical structure of the landscape (Crist and Cicone, 1984), and is sensitive to gradients in forest environments (Cohen et al., 1995). The reflectance values of five spectral bands were extracted from the processed satellite images, and greenness (density of green vegetation) and brightness (overall reflectance, orthogonal to greenness, and correlated with areas of exposed soil) values for each pixel of the image were calculated using the equations and coefficients derived by Dahms et al., 2016 and Schönert et al., 2014:

$$\text{Brightness} = 0.2435\times\text{band1} + 0.3448\times\text{band2} + 0.4881\times\text{band3} + 0.4930\times\text{band4} + 0.5835\times\text{band5}$$

$$\text{Greenness} = (-0.2216\times\text{band1}) + (-0.2319\times\text{band2}) + (-0.4622\times\text{band3}) + (-0.2154\times\text{band4}) + (0.7981\times\text{band5})$$

As with NDVI, greenness and brightness do not have units, only values which can be compared between pixels or sites. These data were then imported into QGIS, and mean greenness and brightness indices were calculated for each site per year. Multicollinearity among explanatory variables was tested using a Spearman correlation test in R.

2.3.4 Modelling approach

The occurrence responses of reptile species to the site variables above were modelled using community-level hierarchical Bayesian occupancy modelling because of its inclusion of both observation and ecological process models, and its flexible Bayesian approach that allows for the inclusion of a hierarchical model structure and random effects (Dorazio and Royle, 2005; Kéry and Royle, 2015; MacKenzie et al., 2002). Species presence records were recorded per site and occasion for each year, and then summed across survey occasions within a year to create a 2-dimensional matrix of species detection frequencies at each site, with a separate matrix for each year. The matrices were then stacked on top of one another and indexed by a year vector.

A single model was created to include all the species detected in all years and combined two logistic regressions: the ecological function and the observational function. The ecological component models the probability of species *k* occurring at site *i* (Ψ_{ik}), giving the presence-absence matrix $z_{i,k}$ where $z_{i,k}$ = 1 if species *k* occurs at site *i* and $z_{i,k} = 0$ if the species is absent. $z_{i,k}$ is treated as a Bernoulli random variable (thus $z_{i,k} \sim \text{Bernoulli}(\Psi_{ik})$). The ecological component included site- and year-specific brightness and greenness indices (‘bright’ and ‘green’ covariates respectively) and distances to the nearest road, settlement and forest edge (‘road’, ‘vill’ and ‘edge’). Continuous covariates were standardised by centring to a mean of zero, as per Kéry and Schaub, 2012. A categorical variable for a site’s location being inside or outside of a forest patch was also included (‘patch’ covariate), as was an interaction between this location and the distance to the forest edge. To account for possible correlation in occupancy among sites within a route and among survey occasions within a year, two random effects (‘routes’ and ‘years’) were included in the ecological model as per Wearn et al., 2017 and Kéry and Royle, 2015 (pg. 602-603). I used standard normal priors for all slope and intercept parameters and uniform hyperpriors for the variance parameters (including for the site covariates and random effects) e.g., $\alpha_k \sim \text{Normal}(\mu_\alpha, S_\alpha)$, where μ is the mean and *S* the precision, defined to be wide enough to be uninformative (judged by the minimal level of autocorrelation between the MCMC chains). Occurrence was assumed to be open (allowing for extinctions, immigrations and emigrations) between years but closed between occasions within a year.

$$\mathrm{logit}(\Psi_{ik}) = \alpha_k + \beta 1_k \times \mathrm{bright}_i + \beta 2_k \times \mathrm{green}_i + \beta 3_k \times \mathrm{road}_i + \beta 4_k \times \mathrm{vill}_i + \beta 5_k \times \mathrm{edge}_i + \beta 6_k \times \mathrm{patch}_i + \beta 7_k \times \mathrm{patch}_i \times \mathrm{edge}_i + \delta_{routes} \times \mathrm{routes}_i + \delta_{years} \times \mathrm{years}_i$$

The observational component models the probability that at least one individual of species k is detected given that it is present (p_k) so that the number of species detections y_{ik} is a realisation of z_{ik} binomial trials ($y_{ik} \sim \mathrm{Binomial}(p_k z_{ik})$). Detection probability was assumed to be constant across sites and years, only differing with species, thus:

$$\mathrm{logit}(p_k) = \mu_k$$

The model was written in the BUGS (Bayesian inference Using Gibbs Sampling) coding language and run in JAGS v 4.3.0 (Plummer, 2017) through R v 3.5.1 (R Core Team, 2014) with the jagsUI v 1.4.9 package (Kellner, 2017). See Appendix 1 for R code. Three MCMC (Markov chain Monte-Carlo) chains were run for 600 000 (MCMC) iterations each, with the first 20 000 iterations being discarded as “burn-in”, and a thinning rate of 110. Convergence was reached when the Gelman-Rubin statistic (“Rhat”) for all parameter estimates was < 1.1. Goodness-of-fit was assessed using Chi-squared discrepancy to compare the posterior distribution of the actual data with the posterior distribution simulated for the model (as per Kéry and Royle, 2015 and Tobler et al., 2015).

Species and site estimates, and their associated 95% credible intervals (CRIs), were derived by the model and then organised and analysed in RStudio (R Core Team, 2014). The credible interval, or Bayesian confidence interval (MacKenzie et al., 2006), is the range of values for which the population parameter has a 95% chance of falling within, directly calculated from the observed dataset and the posterior distribution; this differs from the frequentist ‘confidence interval’ which only defines a fixed, ‘true value’ of the estimate being either within an interval (calculated from repeated samples) or not within the interval (Royle and Dorazio, 2008). Derived estimates included mean site occupancy probability, mean occupancy probability per species, species detection probability, number of species per site, and the effects of site variables (brightness and greenness indices and distances to the nearest road, settlement and forest patch edge) on each species’ occupancy (i.e., the slopes). These estimates were analysed to assess which site characteristics promoted general squamate presence and species richness, as well as the presence of individual species.

2.4 Results

2.4.1 Mean squamate responses to landscape structure

Mean squamate occupancy and detection probability

A total of 6220 terrestrial squamate individuals were detected and 37 species were identified during the study (Table 2.1). Mean squamate occupancy probability was estimated at 0.48 (CRI 0.36, 0.61), which took into account a mean detection probability of all species at all sites of 0.08 (0.01, 0.09). Mean species occupancy probability varied from 0.08 (0.06, 0.11) for *Phelsuma laticauda* to 0.94 (0.89, 0.98) for the most commonly occurring species, *Phelsuma kochi* (Table 2.1). Detection probability ranged from 0.005 (0.001, 0.003) for *Dromicodryas quadrilineatus* to 0.38 (0.35, 0.37) for *Phelsuma kochi* (Table 2.1).

Table 2.1. Mean estimated occupancy probabilities (psi) and detection probabilities (p) and associated Bayesian 95% credible intervals (CRI) of terrestrial squamate species surveyed in Mahamavo, Madagascar from 2012 to 2017.

Species	**psi**	**95% CRI**		**p**	**95% CRI**	
Acrantophis madagascariensis	0.264	0.021	0.900	0.036	0.003	0.009
Blaesodactylus antogilensis	0.250	0.012	0.909	0.021	0.001	0.004
Blaesodactylus sakalava	0.342	0.061	0.888	0.029	0.006	0.013
Dromicodryas bernieri	0.676	0.225	0.990	0.018	0.007	0.011
Dromicodryas quadrilineatus	0.795	0.299	0.991	0.005	0.001	0.003
Furcifer angeli	0.841	0.793	0.885	0.347	0.317	0.337
Furcifer oustaleti	0.818	0.750	0.888	0.276	0.246	0.265
Geckolepis maculata	0.644	0.383	0.915	0.056	0.034	0.045
Geckolepis polylepsis	0.421	0.076	0.919	0.025	0.006	0.011
Geckolepis typica	0.572	0.176	0.952	0.014	0.004	0.008
Hemidactylus mercatorius	0.084	0.025	0.223	0.099	0.024	0.057
Ithycyphus miniatus	0.545	0.053	0.991	0.012	0.002	0.004
Langaha madagascariensis	0.643	0.143	0.989	0.012	0.003	0.006
Langaha pseudoalluaudi	0.407	0.016	0.962	0.013	0.001	0.003
Leioheterodon madagascariensis	0.438	0.121	0.943	0.023	0.006	0.012
Liophidium torquatum	0.159	0.004	0.833	0.025	0.001	0.004
Lygodactylus tolampyae	0.790	0.714	0.866	0.209	0.181	0.199
Madagascarophis colubrinus	0.241	0.087	0.551	0.060	0.018	0.038
Madascincus intermedius	0.174	0.004	0.887	0.026	0.001	0.004
Mimophis mahfalensis	0.794	0.620	0.944	0.087	0.065	0.078
Oplurus cuvieri	0.269	0.140	0.540	0.115	0.047	0.086
Paroedura stumpfii	0.485	0.358	0.647	0.122	0.086	0.107
Paroedura vazimba	0.126	0.030	0.424	0.071	0.012	0.036
Phelsuma kochi	0.938	0.892	0.978	0.377	0.349	0.367
Phelsuma laticauda	0.082	0.055	0.107	0.232	0.152	0.199
Phelsuma lineata	0.084	0.008	0.374	0.065	0.006	0.023
Phelsuma madagascariensis	0.083	0.023	0.216	0.051	0.011	0.027
Phelsuma mutabilis	0.381	0.006	0.960	0.014	0.000	0.002
Sanzinia madagascariensis	0.503	0.123	0.975	0.022	0.006	0.012
Stenophis (Phisalixella) pseudogranuliceps	0.802	0.345	0.995	0.016	0.008	0.012
Stenophis (Phisalixella) variabilis	0.697	0.340	0.944	0.020	0.010	0.015
Trachylepis elegans	0.554	0.339	0.830	0.076	0.044	0.061
Trachylepis gravenhorstii	0.589	0.415	0.805	0.079	0.052	0.068
Uroplatus ebenaui	0.285	0.176	0.464	0.112	0.062	0.091
Uroplatus guentheri	0.501	0.352	0.693	0.077	0.049	0.065
Uroplatus henkeli	0.176	0.015	0.849	0.029	0.002	0.009
Zonosaurus laticaudatus	0.551	0.372	0.756	0.076	0.049	0.064

Effects of site characteristics on mean squamate occupancy

The CRIs (Bayesian 95% credible intervals) included zero for all mean site occupancy responses (effects of site variables on mean occupancy, or regression coefficient estimates) to continuous habitat variables (Table 2.2) indicating that, at a broad scale (overall squamate occupancy rather than species-specific responses), there was high variability among species responses and mean values of these variables had low predictive power in estimating site occupancy.

Table 2.2. Mean squamate site occupancy responses (regression coefficient estimates) to landscape characteristics, and associated Bayesian 95% credible intervals (CRI).

Site variable	Mean occupancy response	95% CRI	
Brightness	-0.374	-0.821	0.016
Greenness	0.433	-0.033	1.020
Road distance	0.068	-0.253	0.375
Settlement distance	0.147	-0.151	0.463
Forest edge distance	-1.093	-2.488	0.142

However, there was a clear distinction between mean reptile occupancy within a forest patch and outside of a forest patch, with higher mean occupancy and variation among sites within a forest patch (0.48 (0.35, 0.61)) than those outside of a forest patch (0.29 (0.18, 0.43) (Figure 2.2(f)). There was suggestive evidence that mean site occupancy decreased with increasing brightness (Table 2.2; Figure 2.2(a)), and increased with increasing greenness and distance to roads and settlements (Table 2.2; Figure 2.2(b), (c) and (d)). With regards to the distance of a site to the edge of the forest patch, the mean squamate occupancy increased towards the periphery of the forest (Table 2.2); the positive trend in Figure 2.2(e) is not reliable, considering that it includes sites both inside and outside of a forest patch (this is clarified later when assessing the estimates of individual species). Therefore, species occupancy was highest within forest patches, and may have been higher at sites with less exposed soil, denser green vegetation, and were further from roads and settlements but closer to the forest patch edge.

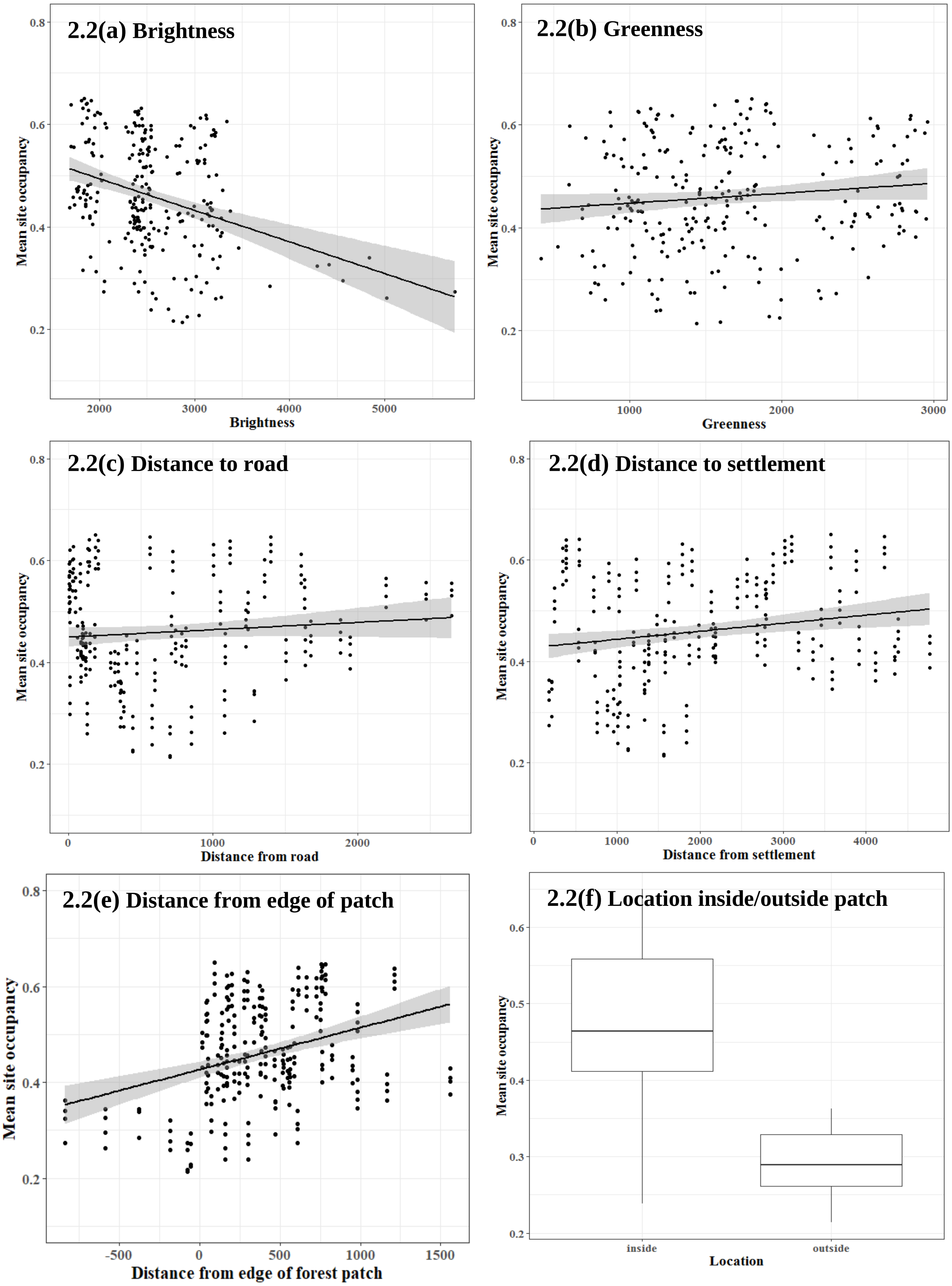


Figure 2.2. Effects of increased soil reflectance (a), vegetation greenness (b), and distance from the nearest point of the nearest road (c), settlement (c) and edge of the occupied forest patch (d) on mean reptile occupancy probability, as well as mean occupancy inside and outside of a forest patch (f), and associate 95% credible intervals.

2.4.2 Species richness

Basic species counts ranged from one species at one site in 2016 to 12 species at another site in 2017 (5 and 19 species in total for all years at the same sites), while model estimates of species numbers at the same sites were considerably higher, at 9 (4, 15) and 25 (20, 30) respectively and a mean over the years of 10 (5, 16) and 24 (18, 29) species respectively. The model estimates of species number in response to each habitat variable showed the same trends as the mean squamate occupancy responses (see Figure 2.3(a)-2.3(f) in Appendix 2). Mean species number was higher at sites within a forest patch (23 (4, 30)) than those outside a forest patch (17 (3, 19)) (Figure 2.3(f)). Species number decreased with increasing soil exposure (Figure 2.3(a)) and increased with increasing greenness and distance from roads and settlements (Figure 2.3(b), (c) and (d)). Again, the positive trend in Figure 2.3(e) is not reliable, considering that it includes sites both inside and outside of a forest patch.

2.4.3 Individual species responses to landscape structure

Many of the occupancy responses to site variables of individual species had model estimates with CRIs including zero (Figure 2.4). I therefore focused primarily on the results of those species with CRIs that did not include zero, and secondarily on those with limits that extended over zero only marginally (-0.2 for a positive estimate, 0.2 for a negative estimate).

Occupancy was negatively associated with increased brightness (soil reflectance) for 36 of the species, with the strongest effect of -1.02 (-2.56, -0.04) being for *Geckolepis maculata*. The only species positively associated with increased brightness, *Furcifer oustaleti,* had a weak response and CRIs including zero (0.06 (-0.55, 0.27)) (Figure 2.4(a)). *Geckolepis maculata* and *Lygodactylus tolampyae* were the most negatively affected of the species by increased brightness and their CRI estimates did not include zero (Figure 2.4(a)). The estimates for *Paroedura vazimba, Acrantophis madagascariensis, Uroplatus guentheri, Furcifer angeli* and *Paroedura stumpfii* suggested that these species may also prefer sites with lower soil reflectance (Figure 2.4(a)).

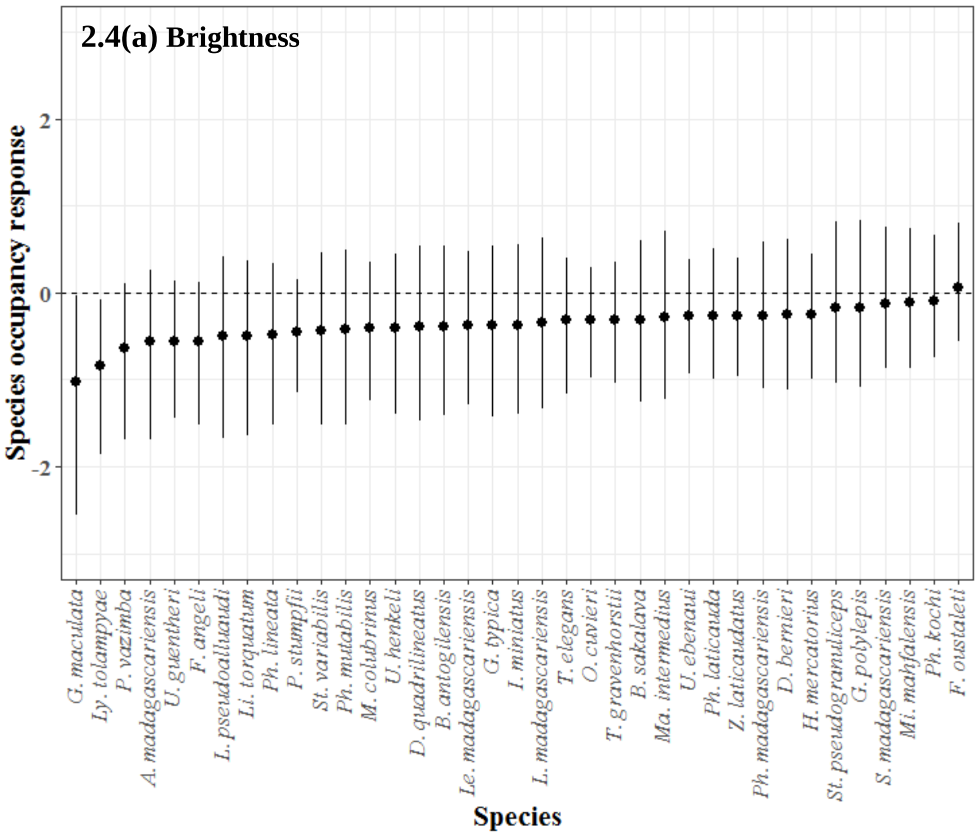
All species had positive associations with increased greenness of a site (Figure 2.4(b)). *Uroplatus ebenaui, Furcifer oustaleti* and *Furcifer angeli* had the strongest preferences of the species for greener sites (up to 0.75 (0.12, 1.53) for *U. ebenaui*), and CRIs that did not include zero (Figure 2.4(b)). There was also suggestive evidence for *Geckolepis polylepis, Mimophis mahfalensis* and *Madagascarophis colubrinus* preferring greener sites (with *Geckolepis polylepis* having the strongest positive response of all species of 0.82 (-0.08, 1.99)), and that *Uroplatus guentheri* and *Paroedura stumpfii* had a moderate preference for greener sites (Figure 2.4(b)).

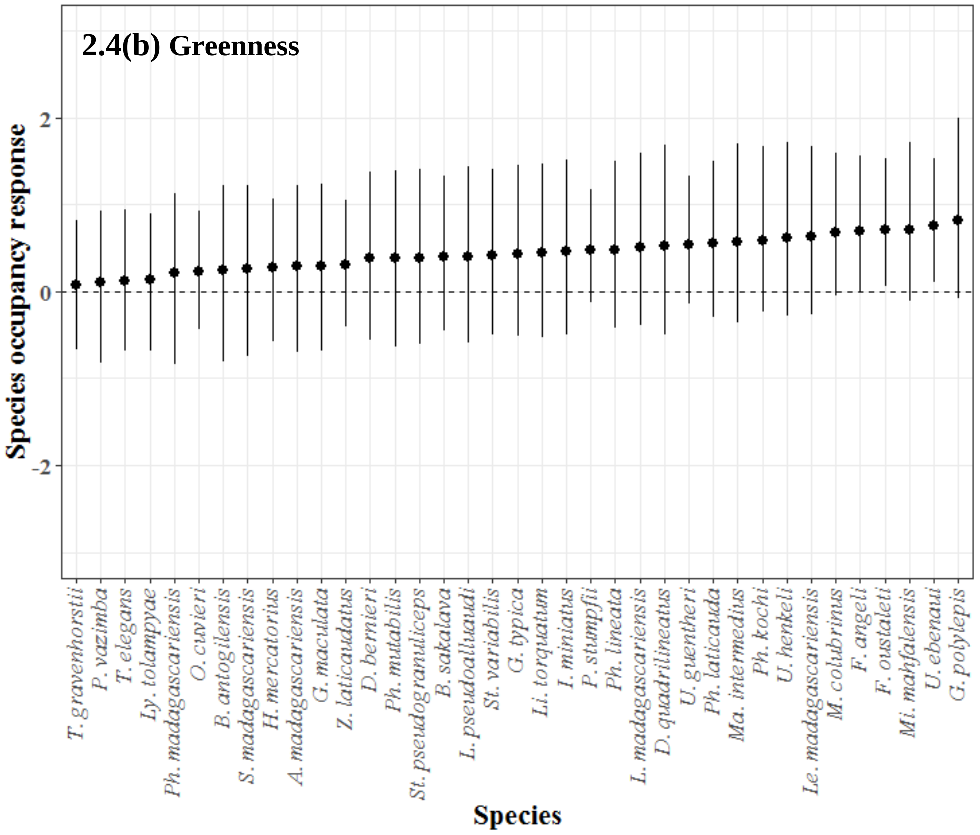
The CRIs for all species occupancy responses to roads included zero, and the responses did not exceed 0.34 (-0.19, 1.24) for *Zonosaurus laticaudatus* and -0.25 for *Furcifer oustaleti* (-0.80, 0.23) (Figure 2.4(c)). The occupancy response estimates and slight extension of the CRIs over zero for *Zonosaurus laticaudatus* and *Uroplatus guentheri* suggested that these species were more likely to occur at sites farther from roads (Figure 2.4(c)).

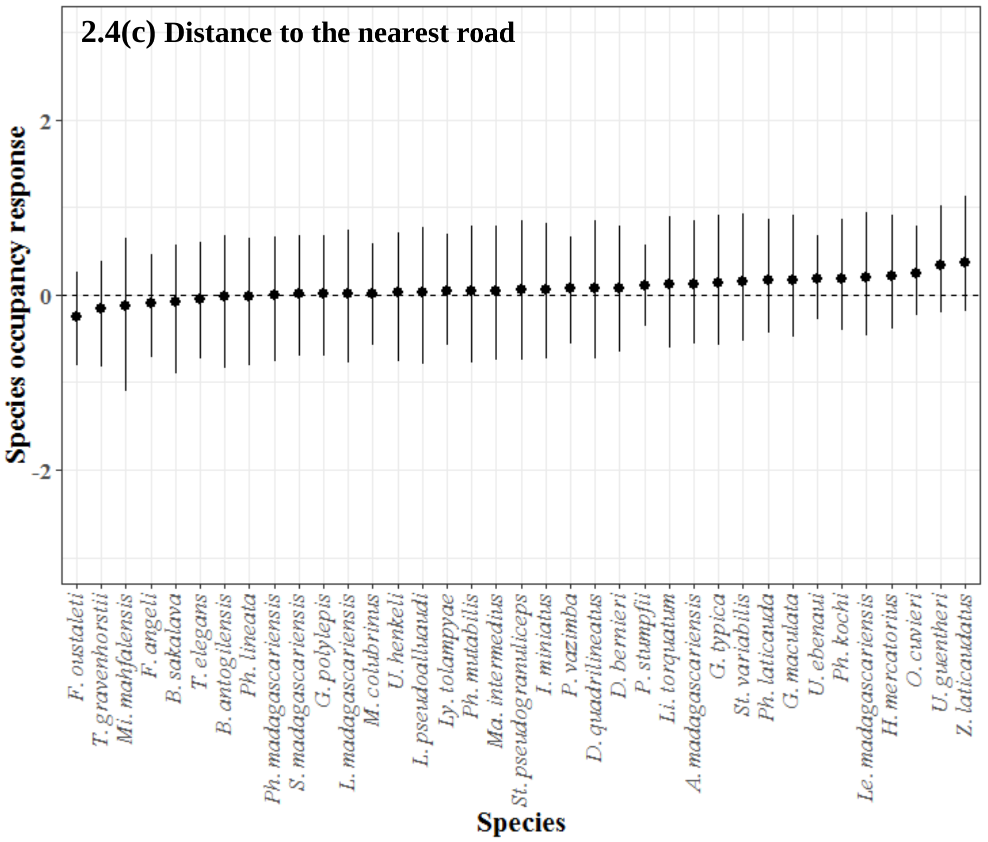
Uroplatus guentheri was the most likely of all the species to occur at sites that were farther from settlements than sites close to settlements (0.81 (0.05, 1.77)) (Figure 2.4(d)). There was some support for *Trachylepis elegans, Trachylepis gravenhorstii* and *Hemidactylus mercatorius* also preferring sites further from settlements (Figure 2.4(d)).

All of the species were negatively associated with increased distance from the forest edge, and the distance to the edge of the forest patch had a strong effect on some species compared to the effects of the other variables (up to -1.94 (-4.28, -0.24)) (Figure 2.4(e)). The five species with CRIs not including zero, *Hemidactylus mercatorius, Phelsuma madagascariensis, Phelsuma laticauda, Madagascarophis colubrinus* and *Furcifer oustaleti,* were the most negatively associated with increased distance from the edge of the forest patch, and there is suggestive evidence that *Dromicodryas bernieri* may also prefer sites closer to the edge of the forest (Figure 2.4(e)).

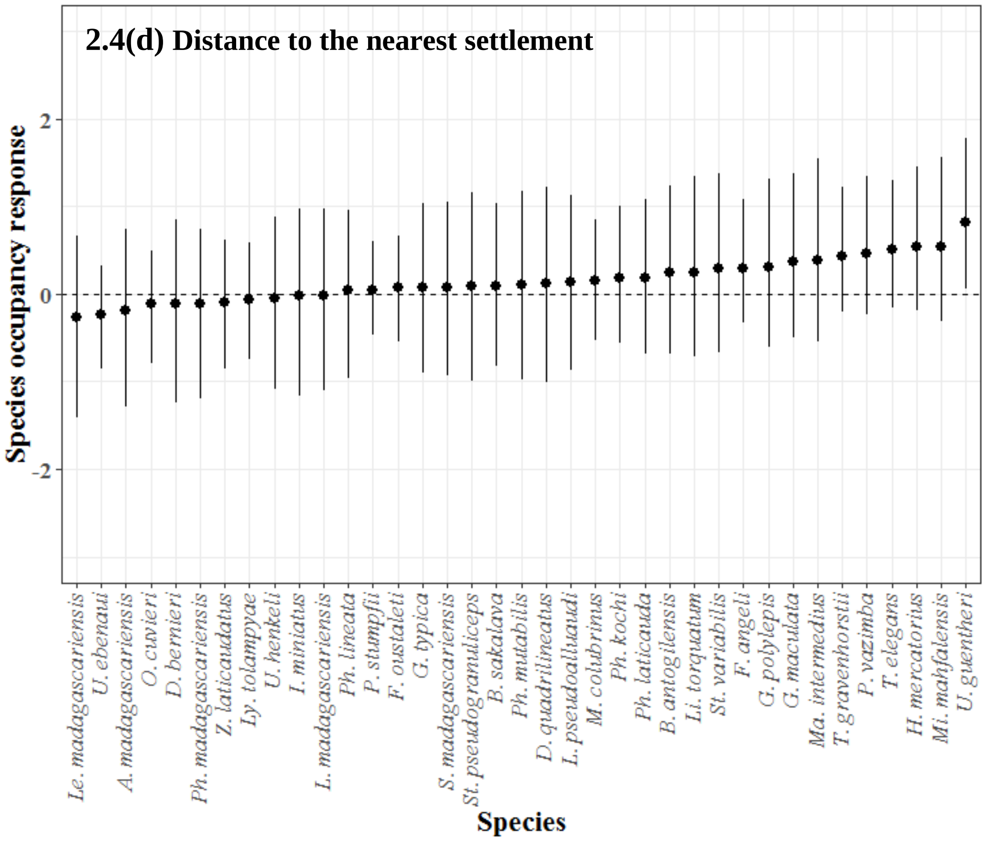
The location of a site inside or outside of a forest patch had the strongest effects on species occupancy of all the habitat variables (note the species occupancy response range in Figure 2.4(f)). 33 species were more likely to occur at sites inside a forest patch, with *Lygodactylus tolampyae* (6.71 (2.76, 8.07)) and *Furcifer angeli* (6.61 (2.97, 10.44) being particularly strongly associated with such sites, followed by *Dromicodryas quadrilineatus, Trachylepis elegans, Mimophis mahfalensis, Phisalixella variabilis, Trachylepis gravenhorstii, Paroedura stumpfii* and *Uroplatus guentheri* (Figure 2.4(f)). There was also some evidence that *Phelsuma kochi* preferred sites inside a forest patch (Figure 2.4(f)). *Phelsuma laticauda* had the strongest preference for sites outside of a forest patch (-4.70 (-8.89, -0.72)) and had the only habitat response estimate for a species with outside-patch preference with CRIs not including zero (Figure 2.4(f)).


2.4(a) Brightness
Species occupancy response
2
0
-2
G. maculata
Ly. tolampyae
P. vazimba
A. madagascariensis
U. guentheri
F. angeli
L. pseudoalluaudi
Li. torquatum
Ph. lineata
P. stumpfii
St. variabilis
Ph. mutabilis
M. colubrinus
U. henkeli
D. quadrilineatus
B. antogilensis
Le. madagascariensis
G. typica
I. miniatus
L. madagascariensis
T. elegans
O. cuvieri
T. gravenhorstii
B. sakalava
Ma. intermedius
U. ebenaui
Ph. laticauda
Z. laticaudatus
Ph. madagascariensis
D. bernieri
H. mercatorius
St. pseudogranuliceps
G. polylepis
S. madagascariensis
Mi. mahfalensis
Ph. kochi
F. oustaleti
Species


2.4(b) Greenness
Species occupancy response
2
0
-2
T. gravenhorstii
P. vazimba
T. elegans
Ly. tolampyae
Ph. madagascariensis
O. cuvieri
B. antogilensis
S. madagascariensis
H. mercatorius
A. madagascariensis
G. maculata
Z. laticaudatus
D. bernieri
Ph. mutabilis
St. pseudogranuliceps
B. sakalava
L. pseudoalluaudi
St. variabilis
G. typica
Li. torquatum
I. miniatus
P. stumpfii
Ph. lineata
I. madagascariensis
D. quadrilineatus
U. guentheri
Ph. laticauda
Ma. intermedius
Ph. kochi
U. henkeli
Le. madagascariensis
M. colubrinus
F. angeli
F. oustaleti
Mi. mahfalensis
U. ebenaui
G. polylepis
Species



2.4(c) Distance to the nearest road



2.4(d) Distance to the nearest settlement

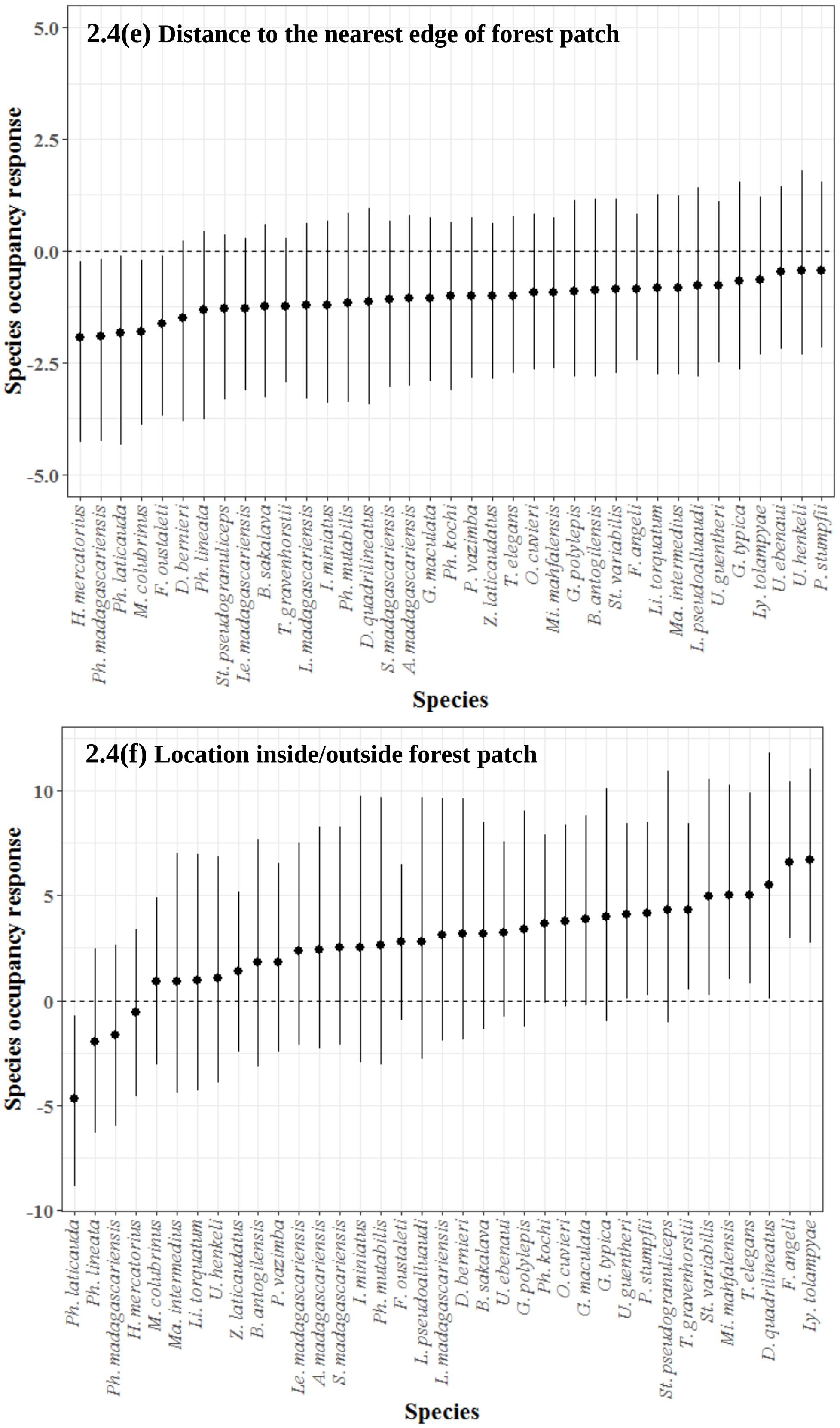


Figure 2.4. Individual species occupancy responses and associated 95% credible intervals to increased soil reflectance (a), vegetation greenness (b), and increased distance from the nearest road (c), settlement (d) and edge of the occupied vegetation patch (e), as well as being inside/outside a forest patch (inside preferences are those above 0) (f). Estimates above the dotted x-axis represent a positive relationship between species occupancy and the site variable, and those below represent a negative relationship.

Species assemblages

Species were grouped into assemblages based on similarity of responses to site variables exhibited in Figure 2.4. Species in parentheses demonstrated suggestive evidence (marginal inclusion of zero of CRIs) in their estimates for responses to site variables.

1. Low brightness: *Geckolepis maculata, Lygodactylus tolampyae (Paroedura vazimba, Acrantophis madagascariensis, Uroplatus guentheri, Furcifer angeli, Paroedura stumpfii)*
2. High greenness: *Uroplatus ebenaui, Furcifer oustaleti, Furcifer angeli (Geckolepis polylepis, Mimophis mahfalensis, Madagascarophis colubrinus, Uroplatus guentheri, Paroedura stumpfii)*
3. Far from roads: *(Zonosaurus laticaudatus, Uroplatus guentheri)*
4. Far from settlements: *Uroplatus guentheri (Trachylepis elegans, Trachylepis gravenhorstii, Hemidactylus mercatorius)*
5. Close to forest patch edge: *Hemidactylus mercatorius, Phelsuma madagascariensis, Phelsuma laticauda, Madagascarophis colubrinus* and *Furcifer oustaleti (Dromicodryas bernieri)*
6. Inside forest patch: *Lygodactylus tolampyae, Furcifer angeli, Dromicodryas quadrilineatus, Trachylepis elegans, Mimophis mahfalensis, Phisalixella variabilis, Trachylepis gravenhorstii, Paroedura stumpfii, Uroplatus guentheri (Phelsuma kochi)*
7. Outside forest patch: *Phelsuma laticauda*

Goodness-of-fit

A Bayesian p-value of 0.22 and a plot of the Pearson goodness-of-fit residuals indicated that the model fits the data sufficiently (Figure 2.5).

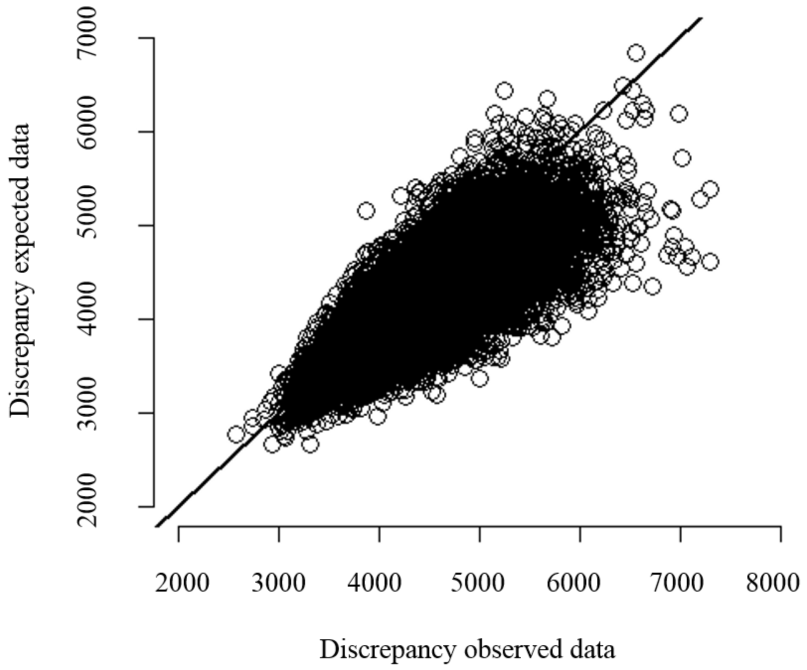


Figure 2.5. Simulated versus observed discrepancy measures of a Pearson goodness-of-fit test of the site occupancy model.

2.5 Discussion

This investigation revealed interesting reptile species occupancy patterns of Mahamavo’s dry forest, with regards to vegetation structure, anthropogenic proximity and patch dynamics. Mean species occurrence and species richness were positively associated with densely vegetated areas inside a forest patch that were closer to the edge of the forest patch than to the interior and, to a lesser extent, were further from settlements. The location of a site within a forest patch had the strongest positive effect on reptile occurrence (although one species, *Phelsuma lineata*, had a strong preference for sites outside of the forest) and road proximity had the weakest effect. The similarities and differences in occupancy patterns seen when investigating the effects of landscape structure, both species-specific distribution patterns and mean reptile occupancy and species richness, have important implications for the management of forest species.

2.5.1 Implications of imperfect detection

Species occupancy did not necessarily increase with detection, a finding that illustrates the importance of accounting for the imperfect observational process in modelling species distributions. If imperfect detection had not been accounted for using repeated surveys and sites, I may have concluded that the species that are the most difficult to detect, such as *Dromicodryas quadrilineatus*, are least likely to occur at a site, when it is in fact *Hemidactylus mercatorius* that had the lowest mean occupancy probability. The model allowed us to make inferences on the effects of landscape structure on species distributions for species which were not detected at certain sites (even those with optimal habitat conditions) on some surveys. In the case of our study, the species that was most easily detected (*Phelsuma kochi*) also occurred most frequently, but without the inclusion of detection probability, we would not have had a measure of how much trust could be put in the occupancy estimate's representation of reality. The importance of accounting for imperfect detection when modelling the distributions of cryptic reptiles has been demonstrated in other studies (Durso et al., 2011; Pearson et al., 2007), and is illustrated well here.

2.5.2 Occurrence inside/outside a forest patch

The strong preference of reptile species for sites within forest patches indicates that they are more likely to occur at such sites and have likely adapted to the resources that these sites offer. A natural step may be to assume that this is because forest patches would naturally contain sites that have denser vegetation and are further from human development than sites outside of forests. However, the species responses to being inside or outside of a forest patch were stronger than to any other variable and there was no correlation between predictor variables. Therefore it may be the combination of these forest characteristics, rather than vegetation or human proximity alone, which affects these species. This was also noted by Brown et al., (2014), which concluded that Madagascan reptile distribution patterns are a result of a complex combination of diversification factors rather than one or two predominant mechanisms.

The preference for sites within a forest patch were demonstrated at a species-level by *Dromicodryas quadrilineatus*, *Phisalixella (Stenophis) variabilis* and *Phelsuma kochi*, which were more likely to occur at sites within, rather than at sites outside of, a forest patch, but do not show associations with individual measures of greenness and brightness levels or human proximity. Brown et al., (2014) found that *Phelsuma* distributions are a result of an array of historic habitat variables, which may be why we see this pattern for *Phelsuma kochi* in this study. *Dromicodryas quadrilineatus* may display these occurrence patterns because of its tendency to travel quickly and far to hunt, and its range of different hunting environments (anthropogenic, open limestone and forest) (Glaw and Vences, 2007; Park, 2017). The investigation into the preference of squamates for sites inside versus outside of a forest patch is an important part of the analysis because without it, the lack of preference for any individual landscape component may have led us to conclude that these are generalist species, when in fact they appear to have a particular preference for a combination of habitat variables rather than a lack of specialisation.

2.5.3 Edge effects

All species were more likely to occur at sites closer to the edge than the interior of the forest, especially *Hemidactylus mercatorius*, *Phelsuma madagascariensis*, *Phelsuma laticauda*, *Madagascarophis colubrinus*, *Furcifer oustaleti* and *Dromicodryas bernieri*. Lehtinen et al., (2003) also found that *F. oustaleti* prefers forest edges in Madagascan rainforest. In the Neotropics however, Schneider-Maunoury et al., (2016) found that more than half of reptile species are negatively associated with forest edges, demonstrating that edge effect responses are very much species- and landscape-specific. *Hemidactulus mercatorius*, *Phelsuma* species, and *F. oustaleti* occur in various habitat types and often inhabit disturbed forest sites (Glaw and Vences, 2007) and therefore it is not surprising that these species occur on the forest fringes, which would offer access to a variety of habitats, both inside and outside of the forest. Forest edges can offer the best thermoregulation opportunities for forest reptile species (Blouin-Demers and Weatherhead, 2001) and so the beneficial presence of both sunny or warm areas in which to bask, as well as the shelter of the nearby forest vegetation, may have contributed to the distributions of the species being positively associated with forest edges.

2.5.4 Impact of vegetation structure

One of the most obvious differences between sites within a forest patch to those outside is the presence of denser vegetation from tree canopy within a forest patch, which would offer shelter from predators, prey and the elements (Beck and Jennings, 2003; Bruton et al., 2016; Masterson et al., 2008; Downes, 2001; Lagarde et al., 2012). The positive association of reptile occurrence and high greenness demonstrated here is reflected by global reptile species richness and abundance patterns, because the distribution of consumers is dependent on the distributions of the producers in a system (Lewin et al., 2016). The importance of forest canopy cover and the heterogeneous habitats provided by forests has been demonstrated in Indonesia (Wanger et al., 2010), China (Qian et al., 2007), and Australia (Garden et al., 2007) where reptile abundance and species richness are higher in such areas.

Furcifer angeli, Furcifer oustaleti, and *Uroplatus ebenaui* show particular preference for higher greenness as well as for being within a forest patch. *Furcifer* species are generally considered to occur in more open or transformed habitats than many of Madagascar's other chameleons, which prefer the sheltered interior of the forest (Andreone et al., 2005; Randrianantoandro et al., 2010; Raxworthy and Nussbaum, 2006). However, the dry forest of our study would indeed be considered more open and less green in comparison to tropical forests elsewhere in Madagascar even if, in the context of our study site, it is more densely canopied compared to the surrounding environment. *Uroplatus ebenaui* would particularly benefit from high-density vegetation, as it is highly adapted to mimicking leaves and would be particularly difficult for predators to detect in the low light given by dense tree canopy. Similarly, the association of *Paroedura stumpfii* and high greenness is likely linked to its habit of climbing on tree trunks, or staying on the ground amongst fallen leaves in which it is well camouflaged, to hunt (Glaw and Vences, 2007).

"Brightness" is a measure of the mean reflectance of soil in an area (Kauth and Thomas, 1976), and had a negative association with reptile occupancy and species richness in this study. The relationship between soil reflectance indices and species distributions or habitat suitability is poorly studied, the focus in the literature tending to be on the presence of vegetation – however, it has been noted that sites that are less vegetated tend to have higher brightness, such as forest stands that have recently been cleared (Healey et al., 2005). In light of this, and the orthogonal nature of the brightness index to the greenness index, brightness is used in this study to complement greenness in assessing the effects of vegetation structure on reptile occurrence. Therefore, the mean preference of reptiles for more densely-vegetated sites (high greenness) is reflected by the preference for sites with lower proportions of exposed reflective soil (lower brightness).

The occupancy responses of *Lygodactylus tolampyae*, *Furcifer angeli*, *Geckolepis maculata*, *Paroedura vazimba* and *Paroedura stumpfii* are negatively associated with brightness, and so are more likely to occur at sites with low densities of exposed reflective soil or rock. These species are all highly reliant on trees for hunting, movement and shelter (Glaw and Vences, 2007), and hence it is not surprising that they prefer densely vegetated sites. *Acrantophis madagascariensis* also demonstrates this occurrence pattern for similar reasons. Being a boid, *A. madagascariensis* is a large-bodied ambush predator and spends much of its time hidden in ground foliage, although it is also known to visit villages to feed on commensal rodents (Vences and Glaw, 2003). Note that *Lygodactylus tolampyae*, *Geckolepis maculata*, *Paroedura vazimba* and *Acrantophis madagascariensis* did not show significant positive responses to high greenness values, which demonstrates the relevance of using more than one index in assessments of landscape vegetation structure.

2.5.5 Proximity to human development

The effect of proximity of anthropogenic development on reptile occupancy is much less apparent than that of vegetation structure. The mean reptile occupancy responses and site species richness estimates indicate that, on average, reptiles may have a slight preference for occurring further away from settlements and roads. Similarly, (Hunt et al., 2013) found that proximity to urbanisation reduces species richness and species occupancy, and Irwin et al., (2010) concluded that anthropogenic disturbance in Madagascan forests reduces reptile species diversity. This is likely due to the heightened risk of a reptile's habitat being exploited and transformed at sites that are accessible to humans (Böhm et al., 2016). *Uroplatus guentheri* and the two *Trachylepis* species show particular preference for sites that are further from settlements. Both *T. elegans* and *T. gravenhorstii* are very generalised in their habitats, frequenting both open and forested areas, whereas *U. guentheri* is restricted to dry forest (Glaw and Vences, 2007), demonstrating that proximity to human development may negatively affect species with very different habits and degrees of habitat-specificity. The absence of significant positive associations of any species with proximity to settlements, even those that are known to be commensal (particularly the *Hemidactylus* and *Phelsuma* geckos and the *Mimophis* and *Acrantophis* snakes) is probably due to the fact that I did not sample the settlements – these species may occur both in forest patches and in settlements, but not in the space in between these habitats.

The very weak effect of roads on mean occupancy, and its negligible effect on individual species occupancy, is perhaps due to the roads being unpaved. Robson and Blouin-Demers (2013) found that eastern hognose snakes (*Heterodon platirhinos*) avoid crossing busy tarred roads, which have faster traffic, but not unpaved roads. Therefore the level of development, and not just the presence of development, may be a pertinent consideration. However, Patrick and Gibbs (2009) did not find an effect of road distance on north American snake species occurrence, despite the roads in the area being heavily travelled. Therefore the presence of roads may be very situation-specific and not a very useful variable for predicting distribution patterns of reptile assemblages in the case of my study.

2.5.6 Conclusion

To promote the presence of the greatest number of species, and the presence of those species that are most 'habitat-specialist' or have the strongest responses to gradients in landscape structure, the conservation of sites that are densely vegetated, are towards the edges of the forest, and are further from settlements should be prioritised. Distance to the edge of the forest patch is clearly a strong effector, with the periphery of the forest being especially important. It is necessary to consider the spatial scale of the landscape under study however, as other studies have found that at a courser resolution (global rather than regional), forest patch interiors tend to hold more species than do forest edges. These results provide a basis for future reptile occupancy studies, and our understanding of reptile landscape-use would be enhanced by incorporating microhabitat data into the analyses and testing the model with data from other forest ecosystems to see whether the model can effectively predict reptile presence elsewhere.

2.6 Literature cited

Adler-Golden, S., Berk, A., Bernstein, L., Richtsmeier, S., Acharya, P., Matthew, M., Anderson, G., Allred, C., Jeong, L., Chetwynd, J., 1998. FLAASH, a MODTRAN4 atmospheric correction package for hyperspectral data retrievals and simulations. Presented at the Proc. 7th Ann. JPL Airborne Earth Science Workshop, JPL Publication Pasadena, CA, pp. 9–14.

Adolph, S.C., 1990. Influence of Behavioral Thermoregulation on Microhabitat Use by Two Sceloporus Lizards. Ecology 71, 315–327. https://doi.org/10.2307/1940271

Alexander, G., Marais, J., 2007. A guide to the reptiles of southern Africa. Struik Pub.

Alves, R.R. da N., Vieira, W.L. da S., Santana, G.G., 2008. Reptiles used in traditional folk medicine: conservation implications. Biodivers. Conserv. 17, 2037–2049. https://doi.org/10.1007/s10531-007-9305-0

Andreone, F., Guarino, F., Randrianirina, J., 2005. Life history traits, age profile, and conservation of the panther chameleon, Furcifer pardalis (Cuvier 1829), at Nosy Be, NW Madagascar. Trop. Zool. 18, 209–225.

Beck, D.D., Jennings, R.D., 2003. Habitat use by Gila monsters: the importance of shelters. Herpetol. Monogr. 17, 111–129.

Bennett, A.F., Radford, J.Q., Haslem, A., 2006. Properties of land mosaics: implications for nature conservation in agricultural environments. Biol. Conserv. 133, 250–264.

Blouin- Demers, G., Weatherhead, P.J., 2001. An experimental test of the link between foraging, habitat selection and thermoregulation in black rat snakes Elaphe obsoleta obsoleta. J. Anim. Ecol. 70, 1006–1013. https://doi.org/10.1046/j.0021-8790.2001.00554.x

Böhm, M., Williams, R., Bramhall, H.R., McMillan, K.M., Davidson, A.D., Garcia, A., Bland, L.M., Bielby, J., Collen, B., 2016. Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. Glob. Ecol. Biogeogr. 25, 391–405.

Bonnet, X., Shine, R., Lourdais, O., 2002. Taxonomic chauvinism. Trends Ecol. Evol. 17, 1–3. https://doi.org/10.1016/S0169-5347(01)02381-3

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., Rodrigues, A.S., 2006. Global biodiversity conservation priorities. science 313, 58–61.

Brown, J.L., Cameron, A., Yoder, A.D., Vences, M., 2014. A necessarily complex model to explain the biogeography of the amphibians and reptiles of Madagascar. Nat. Commun. 5, 5046.

Bruton, M.J., Maron, M., Franklin, C.E., McAlpine, C.A., 2016. The relative importance of habitat quality and landscape context for reptiles in regenerating landscapes. Biol. Conserv. 193, 37–47.

Bruton, M.J., McAlpine, C.A., Maron, M., 2013. Regrowth woodlands are valuable habitat for reptile communities. Biol. Conserv. 165, 95–103. https://doi.org/10.1016/j.biocon.2013.05.018

Butler, M.A., Schoener, T.W., Losos, J.B., 2000. The Relationship Between Sexual Size Dimorphism and Habitat Use in Greater Antillean Anolis Lizards. Evolution 54, 259–272. https://doi.org/10.1111/j.0014-3820.2000.tb00026.x

Cohen, W.B., Spies, T.A., Fiorella, M., 1995. Estimating the age and structure of forests in a multi-ownership landscape of western Oregon, USA. Int. J. Remote Sens. 16, 721–746.

Cowling, R., Pressey, R., Lombard, A., Desmet, P., Ellis, A., 1999. From representation to persistence: requirements for a sustainable system of conservation areas in the species- rich mediterranean- climate desert of southern Africa. Divers. Distrib. 5, 51–71.

Crist, E.P., Cicone, R.C., 1984. A physically-based transformation of Thematic Mapper data---The TM Tasseled Cap. IEEE Trans. Geosci. Remote Sens. 256–263.

Dahms, T., Seissiger, S., Borg, E., Vajen, H., Fichtelmann, B., Conrad, C., 2016. Important Variables of a RapidEye Time Series for Modelling Biophysical Parameters of Winter Wheat. Photogramm.-Fernerkund.-Geoinformation 2016, 285–299.

Diamond, J.M., 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biol. Conserv. 7, 129–146.

Dorazio, R.M., Royle, J.A., 2005a. Estimating size and composition of biological communities by modeling the occurrence of species. J. Am. Stat. Assoc. 100, 389–398.

Dorazio, R.M., Royle, J.A., 2005b. Estimating size and composition of biological communities by modeling the occurrence of species. J. Am. Stat. Assoc. 100, 389–398.

Downes, S., 2001. Trading heat and food for safety: costs of predator avoidance in a lizard. Ecology 82, 2870–2881.

Downes, S., Shine, R., 1998. Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities. Anim. Behav. 55, 1387–1396. https://doi.org/10.1006/anbe.1997.0705

Durso, A.M., Willson, J.D., Winne, C.T., 2011. Needles in haystacks: estimating detection probability and occupancy of rare and cryptic snakes. Biol. Conserv. 144, 1508–1515.

Ferrier, S., Guisan, A., 2006. Spatial modelling of biodiversity at the community level. J. Appl. Ecol. 43, 393–404.

Forman, R.T., Alexander, L.E., 1998. Roads and their major ecological effects. Annu. Rev. Ecol. Syst. 29, 207–231.

Garden, J.G., Mcalpine, C.A., Possingham, H.P., Jones, D.N., 2007. Habitat structure is more important than vegetation composition for local-level management of native terrestrial reptile and small mammal species living in urban remnants: A case study from Brisbane, Australia. Austral Ecol. 32, 669–685. https://doi.org/10.1111/j.1442-9993.2007.01750.x

Gardner, T.A., Barlow, J., Peres, C.A., 2007. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. Biol. Conserv. 138, 166–179.

Glaw, F., Vences, M., 2007. A field guide to the amphibians and reptiles of Madagascar. Vences & Glaw.

Goodman, S.M., Benstead, J.P., 2005. Updated estimates of biotic diversity and endemism for Madagascar. Oryx Camb. 39, 73–77.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009.

Hall, L.S., Krausman, P.R., Morrison, M.L., 1997. The habitat concept and a plea for standard terminology. Wildl. Soc. Bull. 173–182.

Harris, L.D., 1988. Edge effects and conservation of biotic diversity. Conserv. Biol. 2, 330–332.

Hartmann, P.A., Marques, O.A., 2005. Diet and habitat use of two sympatric species of Philodryas (Colubridae), in south Brazil. Amphib.-Reptil. 26, 25–31.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., 2003. Energy, water, and broad- scale geographic patterns of species richness. Ecology 84, 3105–3117.

Healey, S.P., Cohen, W.B., Zhiqiang, Y., Krankina, O.N., 2005. Comparison of Tasseled Cap-based Landsat data structures for use in forest disturbance detection. Remote Sens. Environ. 97, 301–310. https://doi.org/10.1016/j.rse.2005.05.009

Hódar, J.A., Pleguezuelos, J.M., Poveda, J.C., 2000. Habitat selection of the common chameleon (Chamaeleo chamaeleon)(L.) in an area under development in southern Spain: implications for conservation. Biol. Conserv. 94, 63–68.

Huey, R.B., 1991. Physiological Consequences of Habitat Selection. Am. Nat. 137, S91–S115.

Hunt, S.D., Guzy, J.C., Price, S.J., Halstead, B.J., Eskew, E.A., Dorcas, M.E., 2013. Responses of riparian reptile communities to damming and urbanization. Biol. Conserv. 157, 277–284. https://doi.org/10.1016/j.biocon.2012.08.035

Irwin, M.T., Wright, P.C., Birkinshaw, C., Fisher, B.L., Gardner, C.J., Glos, J., Goodman, S.M., Loiselle, P., Rabeson, P., Raharison, J.-L., 2010a. Patterns of species change in anthropogenically disturbed forests of Madagascar. Biol. Conserv. 143, 2351–2362.

Irwin, M.T., Wright, P.C., Birkinshaw, C., Fisher, B.L., Gardner, C.J., Glos, J., Goodman, S.M., Loiselle, P., Rabeson, P., Raharison, J.-L., 2010b. Patterns of species change in anthropogenically disturbed forests of Madagascar. Biol. Conserv. 143, 2351–2362.

IUCN, 2018. The IUCN Red List of Threatened Species. Version 2018-1. [WWW Document]. IUCN Red List Threat. Species. URL https://www.iucnredlist.org/en (accessed 10.22.18).

IUCN, 2016. The IUCN Red List of Threatened Species [WWW Document]. URL http://www.iucnredlist.org/search

Jochimsen D. M., Peterson C. R., Harmon L. J., 2014. Influence of ecology and landscape on snake road mortality in a sagebrush- steppe ecosystem. Anim. Conserv. 17, 583–592. https://doi.org/10.1111/acv.12125

Joseph, L. N., Field, S.A., Wilcox, C., Possingham, H.P., 2006. Presence–absence versus abundance data for monitoring threatened species. Conserv. Biol. 20, 1679–1687.

Kauth, R.J., Thomas, G.S., 1976. The Tasselled Cap -- A Graphic Description of the Spectral-Temporal Development of Agricultural Crops as Seen by LANDSAT 13.

Kellner, K., 2017. jagsUI: A Wrapper Around “rjags” to Streamline “JAGS” Analyses.

Kéry, M., Royle, J.A., 2015. Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1: Prelude and Static Models. Academic Press.

Kéry, M., Schaub, M., 2012. Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective. Academic Press.

Kremen, C., Cameron, A., Moilanen, A., Phillips, S.J., Thomas, C.D., Beentje, H., Dransfield, J., Fisher, B.L., Glaw, F., Good, T.C., Harper, G.J., Hijmans, R.J., Lees, D.C., Louis, E., Nussbaum, R.A., Raxworthy, C.J., Razafimpahanana, A., Schatz, G.E., Vences, M., Vieites, D.R., Wright, P.C., Zjhra, M.L., 2008. Aligning Conservation Priorities Across Taxa in Madagascar with High-Resolution Planning Tools. Science 320, 222–226. https://doi.org/10.1126/science.1155193

Lagarde, F., Louzizi, T., Slimani, T., El Mouden, H., Kaddour, K.B., Moulherat, S., Bonnet, X., 2012. Bushes protect tortoises from lethal overheating in arid areas of Morocco. Environ. Conserv. 39, 172–182.

Laurance, W.F., Goosem, M., Laurance, S.G.W., 2009. Impacts of roads and linear clearings on tropical forests. Trends Ecol. Evol. 24, 659–669. https://doi.org/10.1016/j.tree.2009.06.009

Lehtinen, R.M., Ramanamanjato, J.-B., Raveloarison, J.G., 2003. Edge effects and extinction proneness in a herpetofauna from Madagascar.

Lele, S.R., Merrill, E.H., Keim, J., Boyce, M.S., 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. J. Anim. Ecol. 82, 1183–1191. https://doi.org/10.1111/1365-2656.12141

Lewin, A., Feldman, A., Bauer, A.M., Belmaker, J., Broadley, D.G., Chirio, L., Itescu, Y., LeBreton, M., Maza, E., Meirte, D., 2016a. Patterns of species richness, endemism and environmental gradients of African reptiles. J. Biogeogr. 43, 2380–2390.

Lewin, A., Feldman, A., Bauer, A.M., Belmaker, J., Broadley, D.G., Chirio, L., Itescu, Y., LeBreton, M., Maza, E., Meirte, D., 2016b. Patterns of species richness, endemism and environmental gradients of African reptiles. J. Biogeogr. 43, 2380–2390.

Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385–393.

Long, P., Seing, S.T., Rabenoro, M., Gandola, R., Radespiel, U., Ellis, C., Evans, B., Palfrey, R., Raveloson, B., Rakotondraparany, R., Andriambelo, H., Neaves, J., 2013. Biodiversity surveys of Mariarano and Matsedroy tropical dry forests and associated wetlands, Western Madagascar, Final Report.

Lötter, D., 2010. Agriculture, in: Archer, E., Engelbrecht, F., Landman, W. South African Risk and Vulnerability Atlas. p. 62.

MacKenzie, D., Nichols, J., Royle, J.A., Pollock, K., Bailey, L., Hines, J., 2006. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248–2255.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L., Hines, J.E., 2006. Occupancy in Community-Level Studies, in: Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press, pp. 249–266.

Masterson, G.P., Maritz, B., Alexander, G.J., 2008. Effect of fire history and vegetation structure on herpetofauna in a South African grassland. Appl. Herpetol. 5, 129–143.

Matthiopoulos, J., Fieberg, J., Aarts, G., Beyer, H.L., Morales, J.M., Haydon, D.T., 2015. Establishing the link between habitat selection and animal population dynamics. Ecol. Monogr. 85, 413–436.

McCain, C.M., 2010. Global analysis of reptile elevational diversity. Glob. Ecol. Biogeogr. 19, 541–553.

Morrison, M.L., 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. J. Wildl. Manag. 613–623.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10, 58–62. https://doi.org/10.1016/S0169-5347(00)88977-6

Murphy, A.J., Goodman, S.M., Farris, Z.J., Karpanty, S.M., Andrianjakarivelo, V., Kelly, M.J., 2016. Landscape trends in small mammal occupancy in the Makira–Masoala protected areas, northeastern Madagascar. J. Mammal. gyw168.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Park, J., 2017. Herpetoplogical survey across three distinct habitats in Ankarana National Park: Long-term effects of past land use on species composition in and around the park.

Paterson, J.E., Blouin- Demers, G., 2018. Density- dependent habitat selection predicts fitness and abundance in a small lizard. Oikos 127, 448–459. https://doi.org/10.1111/oik.04758

Patrick, D.A., Gibbs, J.P., 2009. Snake occurrences in grassland associated with road versus forest edges. J. Herpetol. 43, 716–720.

Pearson, R.G., Raxworthy, C.J., Nakamura, M., Townsend Peterson, A., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34, 102–117.

Pike, D.A., Webb, J.K., Shine, R., 2011. Removing forest canopy cover restores a reptile assemblage. Ecol. Appl. 21, 274–280. https://doi.org/10.1890/09-2394.1

Plummer, M., 2017. JAGS: Just Another Gibbs Sampler.

Pollock, J.F., 2006. Detecting population declines over large areas with presence- absence, time- to-encounter, and count survey methods. Conserv. Biol. 20, 882–892.

QGIS Development Team, 2015. QGIS geographic information system. Open Source Geospatial Found. Proj. Disponível Em Httpwww Qgis Org Acesso Em 27.

Qian, H., Wang, X., Wang, S., Li, Y., 2007. Environmental determinants of amphibian and reptile species richness in China. Ecography 30, 471–482.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2013.

Randrianantoandro, C., Razafimahatratra, B., Soazandry, M., Ratsimbazafy, J., Jenkins, R., 2010. Habitat use by chameleons in a deciduous forest in western Madagascar. Amphib.-Reptil. 31, 27–35. https://doi.org/10.1163/156853810790457812

Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A., Peterson, A.T., 2003. Predicting distributions of known and unknown reptile species in Madagascar. Nature 426, 837–841.

Raxworthy, C.J., Nussbaum, R.A., 2006. Six new species of occipital-lobed Calumma chameleons (Squamata: Chamaeleonidae) from montane regions of Madagascar, with a new description and revision of Calumma brevicorne. Copeia 2006, 711–734.

Reed, R.N., Shine, R., 2002. Lying in Wait for Extinction: Ecological Correlates of Conservation Status among Australian Elapid Snakes. Conserv. Biol. 16, 451–461. https://doi.org/10.1046/j.1523-1739.2002.02283.x

Reinert, H., 1993. Habitat selection in snakes. Snakes Ecol. Behav. 201–240.

Rich, L.N., Miller, D.A., Robinson, H.S., McNutt, J.W., Kelly, M.J., 2016. Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. J. Appl. Ecol. 53, 1225–1235.

Robson, L.E., Blouin-Demers, G., 2013. Eastern hognose snakes (Heterodon platirhinos) avoid crossing paved roads, but not unpaved roads. Copeia 2013, 507–511.

Rodríguez, M.Á., Belmontes, J.A., Hawkins, B.A., 2005. Energy, water and large-scale patterns of reptile and amphibian species richness in Europe. Acta Oecologica 28, 65–70.

Royle, J.A., Dorazio, R.M., 2008. Chapter 12: Models of Community Composition and Dynamics, in: Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities. Academic Press.

Rytwinski, T., Fahrig, L., 2012. Do species life history traits explain population responses to roads? A meta-analysis. Biol. Conserv. 147, 87–98. https://doi.org/10.1016/j.biocon.2011.11.023

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., 2000a. Global biodiversity scenarios for the year 2100. science 287, 1770–1774.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., 2000b. Global biodiversity scenarios for the year 2100. science 287, 1770–1774.

Schlaepfer, M.A., Gavin, T.A., 2001. Edge Effects on Lizards and Frogs in Tropical Forest Fragments. Conserv. Biol. 15, 1079–1090. https://doi.org/10.1046/j.1523-1739.2001.0150041079.x

Schneider-Maunoury, L., Lefebvre, V., Ewers, R.M., Medina-Rangel, G.F., Peres, C.A., Somarriba, E., Urbina-Cardona, N., Pfeifer, M., 2016. Abundance signals of amphibians and reptiles indicate strong edge effects in Neotropical fragmented forest landscapes. Biol. Conserv. 200, 207–215.

Schönert, M., Weichelt, H., Zillmann, E., Jürgens, C., 2014. Derivation of tasseled cap coefficients for RapidEye data. Presented at the Earth Resources and Environmental Remote Sensing/GIS Applications V, International Society for Optics and Photonics, p. 92450Q.

Semlitsch, R.D., Bodie, J.R., 2003. Biological Criteria for Buffer Zones around Wetlands and Riparian Habitats for Amphibians and Reptiles. Conserv. Biol. 17, 1219–1228. https://doi.org/10.1046/j.1523-1739.2003.02177.x

Shah, B., Shine, R., Hudson, S., Kearney, M., 2004. Experimental analysis of retreat-site selection by thick-tailed geckosNephrurus milii. Austral Ecol. 29, 547–552. https://doi.org/10.1111/j.1442-9993.2004.01388.x

Shine, R., Barrott, E.G., Elphick, M.J., 2002. SOME LIKE IT HOT: EFFECTS OF FOREST CLEARING ON NEST TEMPERATURES OF MONTANE REPTILES. Ecology 83, 2808–2815. https://doi.org/10.1890/0012-9658(2002)083[2808:SLIHEO]2.0.CO;2

Shine, R., Bonnet, X., 2000. Snakes: a new ‘model organism’ in ecological research? Trends Ecol. Evol. 15, 221–222. https://doi.org/10.1016/S0169-5347(00)01853-X

Shine, R., Lemaster, M., Wall, M., Langkilde, T., Mason, R., 2004. Why Did the Snake Cross the Road? Effects of Roads on Movement and Location of Mates by Garter Snakes (*Thamnophis sirtalis parietalis*). Ecol. Soc. 9. https://doi.org/10.5751/ES-00624-090109

Sutherland, W.J., Pullin, A.S., Dolman, P.M., Knight, T.M., 2004. The need for evidence-based conservation. Trends Ecol. Evol. 19, 305–308.

Tilbury, C.R., 2018. Chameleons of Africa: an atlas: including the chameleons of Europe, the Middle East and Asia. Edition Chimaira.

Tilman, D., Fargione, J., Wolff, B., D’Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. Science 292, 281–284.

Tobler, M.W., Zúñiga Hartley, A., Carrillo- Percastegui, S.E., Powell, G.V., 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. J. Appl. Ecol. 52, 413–421.

Tsairi, H., Bouskila, A., 2004. Ambush Site Selection of a Desert Snake (Echis coloratus) at an Oasis. Herpetologica 60, 13–23.

Vences, M., Glaw, F., 2003. Phylogeography, systematics and conservation status of boid snakes from Madagascar (Sanzinia and Acrantophis).

Vences, M., Wollenberg, K.C., Vieites, D.R., Lees, D.C., 2009a. Madagascar as a model region of species diversification. Trends Ecol. Evol. 24, 456–465. https://doi.org/10.1016/j.tree.2009.03.011

Vences, M., Wollenberg, K.C., Vieites, D.R., Lees, D.C., 2009b. Madagascar as a model region of species diversification. Trends Ecol. Evol. 24, 456–465. https://doi.org/10.1016/j.tree.2009.03.011

Wanger, T.C., Iskandar, D.T., Motzke, I., Brook, B.W., Sodhi, N.S., Clough, Y., Tscharntke, T., 2010. Effects of Land-Use Change on Community Composition of Tropical Amphibians and Reptiles in Sulawesi, Indonesia. Conserv. Biol. 24, 795–802. https://doi.org/10.1111/j.1523-1739.2009.01434.x

Wasko, D.K., Sasa, M., 2012. Food resources influence spatial ecology, habitat selection, and foraging behavior in an ambush-hunting snake (Viperidae: Bothrops asper): an experimental study. Zoology 115, 179–187. https://doi.org/10.1016/j.zool.2011.10.001

Wasko, D.K., Sasa, M., 2009. Activity Patterns of a Neotropical Ambush Predator: Spatial Ecology of the Fer-de-lance (Bothrops asper, Serpentes: Viperidae) in Costa Rica. Biotropica 41, 241–249. https://doi.org/10.1111/j.1744-7429.2008.00464.x

Whitaker, P.B., Shine, R., 2000. Sources of Mortality of Large Elapid Snakes in an Agricultural Landscape. J. Herpetol. 34, 121–128. https://doi.org/10.2307/1565247

Whiting, M.J., Williams, V.L., Hibbitts, T.J., 2013. Animals traded for traditional medicine at the Faraday market in South Africa: species diversity and conservation implications, in: Animals in Traditional Folk Medicine. Springer, pp. 421–473.

Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E., Willis, K.J., 2005. Conservation biogeography: assessment and prospect. Divers. Distrib. 11, 3–23.

Willis, K.J., Seddon, A.W., Long, P.R., Jeffers, E.S., Caithness, N., Thurston, M., Smit, M.G., Hagemann, R., Macias-Fauria, M., 2015. Remote assessment of locally important ecological features across landscapes: how representative of reality? Ecol. Appl. 25, 1290–1302.

CHAPTER 3 – OCCUPANCY TRENDS ALONG TAXONOMIC LINES AND WITHIN THREAT CATEGORIES IN THE REPTILE SPECIES OF MADAGASCAN DRY FOREST

3.1 Abstract

The conservation of reptile species requires efficient land management based on realistic metrics of habitat-use. I used reptile presence records and satellite data, collected over four years, in a community-level occupancy model to investigate reptile distribution patterns in a fragmented Madagascan forest, and assessed whether landscape-use was similar among species within families and IUCN Red List Threat categories. The Opluridae family had the lowest probability of occurring (0.27 (95% credible interval (CRI) 0.14, 0.54)) and the Chamaeleonidae were the most commonly occurring (0.83 (0.77, 0.89)). Regression coefficient estimates indicated that the members of the Chamaeleonidae showed the strongest statistically significant preference for sites with dense green vegetation (0.70 (0.02, 1.55)), and the Pseudoxyrhophiidae and Boidae exhibited highly variable patterns of occurrence (with CRIs of up to (-1.98, 9.13)). Endangered species had the highest mean probability of occurring (0.60 (0.35, 0.82)), demonstrating the importance of considering resolution when exploring Threat Status at a regional scale. Species classified as having an Increasing Population Trend had the lowest mean occupancy probability (0.084 (0.03, 0.22)), indicating that this IUCN categorization may be influenced by imperfect detection, although this would require studying the change in occupancy and abundance over time to ascertain. These results demonstrate that landscape-use trends exist in some Madagascan reptile lineages, and form a basis on which to explore the effects of imperfect detection on the assignment of Threat categories.

3.2 Introduction

Habitat change is currently a primary contributor to biodiversity loss (Lötter, 2010) and is predicted to be responsible for the majority of species extinctions in the future (Sala et al., 2000; Tilman et al., 2001). Not only are species that are currently classified as Threatened, based on IUCN criteria, at risk of extinction, but so too are dominant, abundant species found in changing landscapes (Tilman et al., 1994) and thus research into the conservation of species' habitats is of high relevance. Reptiles are of particular concern in this regard because they are more susceptible to extinction than birds and mammals (IUCN, 2018). Squamates (amphisbaenids, snakes and other lizards) are especially relevant because their behaviour and success can clearly reflect habitat transformation by anthropogenic land-use (Gardner et al., 2007) but they have received relatively little attention with regards to conservation and habitat research, particularly in the Southern Hemisphere (Bonnet et al., 2002; Gardner et al., 2007; Lewin et al., 2016; McCain, 2010).

Understanding the relative importance of habitat characteristics to different species can be used to predict changes in species occurrence in response to landscape transformation, and is therefore fundamental to conservation. This topic falls into the field of 'conservation biogeography' where the principles of biogeography, the study of species' distributions, are applied to conservation (Whittaker et al., 2005). Community-level research that investigates the occurrence of species or groups of species in relation to the landscape tends to be a more cost-effective and practical approach to conservation than are species-specific studies (Ferrier and Guisan, 2006). Carrying out conservation research in a way that is efficient and protects a high number of species that are threatened by human development is especially relevant for species that occur in developing countries, where funding is limited and development often relies on raw resource extraction that transforms natural habitats (Brooks et al., 2006; Myers et al., 2000; Sutherland et al., 2004).

Considering that developing tropical areas tend to be very biodiverse, have many endemic species, and experience high levels of habitat loss (which are criteria for ecological hotpots, see Myers et al., 2000), a surprisingly small number of hotspots have been identified for reptiles, plants and amphibians in the tropics in comparison to temperate areas, suggesting that tropical regions have not received enough attention. Tropical biodiversity is under threat from activities such as mining, logging and farming, which developing countries tend to rely on for trade (Sunderlin et al., 2005). Forests are particularly susceptible to degradation due to the high number of poverty-stricken people who live in or near natural forest and who rely on resources such as firewood or grazing pastures (Jha and Bawa, 2006; Sunderlin et al., 2005).

Madagascar is one such country where the use of multi-taxon approaches is necessary to efficiently conserve biodiversity (Kremen et al. 2008). It is classified as an ecological hotspot (Myers et al., 2000; Harper et al., 2007) and is considered to be a global conservation priority (Brooks et al., 2006; Kremen et al., 2008). The island's forests have experienced considerable deforestation from logging, mining and agriculture (Harper et al., 2007). By the year 2000, less than 10% of its natural habitat remained unaltered (Myers et al., 2000) and forested land continues to be transformed (Grinand et al., 2013). 61% of the human population reside in rural areas and rely on forest resources (Irwin et al., 2010). With the current rate of deforestation, it is predicted that Madagascar will lose many of its species in the near future (Brooks et al., 2002). More than 90% of Madagascan reptiles are endemic to the island (Vences et al., 2009), making them vulnerable to extinction (Brooks et al., 2006). A high proportion of the island's species that are classified as Data Deficient by the IUCN are predicted to be threatened (Bland and Böhm, 2016), but an insufficient amount of research has been carried out to investigate the effects of land transformation resulting from anthropogenic activities on Madagascar's species, and thus it is difficult to address the conservation of broad taxonomic groups such as reptiles (Irwin et al., 2010).

Reptile species occurrence and community composition may be affected by a number of physical habitat attributes. One of the most important components of a terrestrial reptile's habitat, and thus an important predictor of occurrence and species richness, is vegetation (Bennett et al., 2006; Bruton et al., 2016; Lewin et al., 2016; Wanger et al., 2010). Vegetation provides reptiles with shelter (Beck and Jennings, 2003; Bruton et al., 2016; Masterson et al., 2008) which is critical for thermoregulation (Qian et al., 2007; Rodríguez et al., 2005), protection from predators (Downes, 2001), avoiding dehydration (Lagarde et al., 2012), and hunting (Tsairi and Bouskila, 2004; Wasko and Sasa, 2012). Although vegetation cover is thus an important part of a reptile's habitat, the availability of basking areas is also important, because physiological performance is strongly dependent on body temperature (Huey, 1991). Consequently, habitat may be selected based on surfaces or more open areas that enhance heat gain during basking (Blouin- Demers and Weatherhead, 2001; Paterson and Blouin-Demers, 2018; Shah et al., 2004). This may be why squamate occurrence has often been considered to coincide the most with optimal ambient temperature for thermoregulation (Blouin- Demers and Weatherhead, 2001; Hawkins et al., 2003; Reinert, 1993).

As well as the availability of vegetation and basking areas, terrestrial reptile distributions may be affected by the proximity of reptile habitats to humans or human development. Some species are negatively affected by direct human contact (Alves et al., 2008; Whitaker and Shine, 2000; Whiting et al., 2013), or by living in in areas that are highly accessible to humans (Böhm et al., 2016; Tilbury, 2018), while others readily use landscapes transformed by human activity, possibly due to the habitat heterogeneity (and thus, shelters and hunting habitats) available in disturbed habitats (Bruton et al., 2013). The same dichotomy in reptile spatial patterns can be seen in response to roads – some herpetofauna are negatively affected by roads, due to the risk of road mortalities when crossing (Jochimsen et al., 2014; Rytwinski and Fahrig, 2012) or disruption of mate-searching (Shine et al., 2004), while others show a high tolerance to human development in their habitat selection, such as the common chameleon (*Chamaeleo chamaeleon*) which occurs frequently in areas with many roads (Hódar et al., 2000). The location of a reptile's habitat within a forest patch may be related to the chance of encountering humans or stability of environmental conditions, and the findings of edge effect studies are similarly varied in the literature – some reptile species occur at the forest periphery (Blouin-Demers and Weatherhead, 2001; Schlaepfer and Gavin, 2001) but most favour the interior (Lehtinen et al., 2003; Schneider-Maunoury et al., 2016; Semlitsch and Bodie, 2003).

In addition to the physical characteristics of a landscape, species-specific traits are important factors to consider when investigating squamate distributions. The tolerance of a species to habitat traits will affect how susceptible it is to extinction, and may thus be reflected in its IUCN Red List of Threatened Species status. Threat Status is phylogenetically clustered within the squamates, meaning that threatened species tend to be closely related (Tonini et al., 2016) and so one can investigate taxonomic trends in conjunction with Threat Status when studying reptile landscape-use. Range-restricted habitat specialists are at the highest risk of extinction (Böhm et al., 2016; Tingley et al., 2013), and so understanding the habitats that support endemic species would be important when identifying areas of conservation priority. Tolley et al., (2016) and Tonini et al., (2016) concluded that squamate families at the highest risk of extinction include the Chamaeleonidae, Amphisbaenidae, Viperidae, Gekkoniidae and Gerrhosauridae. Investigating trends in habitat preference within Threat categories or families may shed light on how different habitat characteristics promote species that are more threatened or are within a family of interest, which would help in identifying areas of conservation priority.

Many of the methods used to investigate species distributions do not account for the observational process involved in sampling (Dorazio and Royle, 2005; MacKenzie et al., 2006) which can result in biased conclusions being made about species habitat selection, particularly for elusive species (able to camouflage or hide well) or rare species (low abundance or small spatial range) (Durso et al., 2011). This can ultimately lead to inaccurate estimates of population abundance and community structure being used in conservation planning (Tobler et al., 2015; Wearn et al., 2017). Community-level occupancy modelling addresses pseudo-absence and imperfect detection by estimating the probability of detecting species and incorporating this into an ecological model that estimates the probability that species will occur at a site (Dorazio and Royle, 2005; MacKenzie et al., 2006). This method is therefore of great relevance to reptile conservation in Madagascar, because of its many cryptic species that are in need of efficient habitat conservation action.

Using squamate detection/non-detection data and satellite imagery collected annually for four years in a community-level hierarchical occupancy model, I investigated the associations between landscape structure and squamate occurrence in a fragmented forest at risk from human land transformation in north western Madagascar. The objectives were to compare mean occupancy estimates among species within groups (families and Threat Status categories) to assess whether there were any similarities in habitat-preference patterns among species that are classified as Threatened and among species within a family. This topic was explored in order to address the shortage of knowledge regarding reptile land-use in a highly threatened and transformed environment. Considering the findings of previous studies, it is expected that squamates will favour sites with high levels of vegetation greenness that are far from human development, and that groups that are the most threatened (the Endangered and Vulnerable Threat categories and the chameleon, gecko and plated lizard families) will be found most commonly (if not exclusively) in such sheltered sites.

3.3 Methodology

3.3.1 Study area

Data were collected in June and July (the dry season) annually from 2014 to 2017 at the Operation Wallacea research station in the Mahamavo watershed region of north western Madagascar. Reptile presence was sampled along transects that were situated in the two main dry forest patches in the Mahamavo watershed (Figure 3.1). In parts, some routes were also located just outside of the forest patches. The locations of the routes were chosen by Operation Wallacea staff in 2010 to span areas of varying vegetation densities, levels of land transformation and distances to roads. The forest patches were surrounded by transformed areas for rice agriculture, interspersed with meadows and river beds, and there are three small settlements that rely on the forest for resources, the largest being the village of Mariarano (-15.478821, 46.695887). On a global scale, tropical dry forest species are under high risk from anthropogenic land transformation (Miles et al., 2006) and Mahamavo forests are particularly affected by logging and agriculture (Long et al., 2013).

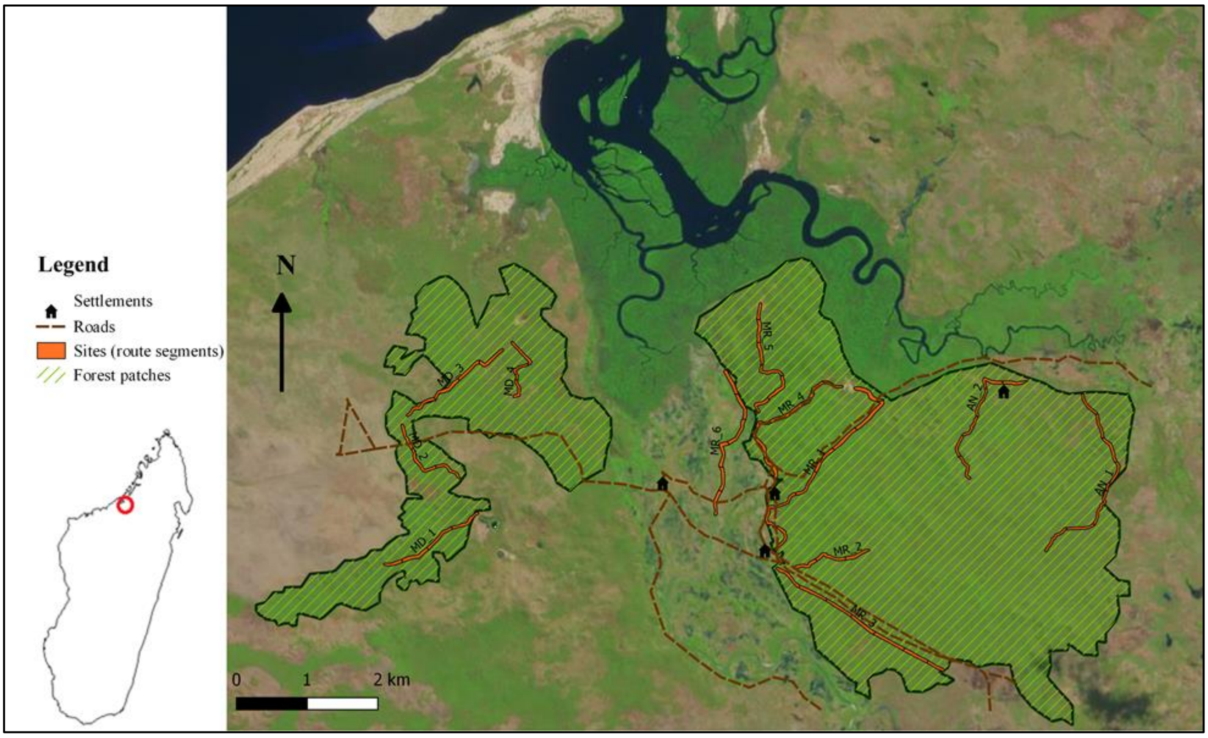


Figure 3.1. Map of the Mahamavo study area, showing sites (route segments) within survey routes sampled in the two main forest patches and nearby roads and settlements.

3.3.2 Study species

From a 2013 survey of Mahamavo, the 46 terrestrial squamate species that occur in the area include geckos, snakes, skinks, iguanas, and chameleons such as the flagship species *Furcifer oustaleti* and *Furcifer angeli* (Long et al., 2013). As on the rest of the island, most of the species in Mahamavo are endemic to Madagascar, and are well-known for their extreme adaptations that aid in camouflage, such as the leaf-like appendages of the leaf-tailed geckos (*Uroplatus* species) and leaf-nosed snakes (*Langaha* species). Some species such as the boids are popular in the exotic pet trade and for the reptile leather industry (IUCN, 2018; Vences and Glaw, 2003).

3.3.3 Experimental design and protocol

Reptile detection/non-detection *data*

A team of ~six people sampled eleven transect routes, each route between 2 and 4 km in length, so that each route was sampled six times per field season (June and July) for four seasons (2014-2017).

The vegetation and ground on either side of the path and overhanging vegetation were scanned and all observed reptiles were identified to species level and their GPS locations recorded.

Defining site areas

The transect routes were plotted in QGIS v2.18 and a fixed-distance buffer of 20 m was drawn around the line of each route, to represent the spatial area occupied by the route's reptile community to be used in analysis. This boundary line encompassed all but a few outlying locality points. Each buffered route polygon was then divided into 500 m length segments, each segment being considered a site and sites within a route being dependant on one another. Species points and raster layers were cropped to these sites.

Proximity of sites to the closest road, settlement and edge of forest patch

The sites layer was overlain with the settlements and roads in the area and the boundaries of the forest patches. I measured the distance of each site to the closest points of the closest road, settlement and edge of the forest patch. For sites that lay outside of the forest patch boundary, distance to the nearest point of the forest edge was multiplied by -1 to distinguish from the sites within the forest patches.

Vegetation indices

I acquired three multispectral images of the study area from the RapidEye satellite (5 m^2 spatial resolution European Space Agency Observation Portal, https://earth.esa.int) and one image from the Sentinel II satellite (10 m^2 spatial resolution; European Space Agency Observation Portal, https://earth.esa.int) to avoid the obscuring of the ground by clouds in the 2016 RapidEye images. The images were pre-processed and atmospherically-corrected in QGIS and ENVI v5.3 and five band reflectance values for each pixel were extracted in ENVI. These values were used to calculate greenness and brightness indices using Tasselled Cap Transformation, a method that combines the reflectance information contained in five spectral bands into principal components which can be used to investigate vegetation gradients in forests (Cohen et al., 1995; Crist and Cicone, 1984; Kauth and Thomas, 1976). A mean greenness (green vegetation density) and brightness (exposed soil and substrate) value was calculated across pixels for each site per year using the following equations and coefficients of Dahms et al., (2016) and Schönert et al., (2014):

Brightness = 0.2435×band1 + 0.3448×band2 + 0.4881×band3 + 0.4930×band4 + 0.5835×band5

Greenness = (-0.2216×band1) + (-0.2319×band2) + (-0.4622×band3) + (-0.2154×band4) + (0.7981×band5)

A Spearman correlation test was used to conclude that there was no multicollinearity among explanatory variables.

3.3.4 Modelling approach

I used community-level hierarchical Bayesian occupancy modelling to calculate the probability that each species occurs at each site (occupancy), the detection probability of each species, the effect of site covariates on species occupancy, and the species richness at each site when taking into account species that may not have been detected. Species locality data were transformed into a presence/absence array for each species at each site on every survey occasion, and then summed across occasions to give a 2-dimensional species detection frequency matrix for easier use in analysis. The data were organized in this manner for each year and each matrix was indexed with a year vector. Occurrence was assumed to be open between years but closed within years.

The model consisted of two logistic regressions and included all species records and site variables for all four years. One regression modelled the latent ecological process (Ψ_{ik}) of species k either occurring ($z_{i,k} = 1$) or not occurring ($z_{i,k} = 0$) given the habitat variables at site i, and $z_{i,k} \sim \text{Bernoulli}(\Psi_{ik})$. The ecological component included coefficients for greenness and brightness and distances to the nearest road, settlement and forest edge, specific to each year and site. These continuous covariates were centred to a mean of zero, as per the standardising method of Kéry and Schaub, 2012. An interaction term between distance to the forest edge and location within or outside of a forest patch was included in the model. The ecological component also included two random effects to account for (1) the dependence among sites (route segments) within a survey route and (2) to account for the dependence between survey occasions within a year, as per Kéry and Royle, 2015 and Wearn et al., 2017. The priors for the slope and intercept parameters were normally distributed, and uniformly distributed for the variance parameters, thus for site covariate β, $\beta_k \sim \text{Normal}(\mu_\beta, S_\beta)$, with μ representing the mean and S, the precision, being uninformative.

$$\text{logit}(\Psi_{ik}) = \alpha_k + \beta 1_k \times \text{bright}_i + \beta 2_k \times \text{green}_i + \beta 3_k \times \text{road}_i + \beta 4_k \times \text{vill}_i + \beta 5_k \times \text{edge}_i + \beta 6_k \times \text{patch}_i + \beta 7_k \times \text{patch}_i \times \text{edge}_i + \delta_{routes} \times \text{routes}_i + \delta_{years} \times \text{years}_i$$

Detection probability p was assumed to be constant across sites but different between species, and so the detection model simply modelled a detection probability for each species, without site covariates. The number of species detections was a model of z_{ik} binomial trials, giving $y_{ik} \sim \text{Binomial}(p_k z_{ik})$.

$$\text{logit}(p_k) = \mu_k$$

The model was written in the BUGS (Bayesian inference Using Gibbs Sampling) language, compiled in R v 3.5.1 (R Core Team, 2014) and run through JAGS v 4.3.0 (Plummer, 2017) with the use of the R package jagsUI v 1.4.9 (Kellner, 2017) (see Appendix 1 for code). Three MCMC (Markov chain Monte-Carlo) chains were run for 600 000 iterations, with 20 000 iterations discarded as ‘burn-in’, and a thinning rate of 110. This was sufficient for convergence of the chains, assessed by the Gelman-Rubin statistic being < 1.1 for all parameters in the output. Goodness-of-fit was investigated using a Chi-square test following the approach of Kéry and Royle, 2015 and Tobler et al., 2015.

The model estimated each species’ occupancy probability, detection probability, and the effects of site habitat variables on each species, as well as 95% credible intervals (CRIs) for each estimate. Mean estimates were then calculated for each species trait category investigated (taxonomic family and IUCN Red List Threat Status and Population Trend). Group estimates were compared to assess how taxonomic and threat groupings may contribute to our understanding of the species’ habitat preferences.

3.4 Results

A total of 6220 individual squamates from 37 species were identified (Table 3.1). Thirteen species belong to three snake families (Boidae, Pseudoxyrhophiidae and Psammophiidae), seventeen to the geckos (Gekkonidae), two to the chameleons (Chamaeleonidae), three to the skinks (Scincidae), one to the iguanas (Opluridae), and one to the plated lizards (Gerrhosauridae) (IUCN, 2018) (Table 3.1). The majority of the species (31) were classified as Least Concern by the IUCN Red List, three were Vulnerable, two Endangered and one was Data Deficient (IUCN, 2018) (Table 3.1). The Red List estimated 15 species to have Stable Population Trends, ten Decreasing, nine Unknown and one Increasing (Table 3.1).

Many of the group occupancy responses to site variables had CRIs including zero and therefore I also considered estimates that marginally include zero (by -0.2 for a positive estimate and 0.2 for a negative estimate) and therefore demonstrate suggestive responses. Mean occupancy responses (regression coefficient estimates) to greenness were positive for all groups. All group responses to brightness were negative, but all had CRIs that included zero (< -0.2) and so were not explored further. With regards to the group responses to distance to roads and settlements, all CRIs included zero, but those that showed suggestive evidence of a response were explored.

Table 3.1. Terrestrial squamate species recorded in Mahamavo, Madagascar between 2012 and 2017 and their corresponding taxonomic families, Threat Statuses (LC: Least Concern, NA: Not Assessed, DD: Data Deficient, EN: Endangered, CR: Critically Endangered, VU: Vulnerable) and predicted Population Trends (S: Stable, D: Decreasing, U: Unknown, I: Increasing).

Species	**Family***	**Threat Status***	**Population Trend***
Acrantophis madagascariensis	Boidae	LC	S
Blaesodactylus antogilensis	Gekkonidae	LC	D
Blaesodactylus sakalava	Gekkonidae	LC	D
Dromicodryas bernieri	Pseudoxyrhophiidae	LC	S
Dromicodryas quadrilineatus	Pseudoxyrhophiidae	LC	S
Furcifer angeli	Chamaeleonidae	LC	S
Furcifer oustaleti	Chamaeleonidae	LC	S
Geckolepis maculata	Gekkonidae	LC	U
Geckolepis polylepsis	Gekkonidae	DD	U
Geckolepis typica	Gekkonidae	LC	U
Hemidactylus mercatorius	Gekkonidae	LC	I
Ithycyphus miniatus	Pseudoxyrhophiidae	LC	U
Langaha madagascariensis	Pseudoxyrhophiidae	LC	D
Langaha pseudoalluaudi	Pseudoxyrhophiidae	LC	D
Leioheterodon madagascariensis	Pseudoxyrhophiidae	LC	S
Liophidium torquatum	Pseudoxyrhophiidae	LC	U
Lygodactylus tolampyae	Gekkonidae	LC	D
Madagascarophis colubrinus	Pseudoxyrhophiidae	LC	U
Madascincus intermedius	Scincidae	LC	S
Mimophis mahfalensis	Psammophiidae	LC	S
Oplurus cuvieri	Opluridae	LC	S
Paroedura stumpfii	Gekkonidae	LC	S
Paroedura vazimba	Gekkonidae	VN	D
Phelsuma kochi	Gekkonidae	LC	D
Phelsuma laticauda	Gekkonidae	LC	S
Phelsuma lineata	Gekkonidae	LC	S
Phelsuma madagascariensis	Gekkonidae	LC	D
Phelsuma mutabilis	Gekkonidae	LC	U
Sanzinia madagascariensis	Boidae	LC	S
Stenophis (Phisalixella) pseudogranuliceps	Pseudoxyrhophiidae	LC	D
Stenophis (Phisalixella) variabilis	Pseudoxyrhophiidae	EN	D
Trachylepis elegans	Scincidae	LC	S
Trachylepis gravenhorstii	Scincidae	LC	S
Uroplatus ebenaui	Gekkonidae	VN	D
Uroplatus guentheri	Gekkonidae	EN	D
Uroplatus henkeli	Gekkonidae	VN	U
Zonosaurus laticaudatus	Gerrhosauridae	LC	U

* The IUCN Red List of Threatened Species. Version 2018-1. www.iucnredlist.org

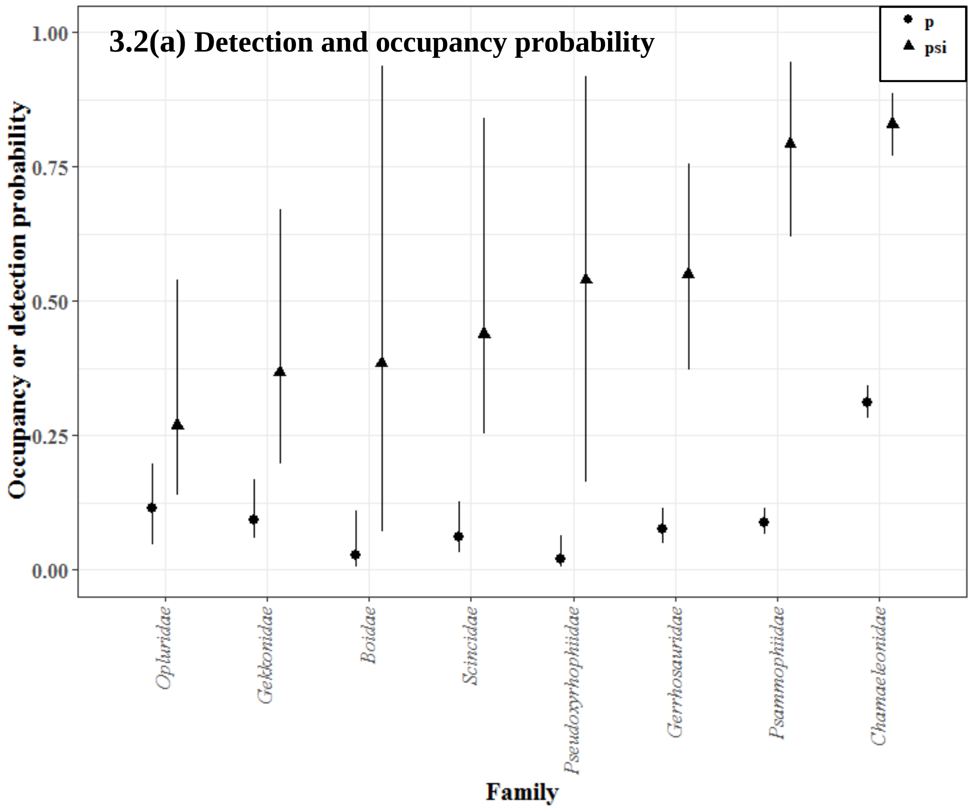
3.4.1 Family

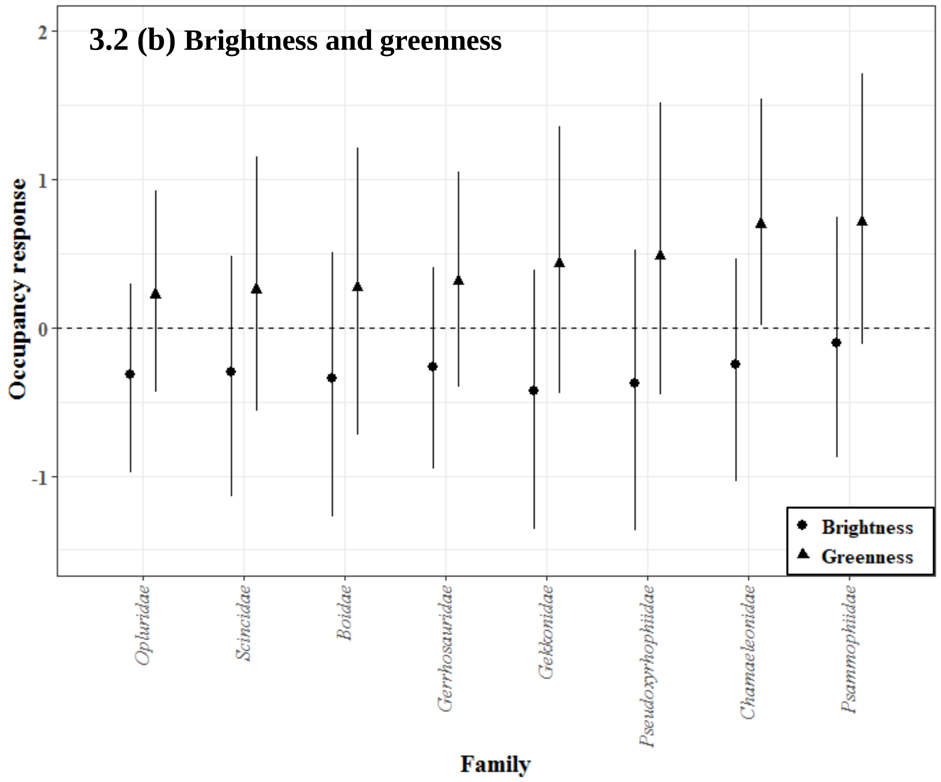
The Opluridae family, the Madagascan iguanas, had the lowest mean occupancy probability of 0.27 (95% CRI 0.14, 0.54) (note, however, that the Opluridae family had only one species member in this study and therefore it was not possible to conclude that this was a family trend) and the Chamaeleonidae family had the highest of 0.83 (0.77, 0.89), as well as the highest detectability of 0.31 (0.28, 0.34) (Figure 3.2(a)). The Pseudoxyrhophiidae snakes were the least likely to be detected (0.02 (0.01, 0.07)) (Figure 3.2(a)). The Boidae had the widest 95% CRI for occupancy of 0.07-0.94, and the Chamaeleonidae had the narrowest (0.77, 0.89) (Figure 3.2(a)).

The Chamaeleonidae family had the strongest significant association (positive) with greenness (0.70 (0.02, 1.55)) and there was suggestive evidence for the Psammophiidae having a similarly strong response (0.71 (-0.11, 1.72) (Figure 3.2(b)), although I could not conclude this to be a family response because there was only one species in the Psammophiidae family in this study. The Pseudoxyrhophiidae and Boidae had the widest brightness response CRIs (-0.45, 1.52 and -0.73, 1.22) (Figure 3.2(b)).

The Gerrhosauridae responses to road distance (0.38 (-0.19, 1.12) suggested that the occurrence of this family increased with increased distance from roads (Figure 3.2(c)) although, as the family contained only one species in this study, this could not be considered a family-based character. The inclusion of zero in the CRIs of the other groups indicated that species within a family differed in their preference for distance to settlements.

The mean occupancy responses (regression coeffiecient estimates) of all families were positively associated with being within a forest patch, and were the strongest responses of all the habitat variables tested. The Psammophiidae (5.00 (1.00, 10.27)) and the Chamaeleonidae (4.71 (1.02, 8.46)) had the strongest responses to being within a patch (Figure 3.2(d)). All CRIs of the family edge responses clearly included zero, and so sensitivity to forest edge distance could not be explained by family. The snake families had the widest response CRIs to being within/outside of a forest patch, with the Pseudoxyrhophiidae having the widest for both patch response (-1.98, 9.13) and edge distance (-3.27, 0.67) (Figure 3.2(d)).


3.2(a) Detection and occupancy probability
p
psi
Occupancy or detection probability
1.00
0.75
0.50
0.25
0.00
Opluridae
Gekkonidae
Boidae
Scincidae
Pseudoxyrhophiidae
Gerrhosauridae
Psammophiidae
Chamaeleonidae
Family


3.2 (b) Brightness and greenness
Occupancy response
2
1
0
-1
Brightness
Greenness
Opluridae
Scincidae
Boidae
Gerrhosauridae
Gekkonidae
Pseudoxyrhophiidae
Chamaeleonidae
Psammophiidae
Family

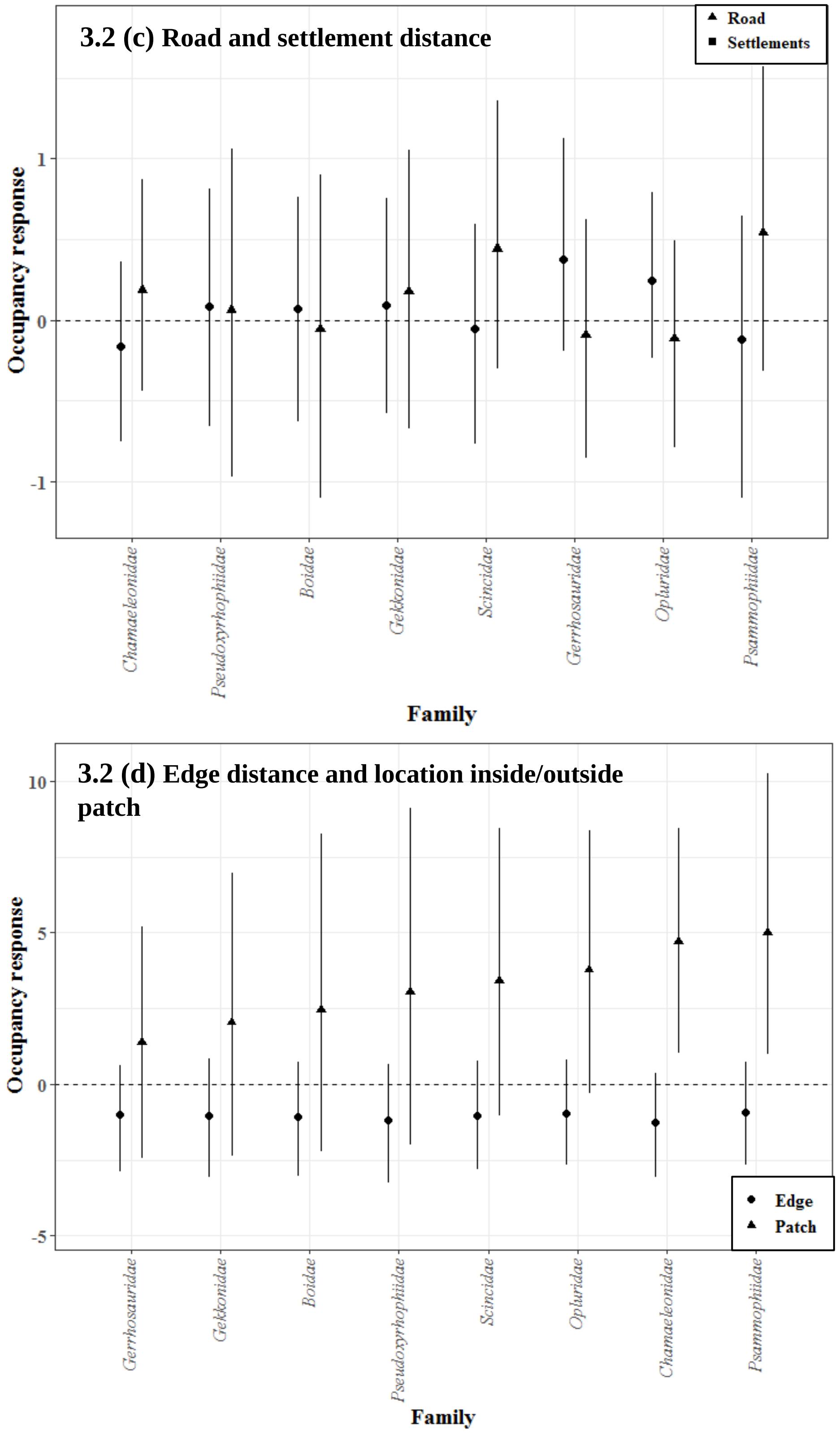


Figure 3.2. Estimates and associated 95% credible intervals of detection (p) and occupancy (psi) probability (a), and occupancy responses to increased soil reflectance and vegetation greenness (b), distance from the nearest road and settlement (c), and distance from edge of the occupied forest patch and being located within or outside of a patch (d), for each squamate family in Mahamavo. Response estimates above the x-intercept indicate increased species occupancy with an increased value of the site variable.

3.4.2 Threat Status

Mean occupancy was lowest in Vulnerable species (0.20 (0.07, 0.58)) and highest for Endangered species (0.60 (0.35, 0.82)) (Figure 3.3(a)). Detection probability was highest at 0.08 (0.06, 0.15) for species classified as Least Concern, and lowest at 0.03 for Data Deficient species (0.01, 0.08) (Figure 3.3(a)). The Data Deficient group had the widest 95% CRI (0.08, 0.92) for occupancy, even though this category contained only one species in this study (Figure 3.3(a)).

All mean occupancy responses (regression coeffiecient estimates) to greenness, brightness, road distance and settlement distance per Threat Status group had CRIs including zero (Figure 3.3(b) and (c)). There was suggestive evidence that the Data Deficient group was the most strongly associated with increased greenness (0.820 (-0.08, 1.99)) (Figure 3.3(b)), but there were no reliable trends within Threat Status groups regarding reptile responses to brightness or distance to anthropogenic development. The CRIs for the responses to road and settlement proximity were similar among the Threat Statuses, with mean CRI for the Data Deficient group being marginally widest for both road distance (-0.71, 0.69) and settlement distance (-0.60, 1.31) (Figure 3.3(c)).

The Endangered species showed a strong positive mean response to being within a forest patch (4.51 (0.15, 9.50)) (Figure 3.3(d)). The other Threat categories did not have significant responses to being inside/outside of a patch, or to forest edge proximity. The Data Deficient category had the widest response CRIs (-1.29, 9.00) to being inside/outside of a patch (-2.829, 1.120) and to edge proximity (Figure 3.3(d)).

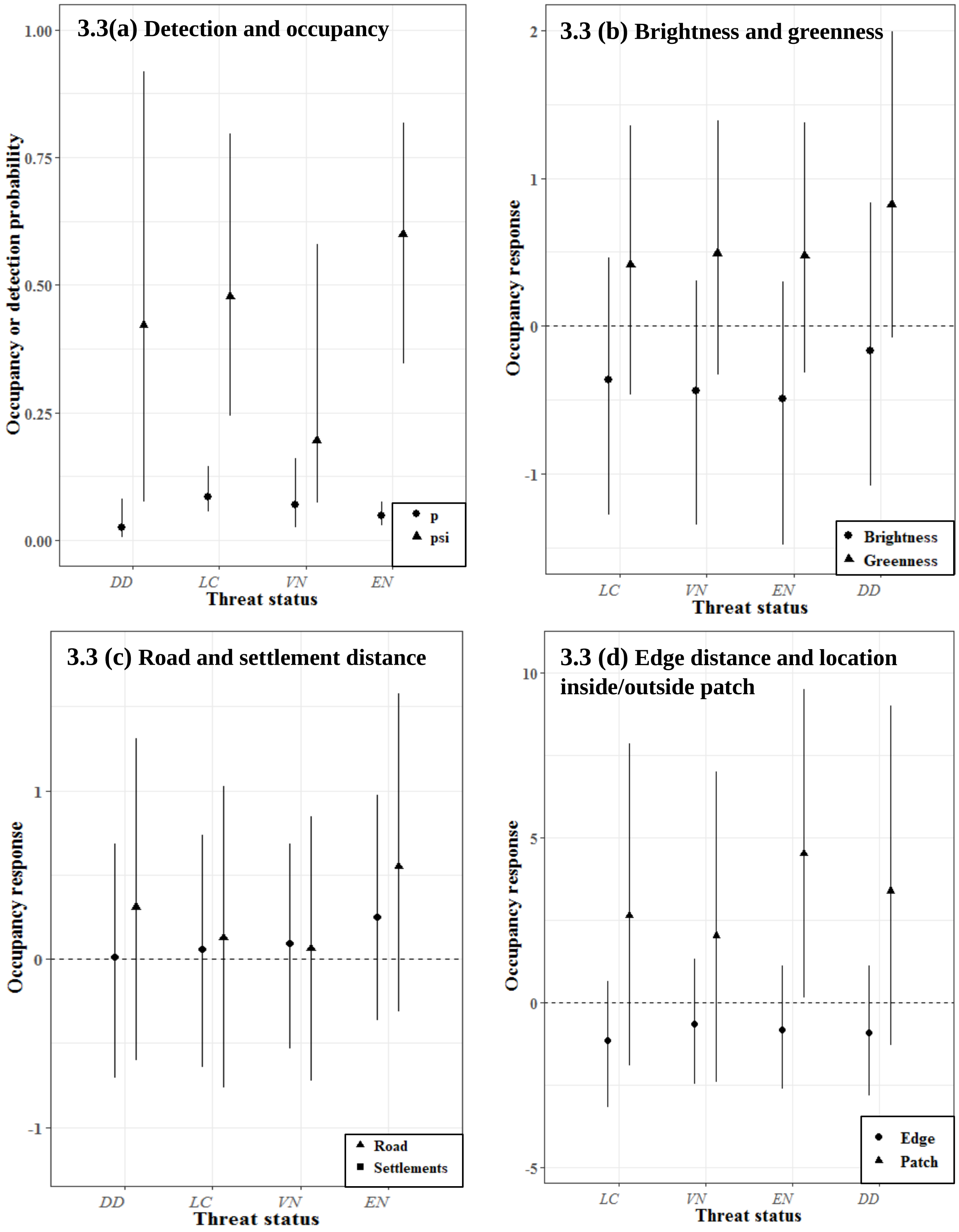


Figure 3.3. Estimates and associated 95% credible intervals of detection (p) and occupancy (psi) probability (a), and occupancy responses to increased soil reflectance and vegetation greenness (b), increased distance from the nearest road and settlement (c), and increased distance to the edge of the occupied vegetation patch and being located within or outside of a patch (d), for each Threat Status of reptiles in Mahamavo. Response estimates above the x-intercept indicate increased species occupancy with increased value of the site variable.

3.4.3 Population Trend

The mean occupancy probability of the Increasing category of 0.084 (0.03, 0.22) was notably lower than the other categories, with the other categories ranging from 0.41 (0.13, 0.86) for Unknown species to 0.49 (0.29, 0.78) for the Stable category (Figure 3.4(a)). The Unknown category had the lowest detection probability of 0.03 (0.01, 0.10) and the widest 95% CRI of 0.13-0.86 (Figure 3.4(a)).

The mean occupancy responses (regression coefficient estimates) to all site variables of all Population Trend categories had CRIs that included zero (Figure 3.4(b), (c) and (d)), except for the Increasing category which had a negative association with increased distance to the edge of the forest patch (-1.94 (-4.28, -0.24)) (Figure 3.4(d)), and a marginal positive effect of increased distance from the nearest settlement, although with there being only one species in this category, these were not reliable representations of the whole group. The Unknown Population Trend category had the widest response CRI (-2.47, 7.91) to a site being located inside or outside of a forest patch (Figure 3.4(d)).

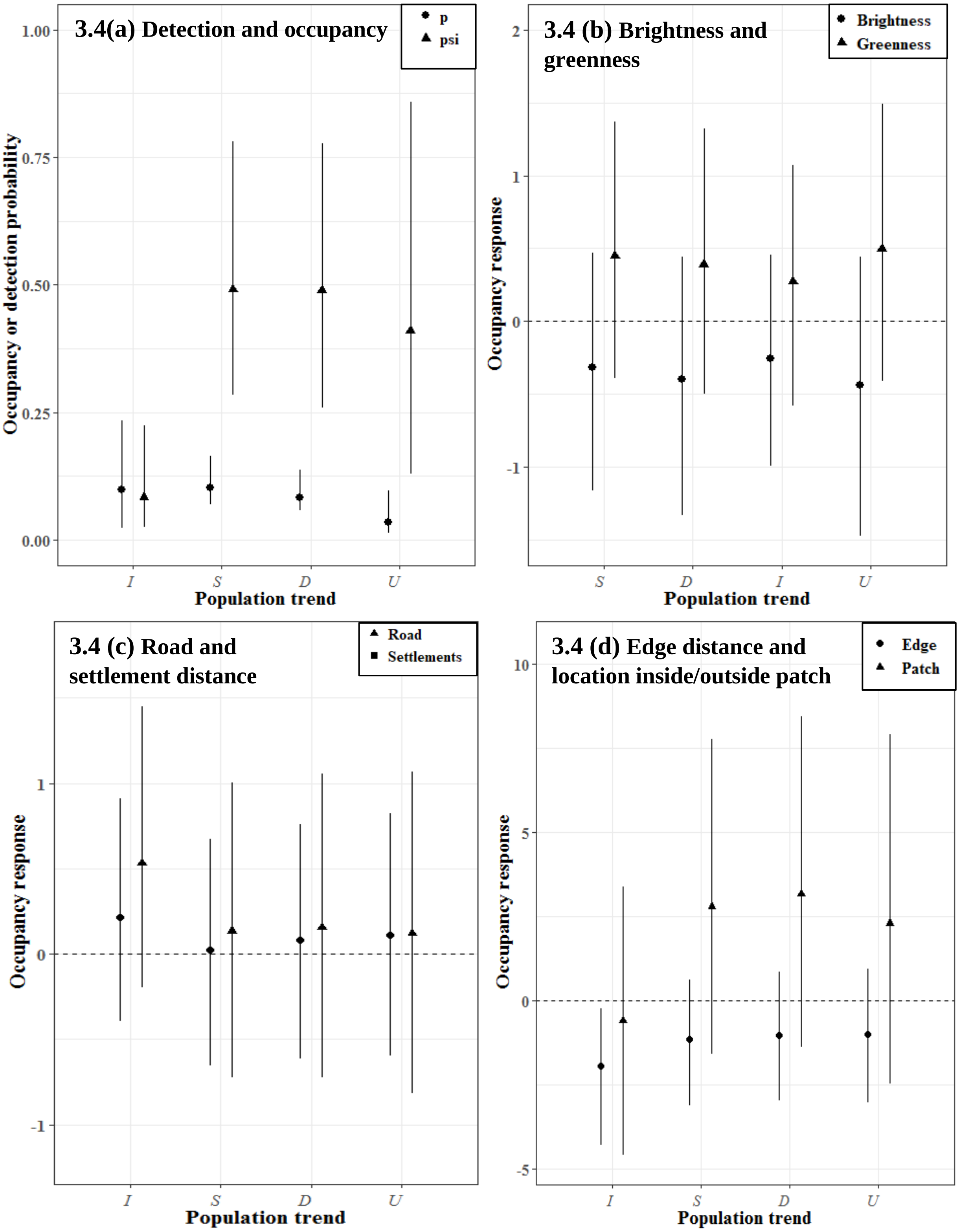


Figure 3.4. Estimates and associated 95% credible intervals of detection (p) and occupancy (psi) probability (a), and occupancy responses to increased soil reflectance and vegetation greenness (b), increased distance from the nearest road and settlement (c), and increased distance to the edge of the occupied vegetation patch and being located within or outside of a patch (d), for each Population Trend category of reptiles in Mahamavo. Response estimates above the x-intercept indicate increased species occupancy with increased values of the site variable.

Goodness-of-fit

The Bayesian p-value of 0.22 and the relationship between the expected and observed data (Figure 3.5) indicated the model fit the data adequately.

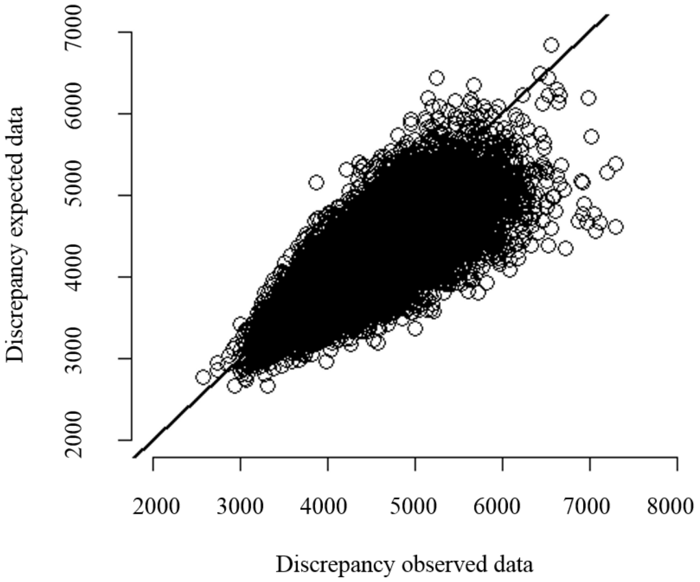


Figure 3.5. Simulated versus observed discrepancy measures of a Pearson goodness-of-fit test of the multi-species site occupancy model.

3.5. Discussion

Our results demonstrate how the use of mean estimates of species groups may yield interesting trends but also results in the loss of important species-level patterns. The grouping that was most valuable in predicting habitat selection was family, where the Chamaeleonidae family stood out for its high probability of occurring at a site and strong preference for sites with dense, green vegetation within a forest patch. The Pseudoxyrhophiidae and the Boidae had the widest credible intervals, indicating high variation within the groups' distributions. The Red List Threat Status was less effective in predicting species site distributions, but the use of this grouping still highlighted some notable occupancy and detection patterns, such as the Vulnerable species group having the lowest occupancy estimate and the Endangered having the highest. Additionally, the Increasing Population Trend group had the lowest mean occupancy estimate but a relatively high detection probability, while the Decreasing and Stable groups had the highest occupancy estimates, although it is difficult to draw conclusions with regards to IUCN Population Trend groupings without testing occupancy change over time.

3.5.1 Family responses to landscape structure

Irwin et al., (2010) found that phylogenetic groupings such as families could not be used to predict occurrence responses at a multi-taxon scale to anthropogenic disturbance in Madagascar because species within a group differ too greatly from one another. Similarly, occupancy responses to soil reflectance and the proximity to forest edges and human development did not appear to be family-based in Mahamavo reptile species in our study. However, the Chamaeleonidae family did show a strong preference for sites with dense green vegetation that were within a forest patch. Some studies have found similar patterns in the occurrence of chameleons being positively associated with primary, intact forests or low-disturbance forest patches, which offer shelter and aid in movement between vegetation (Brady and Griffiths, 1999; Jenkins et al., 2003). Other studies, however, have concluded that species such as *Chamaeleo chamaeleon* in Spain and some southern African *Bradypodion* species are not restricted to intact or green forest (Hódar et al., 2000; Reisinger et al., 2006), possibly as a result of the basking opportunities offered by sparser vegetation or edges of forest clearings. Consequently, although it is useful to investigate distribution patterns at a group level to gauge broad trends, it is also important to investigate the individual species within the groups.

Although the conflicting results in the literature mean that the association of chameleon occurrence with the distribution of dense, green forest patches cannot be applied confidently to all species within the global Chamaeleonidae family, this finding may still be useful when investigating the distribution of the *Furcifer* genus, which contains the flagship species *F. oustaleti* and *F. angeli*. The *Furcifer* chameleons in the Mahamavo forest exhibited high occupancy estimates and favour intact, green forest patches; considering that the Chamaeleonidae tend to be at a high risk of extinction, particularly in degraded environments like those in much of Madagascar (Tolley et al., 2016; Tonini et al., 2016), these intact forest patches may serve as important refuges for the *Furcifer* genus. Conversely, Glaw and Vences (2007) note that *Furcifer oustaleti* occupies disturbed and less-vegetated sites and is rare in primary forest. However, this was concluded based on a broad-scale survey of the species' distribution on the island, which includes rainforests, where it may have appeared to occur in comparatively sparsely-vegetated areas, whereas our results indicate that, at a regional scale, *Furcifer* species favour densely-vegetated dry forest.

The wide CRIs of the habitat responses of the Boidae and Pseudoxyrhophiidae may be interpreted in two ways: either the species within a family are habitat-generalists, or the species within a family differ among one another in their landscape-use. The boid genera *Sanzinia* and *Acrantophis* are found in a broad range of habitats (Glaw and Vences, 2007; Vences and Glaw, 2003) and therefore their variation is likely due to variability of habitat, with individuals moving between (and being detected in) different parts of the landscape. The Pseudoxyrhophiidae family includes a number of species with notably different habits, such as the small, camouflaging arboreal *Langaha* and the larger, terrestrial *Dromicodryas* active-foragers; in this case, the variability in landscape-use is likely between species (*Langaha* and *Dromicodryas* occurring in different terrains) as well as within species (as with the boids, *Dromicodryas* individuals occurring in a wide range of different terrains). These results again demonstrate that although grouping landscape-use into mean family responses may provide some useful insight, it is important to investigate further at the individual species-level to understand variability in landscape-use.

3.5.2 Assessing occupancy trends in Threat Status

With regard to Threat Status, the Least Concern group in our study demonstrated the highest mean detection probability of the Threat Statuses but not the highest occupancy probability as might be expected, which instead belonged to the Endangered species category. This raises the question of whether Least Concern species are actually more at risk than Endangered species at a regional scale than their Threat Status implies. A species is classified as Endangered on the IUCN Red List when it has shown a high reduction in its population size (> 50% or > 70% depending on the situation) over the last decade or three generations, has a small (< 5 000 km^2) extent of occurrence (the spatial range of the species as one continuous distribution), or has few individuals (250 adults per population, and <

2500 in total) (IUCN Standards and Petitions Subcommittee, 2017). The two Endangered species in this study, *Uroplatus guentheri* and *Phisalixella (Stenophis) variabilis*, were classified as such because of their small extents of occurrence (IUCN, 2018). Although these species showed a high probability of occurring in the study area, when investigated at a different spatial scale (i.e., the whole island), they are considered to be at a high risk of extinction because their small ranges increase the likelihood that the entire species would be extirpated by a stochastic event (Nicholson et al., 2009). This again demonstrates the importance of conserving primary forest fragments such as those in our study, and shows how IUCN Red List categories, which are assigned based on global assessments, may not be applicable at a regional scale.

The importance of investigating Threat Status at a regional scale is reiterated by the Vulnerable species in our results having the lowest mean occupancy estimate. *Paroedura vazimba*, *Uroplatus ebenaui* and *Uroplatus henkeli* are classified as Vulnerable because of their small extents of occurrence (< 20 000 km^2) (IUCN, 2018). Although these Vulnerable species are considered by the IUCN Red List to be at a lower risk of extinction than the Endangered species (because Vulnerable species have larger ranges), their low occupancy in the area indicates that they should still be monitored at a regional level because they could easily become Endangered if forest patches such as those in Mahamavo are destroyed. This limitation has been identified by the IUCN, which urges users to consider the effects of scale and regional assessments in the light of Threat Status being based off global assessments (IUCN Species Survival Commission, 2012). Communities that are investigated at a coarse resolution tend to appear less threatened than those at a fine scale Kirkpatrick 1998, (Nicholson et al., 2009). This is particularly relevant to studies conducted in Madagascar, where the fine-scale endemicity, and the associated small geographic ranges and high habitat specialization, make species vulnerable to large changes in their populations (Böhm et al., 2016). Spatial resolution is also important to consider when investigating landscape use, because some reptile distributions can be predicted by habitat variables at some resolutions but not others (Fischer et al., 2004) – perhaps at a different spatial resolution, we may have been able to see trends in landscape-occupancy patterns within threat categories, which were absent in the results of our study.

3.5.3 Occupancy and Population Trend

The relevance of considering detection probability, as well as understanding how the Red List assigns species to categories, is demonstrated by the mean occupancy estimates of the Red List's Population Trend categories. The Stable and Increasing Population Trend groups had the highest detection probabilities, but the Increasing group had the lowest occupancy probability and the occupancy estimate for the Decreasing group is relatively high. Although these Population Trends are based on abundance of individuals rather than species presence/absence involved with occupancy analysis, it is expected that where individuals are abundant, occupancy will be higher because there is a higher chance of encountering an individual. This may be an implication of the Red List's Population Trend category being assigned based on the assessor's subjective estimate, unlike Threat Status which uses data to test hypotheses (G.A. pers. comm.; Rodrigues et al., 2006). However, a species may have a high abundance of individuals but still be decreasing and, therefore, to assess whether it is in fact decreasing, occupancy over time would need to be investigated.

3.5.4 Conclusion

Our assessment indicates that densely vegetated forest fragments are of great conservation importance, particularly to chameleons, and that although taxonomic grouping may yield some insight into the effect of landscape structure on reptile occurrence, more meaningful assessment may result from investigating reptile patterns at the level of species or genus. Our results also demonstrate the importance of considering the spatial scale at which the Red List Threat Status is applied and using caution when making assumptions at a regional level. Further study is required to ascertain the effect of using the IUCN Red List Population Trend categorization, but initial assessment indicates that the assignment of Increasing, Decreasing and Stable trends may be heavily influenced by detection probability. Future investigations could explore the distributions of snake taxa with different foraging strategies (active and passive) and assess the effectiveness of using different taxonomic groupings such as genus to characterise patterns of landscape-use.

3.6 Literature cited

Alves, R.R. da N., Vieira, W.L. da S., Santana, G.G., 2008. Reptiles used in traditional folk medicine: conservation implications. Biodivers. Conserv. 17, 2037–2049. https://doi.org/10.1007/s10531-007-9305-0

Beck, D.D., Jennings, R.D., 2003. Habitat use by Gila monsters: the importance of shelters. Herpetol. Monogr. 17, 111–129.

Bennett, A.F., Radford, J.Q., Haslem, A., 2006. Properties of land mosaics: implications for nature conservation in agricultural environments. Biol. Conserv. 133, 250–264.

Bland, L.M., Böhm, M., 2016. Overcoming data deficiency in reptiles. Biol. Conserv., Advancing reptile conservation: Addressing knowledge gaps and mitigating key drivers of extinction risk 204, 16–22. https://doi.org/10.1016/j.biocon.2016.05.018

Blouin- Demers, G., Weatherhead, P.J., 2001. An experimental test of the link between foraging, habitat selection and thermoregulation in black rat snakes Elaphe obsoleta obsoleta. J. Anim. Ecol. 70, 1006–1013. https://doi.org/10.1046/j.0021-8790.2001.00554.x

Böhm, M., Williams, R., Bramhall, H.R., McMillan, K.M., Davidson, A.D., Garcia, A., Bland, L.M., Bielby, J., Collen, B., 2016. Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. Glob. Ecol. Biogeogr. 25, 391–405.

Bonnet, X., Shine, R., Lourdais, O., 2002. Taxonomic chauvinism. Trends Ecol. Evol. 17, 1–3. https://doi.org/10.1016/S0169-5347(01)02381-3

Brady, L.D., Griffiths, R.A., 1999. Status assessment of chameleons in Madagascar. IUCN Species Survival Commission Gland, Cambridge.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., Rodrigues, A.S., 2006. Global biodiversity conservation priorities. science 313, 58–61.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., Hilton-Taylor, C., 2002. Habitat Loss and

Extinction in the Hotspots of Biodiversity. Conserv. Biol. 16, 909–923. https://doi.org/10.1046/j.1523-1739.2002.00530.x

Bruton, M.J., Maron, M., Franklin, C.E., McAlpine, C.A., 2016. The relative importance of habitat quality and landscape context for reptiles in regenerating landscapes. Biol. Conserv. 193, 37–47.

Bruton, M.J., McAlpine, C.A., Maron, M., 2013. Regrowth woodlands are valuable habitat for reptile communities. Biol. Conserv. 165, 95–103. https://doi.org/10.1016/j.biocon.2013.05.018

Cohen, W.B., Spies, T.A., Fiorella, M., 1995. Estimating the age and structure of forests in a multi-ownership landscape of western Oregon, USA. Int. J. Remote Sens. 16, 721–746.

Crist, E.P., Cicone, R.C., 1984. A physically-based transformation of Thematic Mapper data---The TM Tasseled Cap. IEEE Trans. Geosci. Remote Sens. 256–263.

Dahms, T., Seissiger, S., Borg, E., Vajen, H., Fichtelmann, B., Conrad, C., 2016. Important Variables of a RapidEye Time Series for Modelling Biophysical Parameters of Winter Wheat. Photogramm.-Fernerkund.-Geoinformation 2016, 285–299.

Dorazio, R.M., Royle, J.A., 2005a. Estimating size and composition of biological communities by modeling the occurrence of species. J. Am. Stat. Assoc. 100, 389–398.

Dorazio, R.M., Royle, J.A., 2005b. Estimating size and composition of biological communities by modeling the occurrence of species. J. Am. Stat. Assoc. 100, 389–398.

Downes, S., 2001. Trading heat and food for safety: costs of predator avoidance in a lizard. Ecology 82, 2870–2881.

Durso, A.M., Willson, J.D., Winne, C.T., 2011. Needles in haystacks: estimating detection probability and occupancy of rare and cryptic snakes. Biol. Conserv. 144, 1508–1515.

Ferrier, S., Guisan, A., 2006. Spatial modelling of biodiversity at the community level. J. Appl. Ecol. 43, 393–404.

Fischer, J., Lindenmayer, D.B., Cowling, A., 2004. The challenge of managing multiple species at multiple scales: reptiles in an Australian grazing landscape. J. Appl. Ecol. 41, 32–44. https://doi.org/10.1111/j.1365-2664.2004.00869.x

Gardner, T.A., Barlow, J., Peres, C.A., 2007a. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. Biol. Conserv. 138, 166–179.

Gardner, T.A., Barlow, J., Peres, C.A., 2007b. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. Biol. Conserv. 138, 166–179.

Glaw, F., Vences, M., 2007. A field guide to the amphibians and reptiles of Madagascar. Vences & Glaw.

Grinand, C., Rakotomalala, F., Gond, V., Vaudry, R., Bernoux, M., Vieilledent, G., 2013. Estimating deforestation in tropical humid and dry forests in Madagascar from 2000 to 2010 using multi-date Landsat satellite images and the random forests classifier. Remote Sens. Environ. 139, 68–80.

Harper, G.J., Steininger, M.K., Tucker, C.J., Juhn, D., Hawkins, F., 2007. Fifty years of deforestation and forest fragmentation in Madagascar. Environ. Conserv. 34, 325–333.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O’Brien, E.M., 2003. Energy, water, and broad- scale geographic patterns of species richness. Ecology 84, 3105–3117.

Hódar, J.A., Pleguezuelos, J.M., Poveda, J.C., 2000. Habitat selection of the common chameleon (Chamaeleo chamaeleon)(L.) in an area under development in southern Spain: implications for conservation. Biol. Conserv. 94, 63–68.

Huey, R.B., 1991. Physiological Consequences of Habitat Selection. Am. Nat. 137, S91–S115.

Irwin, M.T., Wright, P.C., Birkinshaw, C., Fisher, B.L., Gardner, C.J., Glos, J., Goodman, S.M., Loiselle, P., Rabeson, P., Raharison, J.-L., 2010a. Patterns of species change in anthropogenically disturbed forests of Madagascar. Biol. Conserv. 143, 2351–2362.

Irwin, M.T., Wright, P.C., Birkinshaw, C., Fisher, B.L., Gardner, C.J., Glos, J., Goodman, S.M., Loiselle, P., Rabeson, P., Raharison, J.-L., 2010b. Patterns of species change in anthropogenically disturbed forests of Madagascar. Biol. Conserv. 143, 2351–2362.

IUCN, 2018. The IUCN Red List of Threatened Species. Version 2018-1. [WWW Document]. IUCN Red List Threat. Species. URL https://www.iucnredlist.org/en (accessed 10.22.18).

IUCN, 2016. The IUCN Red List of Threatened Species [WWW Document]. URL http://www.iucnredlist.org/search

IUCN Species Survival Commission, 2012. IUCN Red List Categories and Criteria: Version 3.1 (No. Second edition). IUCN Council, Gland, Switzerland and Cambridge, UK.

IUCN Standards and Petitions Subcommittee, 2017. Guidelines for Using the IUCN Red List Categories and Criteria. Version 13. (No. Second edition).

Jenkins, R.K.B., Brady, L.D., Bisoa, M., Rabearivony, J., Griffiths, R.A., 2003. Forest disturbance and river proximity influence chameleon abundance in Madagascar. Biol. Conserv. 109, 407–415. https://doi.org/10.1016/S0006-3207(02)00166-0

Jha, S., Bawa, K.S., 2006. Population growth, human development, and deforestation in biodiversity hotspots. Conserv. Biol. 20, 906–912.

Jochimsen D. M., Peterson C. R., Harmon L. J., 2014. Influence of ecology and landscape on snake road mortality in a sagebrush- steppe ecosystem. Anim. Conserv. 17, 583–592. https://doi.org/10.1111/acv.12125

Kauth, R.J., Thomas, G.S., 1976. The Tasselled Cap -- A Graphic Description of the Spectral-Temporal Development of Agricultural Crops as Seen by LANDSAT 13.

Kellner, K., 2017. jagsUI: A Wrapper Around “rjags” to Streamline “JAGS” Analyses.

Kéry, M., Royle, J.A., 2015. Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1: Prelude and Static Models. Academic Press.

Kéry, M., Schaub, M., 2012. Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective. Academic Press.

Kremen, C., Cameron, A., Moilanen, A., Phillips, S.J., Thomas, C.D., Beentje, H., Dransfield, J., Fisher, B.L., Glaw, F., Good, T.C., Harper, G.J., Hijmans, R.J., Lees, D.C., Louis, E., Nussbaum, R.A., Raxworthy, C.J., Razafimpahanana, A., Schatz, G.E., Vences, M., Vieites, D.R., Wright, P.C., Zjhra, M.L., 2008. Aligning Conservation Priorities Across Taxa in

Madagascar with High-Resolution Planning Tools. Science 320, 222–226. https://doi.org/10.1126/science.1155193

Lagarde, F., Louzizi, T., Slimani, T., El Mouden, H., Kaddour, K.B., Moulherat, S., Bonnet, X., 2012. Bushes protect tortoises from lethal overheating in arid areas of Morocco. Environ. Conserv. 39, 172–182.

Lehtinen, R.M., Ramanamanjato, J.-B., Raveloarison, J.G., 2003. Edge effects and extinction proneness in a herpetofauna from Madagascar.

Lewin, A., Feldman, A., Bauer, A.M., Belmaker, J., Broadley, D.G., Chirio, L., Itescu, Y., LeBreton, M., Maza, E., Meirte, D., 2016a. Patterns of species richness, endemism and environmental gradients of African reptiles. J. Biogeogr. 43, 2380–2390.

Lewin, A., Feldman, A., Bauer, A.M., Belmaker, J., Broadley, D.G., Chirio, L., Itescu, Y., LeBreton, M., Maza, E., Meirte, D., 2016b. Patterns of species richness, endemism and environmental gradients of African reptiles. J. Biogeogr. 43, 2380–2390.

Long, P., Seing, S.T., Rabenoro, M., Gandola, R., Radespiel, U., Ellis, C., Evans, B., Palfrey, R., Raveloson, B., Rakotondraparany, R., Andriambelo, H., Neaves, J., 2013. Biodiversity surveys of Mariarano and Matsedroy tropical dry forests and associated wetlands, Western Madagascar, Final Report.

Lötter, D., 2010. Agriculture, in: Archer, E., Engelbrecht, F., Landman, W. South African Risk and Vulnerability Atlas. p. 62.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L., Hines, J.E., 2006. Occupancy in Community-Level Studies, in: Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press, pp. 249–266.

Masterson, G.P., Maritz, B., Alexander, G.J., 2008. Effect of fire history and vegetation structure on herpetofauna in a South African grassland. Appl. Herpetol. 5, 129–143.

McCain, C.M., 2010. Global analysis of reptile elevational diversity. Glob. Ecol. Biogeogr. 19, 541–553.

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V., Gordon, J.E., 2006. A global overview of the conservation status of tropical dry forests. J. Biogeogr. 33, 491–505. https://doi.org/10.1111/j.1365-2699.2005.01424.x

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Nicholson, E., Keith, D.A., Wilcove, D.S., 2009. Assessing the Threat Status of Ecological Communities. Conserv. Biol. 23, 259–274. https://doi.org/10.1111/j.1523-1739.2008.01158.x

Paterson, J.E., Blouin- Demers, G., 2018. Density- dependent habitat selection predicts fitness and abundance in a small lizard. Oikos 127, 448–459. https://doi.org/10.1111/oik.04758

Plummer, M., 2017. JAGS: Just Another Gibbs Sampler.

Qian, H., Wang, X., Wang, S., Li, Y., 2007. Environmental determinants of amphibian and reptile species richness in China. Ecography 30, 471–482.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2013.

Reinert, H., 1993. Habitat selection in snakes. Snakes Ecol. Behav. 201–240.

Reisinger, W.J., Stuart-Fox, D.M., Erasmus, B.F.N., 2006. Habitat associations and conservation status of an endemic forest dwarf chameleon (Bradypodion sp.) from South Africa. Oryx 40, 183. https://doi.org/10.1017/S0030605306000408

Rodrigues, A.S.L., Pilgrim, J.D., Lamoreux, J.F., Hoffmann, M., Brooks, T.M., 2006. The value of the IUCN Red List for conservation. Trends Ecol. Evol. 21, 71–76. https://doi.org/10.1016/j.tree.2005.10.010

Rodríguez, M.Á., Belmontes, J.A., Hawkins, B.A., 2005. Energy, water and large-scale patterns of reptile and amphibian species richness in Europe. Acta Oecologica 28, 65–70.

Rytwinski, T., Fahrig, L., 2012. Do species life history traits explain population responses to roads? A meta-analysis. Biol. Conserv. 147, 87–98. https://doi.org/10.1016/j.biocon.2011.11.023

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., 2000. Global biodiversity scenarios for the year 2100. science 287, 1770–1774.

Schlaepfer, M.A., Gavin, T.A., 2001. Edge Effects on Lizards and Frogs in Tropical Forest Fragments. Conserv. Biol. 15, 1079–1090. https://doi.org/10.1046/j.1523-1739.2001.0150041079.x

Schneider-Maunoury, L., Lefebvre, V., Ewers, R.M., Medina-Rangel, G.F., Peres, C.A., Somarriba, E., Urbina-Cardona, N., Pfeifer, M., 2016. Abundance signals of amphibians and reptiles indicate strong edge effects in Neotropical fragmented forest landscapes. Biol. Conserv. 200, 207–215.

Schönert, M., Weichelt, H., Zillmann, E., Jürgens, C., 2014. Derivation of tasseled cap coefficients for RapidEye data. Presented at the Earth Resources and Environmental Remote Sensing/GIS Applications V, International Society for Optics and Photonics, p. 92450Q.

Semlitsch, R.D., Bodie, J.R., 2003. Biological Criteria for Buffer Zones around Wetlands and Riparian Habitats for Amphibians and Reptiles. Conserv. Biol. 17, 1219–1228. https://doi.org/10.1046/j.1523-1739.2003.02177.x

Shah, B., Shine, R., Hudson, S., Kearney, M., 2004. Experimental analysis of retreat-site selection by thick-tailed geckosNephrurus milii. Austral Ecol. 29, 547–552. https://doi.org/10.1111/j.1442-9993.2004.01388.x

Shine, R., Lemaster, M., Wall, M., Langkilde, T., Mason, R., 2004. Why Did the Snake Cross the Road? Effects of Roads on Movement and Location of Mates by Garter Snakes (*Thamnophis sirtalis parietalis*). Ecol. Soc. 9. https://doi.org/10.5751/ES-00624-090109

Sunderlin, W.D., Angelsen, A., Belcher, B., Burgers, P., Nasi, R., Santoso, L., Wunder, S., 2005. Livelihoods, forests, and conservation in developing countries: an overview. World Dev. 33, 1383–1402.

Sutherland, W.J., Pullin, A.S., Dolman, P.M., Knight, T.M., 2004. The need for evidence-based conservation. Trends Ecol. Evol. 19, 305–308.

Tilbury, C.R., 2018. Chameleons of Africa: an atlas: including the chameleons of Europe, the Middle East and Asia. Edition Chimaira.

Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. Nature 371, 65–66.

Tingley, R., Hitchmough, R.A., Chapple, D.G., 2013. Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. Biol. Conserv. 165, 62–68. https://doi.org/10.1016/j.biocon.2013.05.028

Tobler, M.W., Zúñiga Hartley, A., Carrillo- Percastegui, S.E., Powell, G.V., 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. J. Appl. Ecol. 52, 413–421.

Tolley, K.A., Alexander, G.J., Branch, W.R., Bowles, P., Maritz, B., 2016. Conservation status and threats for African reptiles. Biol. Conserv., Advancing reptile conservation: Addressing knowledge gaps and mitigating key drivers of extinction risk 204, 63–71. https://doi.org/10.1016/j.biocon.2016.04.006

Tonini, J.F.R., Beard, K.H., Ferreira, R.B., Jetz, W., Pyron, R.A., 2016. Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. Biol. Conserv., Advancing reptile conservation: Addressing knowledge gaps and mitigating key drivers of extinction risk 204, 23–31. https://doi.org/10.1016/j.biocon.2016.03.039

Tsairi, H., Bouskila, A., 2004. Ambush Site Selection of a Desert Snake (Echis coloratus) at an Oasis. Herpetologica 60, 13–23.

Vences, M., Glaw, F., 2003. Phylogeography, systematics and conservation status of boid snakes from Madagascar (Sanzinia and Acrantophis).

Vences, M., Wollenberg, K.C., Vieites, D.R., Lees, D.C., 2009. Madagascar as a model region of species diversification. Trends Ecol. Evol. 24, 456–465. https://doi.org/10.1016/j.tree.2009.03.011

Wanger, T.C., Iskandar, D.T., Motzke, I., Brook, B.W., Sodhi, N.S., Clough, Y., Tscharntke, T., 2010. Effects of Land-Use Change on Community Composition of Tropical Amphibians and Reptiles in Sulawesi, Indonesia. Conserv. Biol. 24, 795–802. https://doi.org/10.1111/j.1523-1739.2009.01434.x

Wasko, D.K., Sasa, M., 2012. Food resources influence spatial ecology, habitat selection, and foraging behavior in an ambush-hunting snake (Viperidae: Bothrops asper): an experimental study. Zoology 115, 179–187. https://doi.org/10.1016/j.zool.2011.10.001

Wearn, O.R., Rowcliffe, J.M., Carbone, C., Pfeifer, M., Bernard, H., Ewers, R.M., 2017. Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling approach. Biol. Conserv. 212, 162–171.

Whitaker, P.B., Shine, R., 2000. Sources of Mortality of Large Elapid Snakes in an Agricultural Landscape. J. Herpetol. 34, 121–128. https://doi.org/10.2307/1565247

Whiting, M.J., Williams, V.L., Hibbitts, T.J., 2013. Animals traded for traditional medicine at the Faraday market in South Africa: species diversity and conservation implications, in: Animals in Traditional Folk Medicine. Springer, pp. 421–473.

Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E., Willis, K.J., 2005. Conservation biogeography: assessment and prospect. Divers. Distrib. 11, 3–23.

CHAPTER 4 – SYNTHESIS AND CONCLUSIONS

The aim of this dissertation was to explore the patterns of terrestrial reptile land-use in a discontinuous dry forest. This was approached in Chapter 2 by assessing species occupancy in response to vegetation gradients and proximity to anthropogenic development, and characterizing species assemblages based on similarities in distribution responses to landscape variables. The species landscape-use patterns were investigated further in Chapter 3 by testing whether any trends in mean reptile occupancy exist in taxonomic families and IUCN Red List Threat categories. The results of both chapters are summarized and compared in Table 4.1. Investigating and comparing occupancy patterns at mean reptile-level, group-level and species-level provided useful summaries of landscape-use, as well as species-specific distribution trends.

4.1. Summary of findings

Sites that are within, but are towards the periphery of, forest patches that have high densities of green vegetation are of the highest conservation value for reptiles in Madagascan dry forest. This combination of landscape variables supports 1) a high number of species, 2) species (such as *Geckolepis maculata* and *Hemidactylus mercatorius*) that have strong responses to landscape structure gradients as well as low occupancy probabilities, and are therefore sensitive to change 3) families (such as the Chamaeleonidae) that have the strongest responses to landscape structure gradients and are therefore the most sensitive to change, and 3) species that are classified as Endangered (EN) and Data Deficient (DD) by the IUCN Red List. It is important to note, however, that *Phelsuma laticauda*, which is more likely to occur outside of a forest patch but still close to the edge of a patch, would be excluded if we were to conserve only these areas. Distances to rural settlements and roads appear to be less important determinants of reptile occurrence, although the Endangered *Uroplatus guentheri* demonstrates some preference for sites further from settlements.

The results also suggest that the conservation of snake habitats may prove difficult because of the complexity of their occurrence patterns and landscape-use. This is particularly the case for the boid species in the area, which are wide-ranging and therefore prone to local extinction (Glaw and Vences, 2007; Vences and Glaw, 2003; Woodroffe, 1998). Although not classified as Threatened by the IUCN, both boid species are listed on CITES Appendix I and are therefore considered to be threatened with extinction (CITES, 2016). Additionally, *Sanzinia madagascariensis volontany* is only found in the north western parts of Madagascar and so, although at a species level *S. madagascariensis* is not Threatened, the restricted range of this subspecies makes it vulnerable to extinction (Vences and Glaw, 2003).

This study highlights the importance of detection probability in distribution studies, and of considering spatial scale when investigating Threat Status. With the use of occupancy modelling, I was able to calculate species occurrence estimates that were not biased by differences in species detectability, demonstrated by how detection probability was not correlated with occupancy probability. The measures of detection probability also provided insight into the Red List's Population Trend classification, where species classified as Increasing may have been classified thus due to being easily detected. Occupancy patterns relating to Threat category should be interpreted with caution at a regional population level, however, because Threat Status and Population Trend are based on global assessments using absolute criteria rather than relative or local measures.

4.2 Comparison with other studies

My results are in broad agreement with the current literature on reptile habitat-selection and also demonstrate some interesting contrasts. The increase of reptile presence and species richness with increased vegetation density is consistent with studies conducted at both global and local scales (Bennett et al., 2006; Bruton et al., 2016; Lewin et al., 2016; Wanger et al., 2010) and is likely due to the hunting and shelter opportunities present at more densely-vegetated sites with greater levels of habitat heterogeneity (Beck and Jennings, 2003; Bruton et al., 2016; Masterson et al., 2008; Tsairi and Bouskila, 2004; Wasko and Sasa, 2012). The distance to roads or settlements did not have a pronounced effect on reptile site-selection, which may reflect the mixed results of both positive (Hódar et al., 2000; Bruton et al., 2013) and negative (Böhm et al., 2016; Tilbury, 2018; Jochimsen et al., 2014; Rytwinski and Fahrig, 2012) relationships between reptile distributions and human presence that have been described by other studies, although human impact on reptile distributions is not a particularly common topic in the literature.

There was a clear preference among reptile species for forest edges, which is in contrast to the decrease in reptile presence with increased proximity to forest edges in the Neotropics found by Schneider-Maunoury et al., (2016), to the results of Lehtinen et al., (2003) where some reptile species in Madagascar were strong edge-avoiders, and to Dixo and Martins (2008), which found no difference in reptile species richness or abundance between interior and edge sites in Brazillian forest. However, Schlaepfer and Gavin (2001) found that some anoline lizards were more abundant along forest edges than the forest interior in Costa Rica during the dry season. My results regarding edge effects may be owing to the presence of better basking sites (Blouin-Demers and Weatherhead (2001) or lower parasite occurrence (Schlaepfer and Gavin (2001) on the edges of forests than the interior. In terms of family groupings, I concluded that the Chamaeleonidae and Gekkonidae are habitat-specialized and therefore at high risk from habitat transformation, which is consistent with the conclusions of Tolley et al. (2016) and Tonini et al. (2016) that chameleons and geckos are at a high risk of extinction.

4.3 The implications of grouping species based on landscape-use

The lack of significant habitat preferences found when grouping species by Threat Status and Population Trend investigated in Chapter 3 is clarified when we group species into assemblages based on habitat preference in Chapter 2 (Table 4.1). Although this approach of looking for patterns *post hoc* in the results in this manner may be criticized as deviating from hypothesis-based science, in this situation one may gain a better understanding not by comparing the means of species groups, but rather assessing if species seem to show patterns based on being within a group. Vulnerable (VN), Least Concern (LC) and Endangered (EN) species are dispersed widely among the assemblages (Table 4.1) and therefore, other than EN species preferring sites within a forest, landscape-use is not well predicted by Threat Status. Chapter 2 indicated that all species that prefer forest edges are LC, whereas Chapter 3 did not show any significant patterns in LC species preferences.

With regards to family trends, families are dispersed fairly evenly amongst the Chapter 2 assemblages but some trends are still apparent (Table 4.1). Both Chapter 2 and Chapter 3 indicate that the Chamaeleonidae are habitat-specific, inferred from their strong occupancy responses to site variables. However, this agreement of results between chapters was not the case for the Gekkoniidae. The majority of the significant responses to landscape variables demonstrated in the assemblages of Chapter 2 are made up of gecko species, and four of the eleven habitat response types (inside & outside patch, far from settlements and low brightness) consist only of gecko species (Table 4.1). *Uroplatus guentheri*, *Paroedura stumpfii* and *Furcifer angeli* in particular have the greatest numbers of habitat preferences, indicating specificity for a particular combination of landscape variables. This is across multiple genera, and therefore these patterns are likely truly family-based rather than simply resulting from random individual species traits. Similarly, these patterns are not only based on genus, because species in the same genus can respond differently (such as *Uroplatus* and *Paroedura* species). In contrast, Chapter 3 failed to demonstrate this habitat-specificity or sensitivity of the Gekkoniidae because mean family estimates do not distinguish between within-species variation and between-species variation within a family.

Table 4.1. Species grouped into assemblages based on similar landscape-use, and the corresponding family, Threat Status and estimated Population Trend of each species. Species with CRI marginally including zero are indicated as suggestive responses.

Site preference	Species	Family *	Threat Status*	Pop. Trend *
Low brightness	*Geckolepis maculata*	Gekkonidae	LC	U
	Lygodactylus tolampyae	Gekkonidae	LC	D
Low brightness (marginal)	*Acrantophis madagascariensis*	Boidae	LC	S
	Furcifer angeli	Chamaeleonidae	LC	S
	Paroedura stumpfii	Gekkonidae	LC	S
	Paroedura vazimba	Gekkonidae	VN	D
	Uroplatus guentheri	Gekkonidae	EN	D
High greenness	*Furcifer oustaleti*	Chamaeleonidae	LC	S
	Furcifer angeli	Chamaeleonidae	LC	S
	Uroplatus ebenaui	Gekkonidae	VN	D
High greenness (marginal)	*Geckolepis polylepis*	Gekkonidae	DD	U
	Uroplatus guentheri	Gekkonidae	EN	D
	Paroedura stumpfii	Gekkonidae	LC	S
	Mimophis mahfalensis	Psammophiidae	LC	S
	Madagascarophis colubrinus	Pseudoxyrhophiidae	LC	U
Far from roads (marginal)	*Zonosaurus laticaudatus*	Gerrhosauridae	LC	U
	Uroplatus guentheri	Gekkonidae	EN	D
Far from settlements	*Uroplatus guentheri*	Gekkonidae	EN	D
Far from settlements (marginal)	*Hemidactylus mercatorius*	Gekkonidae	LC	I
	Trachylepis elegans	Scincidae	LC	S
	Trachylepis gravenhorstii	Scincidae	LC	S
Close to forest patch edge	*Furcifer oustaleti*	Chamaeleonidae	LC	S
	Hemidactylus mercatorius	Gekkonidae	LC	I
	Phelsuma madagascariensis	Gekkonidae	LC	D
	Phelsuma laticauda	Gekkonidae	LC	S
	Madagascarophis colubrinus	Pseudoxyrhophiidae	LC	U
Close to forest patch edge (marginal)	*Dromicodryas bernieri*	Pseudoxyrhophiidae	LC	S
Inside forest patch	*Furcifer angeli*	Chamaeleonidae	LC	S
	Lygodactylus tolampyae	Gekkonidae	LC	D
	Paroedura stumpfii	Gekkonidae	LC	S
	Uroplatus guentheri	Gekkonidae	EN	D
	Dromicodryas quadrilineatus	Pseudoxyrhophiidae	LC	S
	Mimophis mahfalensis	Psammophiidae	LC	S
	Stenophis (Phisalixella) variabilis	Pseudoxyrhophiidae	LC	D
	Trachylepis gravenhorstii	Scincidae	LC	S
	Trachylepis elegans	Scincidae	LC	S
Inside forest patch (marginal)	*Phelsuma kochi*	Gekkonidae	LC	S
Outside forest patch:	*Phelsuma laticauda*	Gekkonidae	LC	S

* The IUCN Red List of Threatened Species. Version 2017-3. www.iucnredlist.org

4.4 Conclusions

Dry forests are under high threat from habitat transformation (Miles et al., 2006) and therefore prioritizing sites with characteristics that promote the persistence of a high number of species, as well as the species sensitive to habitat transformation, is of high relevance to conservation. The results of both species-specific and group investigations indicate that sites on the edges of forest patches which have relatively dense vegetation are important for the reptile species of Mahamavo dry forests, and that geckos and chameleons are likely highly sensitive to habitat transformation. The conservation of sites on the edges of forest patches would promote both high species richness and the persistence of geckos and chameleons in the area. Sites that are further from settlements may also be worth consideration for gecko conservation.

The model created in this study could be tested by identifying, from satellite imagery, other areas with high greenness and low brightness that are closer to forest edges but further from settlements, and investigating whether the occupancy patterns estimated by our model apply elsewhere. Additionally, using a model-selection approach may result in better model fit. Comparing reptile occupancy in forest patches of different sizes and shapes would be a valuable avenue for future study, as would be assessing how occupancy patterns compare between night and day surveys, between nocturnal and diurnal species, and among sites in areas subjected to different levels of development.

4.5 Literature cited

Beck, D.D., Jennings, R.D., 2003. Habitat use by Gila monsters: the importance of shelters. Herpetol. Monogr. 17, 111–129.

Bennett, A.F., Radford, J.Q., Haslem, A., 2006. Properties of land mosaics: implications for nature conservation in agricultural environments. Biol. Conserv. 133, 250–264.

Blouin- Demers, G., Weatherhead, P.J., 2001. An experimental test of the link between foraging, habitat selection and thermoregulation in black rat snakes Elaphe obsoleta obsoleta. J. Anim. Ecol. 70, 1006–1013. https://doi.org/10.1046/j.0021-8790.2001.00554.x

Böhm, M., Williams, R., Bramhall, H.R., McMillan, K.M., Davidson, A.D., Garcia, A., Bland, L.M., Bielby, J., Collen, B., 2016. Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. Glob. Ecol. Biogeogr. 25, 391–405.

Bruton, M.J., Maron, M., Franklin, C.E., McAlpine, C.A., 2016. The relative importance of habitat quality and landscape context for reptiles in regenerating landscapes. Biol. Conserv. 193, 37–47.

Bruton, M.J., McAlpine, C.A., Maron, M., 2013. Regrowth woodlands are valuable habitat for reptile communities. Biol. Conserv. 165, 95–103. https://doi.org/10.1016/j.biocon.2013.05.018

CITES, 2016. Appendices I, II and III [WWW Document]. URL https://cites.org/sites/default/files/notif/E-Notif-2016-064-A.pdf (accessed 11.20.18).

Dixo, M., Martins, M., 2008. Are leaf-litter frogs and lizards affected by edge effects due to forest fragmentation in Brazilian Atlantic forest? J. Trop. Ecol. 24, 551–554.

Glaw, F., Vences, M., 2007. A field guide to the amphibians and reptiles of Madagascar. Vences & Glaw.

Hódar, J.A., Pleguezuelos, J.M., Poveda, J.C., 2000. Habitat selection of the common chameleon (Chamaeleo chamaeleon)(L.) in an area under development in southern Spain: implications for conservation. Biol. Conserv. 94, 63–68.

Jochimsen D. M., Peterson C. R., Harmon L. J., 2014. Influence of ecology and landscape on snake road mortality in a sagebrush-steppe ecosystem. Anim. Conserv. 17, 583–592. https://doi.org/10.1111/acv.12125

Lehtinen, R.M., Ramanamanjato, J.-B., Raveloarison, J.G., 2003. Edge effects and extinction proneness in a herpetofauna from Madagascar.

Lewin, A., Feldman, A., Bauer, A.M., Belmaker, J., Broadley, D.G., Chirio, L., Itescu, Y., LeBreton, M., Maza, E., Meirte, D., 2016. Patterns of species richness, endemism and environmental gradients of African reptiles. J. Biogeogr. 43, 2380–2390.

Masterson, G.P., Maritz, B., Alexander, G.J., 2008. Effect of fire history and vegetation structure on herpetofauna in a South African grassland. Appl. Herpetol. 5, 129–143.

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V., Gordon, J.E., 2006. A global overview of the conservation status of tropical dry forests. J. Biogeogr. 33, 491–505. https://doi.org/10.1111/j.1365-2699.2005.01424.x

Schlaepfer, M.A., Gavin, T.A., 2001. Edge Effects on Lizards and Frogs in Tropical Forest Fragments. Conserv. Biol. 15, 1079–1090. https://doi.org/10.1046/j.1523-1739.2001.0150041079.x

Schneider-Maunoury, L., Lefebvre, V., Ewers, R.M., Medina-Rangel, G.F., Peres, C.A., Somarriba, E., Urbina-Cardona, N., Pfeifer, M., 2016. Abundance signals of amphibians and reptiles indicate strong edge effects in Neotropical fragmented forest landscapes. Biol. Conserv. 200, 207–215.

Tolley, K.A., Alexander, G.J., Branch, W.R., Bowles, P., Maritz, B., 2016. Conservation status and threats for African reptiles. Biol. Conserv., Advancing reptile conservation: Addressing knowledge gaps and mitigating key drivers of extinction risk 204, 63–71. https://doi.org/10.1016/j.biocon.2016.04.006

Tonini, J.F.R., Beard, K.H., Ferreira, R.B., Jetz, W., Pyron, R.A., 2016. Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. Biol. Conserv., Advancing reptile conservation: Addressing knowledge gaps and mitigating key drivers of extinction risk 204, 23–31. https://doi.org/10.1016/j.biocon.2016.03.039

Vences, M., Glaw, F., 2003. Phylogeography, systematics and conservation status of boid snakes from Madagascar (Sanzinia and Acrantophis).

Wanger, T.C., Iskandar, D.T., Motzke, I., Brook, B.W., Sodhi, N.S., Clough, Y., Tscharntke, T., 2010. Effects of Land-Use Change on Community Composition of Tropical Amphibians and Reptiles in Sulawesi, Indonesia. Conserv. Biol. 24, 795–802. https://doi.org/10.1111/j.1523-1739.2009.01434.x

Woodroffe, R., 1998. Edge Effects and the Extinction of Populations Inside Protected Areas. Science 280, 2126–2128. https://doi.org/10.1126/science.280.5372.2126

APPENDIX 1.

```
#R code for running model through JAGS

# Load packages
library(jagsUI)
library(abind)

# Data were arranged as a matrix of site (y) vs species (x), with each
# record being the detection frequency of each species at each site
# (detections summed across occasions in a year).
# Separate matrices for each year were stacked under one another in the datasheet
# Matrix includes index columns for 'year', 'route' and 'patch',
# and columns with site variable values (vegetation indices and human proximity)

data1 <- read.csv2("NewEdgeCovar_Years_Stacked_37Sp.csv", header = T, sep = ",", dec= ".")

# Define vegetation indices as vectors BRIGHT (brightness) & GREEN (greenness)
bright1 <- data1$B_TCT
green1 <- data1$G_TCT

# Standardize means around zero
mean.bright <- mean(bright1, na.rm = TRUE)
sd.bright <- sd(bright1[!is.na(bright1)])
BRIGHT <- (bright1-mean.bright)/sd.bright
BRIGHT [is.na(BRIGHT )] <- 0
mean.green <- mean(green1, na.rm = TRUE)
sd.green <- sd(green1[!is.na(green1)])
GREEN <- (green1-mean.green)/sd.green
GREEN[is.na(GREEN)] <- 0

# Define distances of sites to nearest road, village and edge of forest patch
# as vectors ROAD, VILL and EDGE
distRoad <- data1$RoadDist
distVillage <- data1$VillageDist
```

```
distEdge <- data1$EdgeDist

# Standardize means around zero
mean.road <- mean(distRoad, na.rm = TRUE)
sd.road <- sd(distRoad[!is.na(distRoad)])
ROAD <- (distRoad-mean.road)/sd.road
ROAD[is.na(ROAD)] <- 0
mean.vill <- mean(distVillage, na.rm = TRUE)
sd.vill <- sd(distVillage[!is.na(distVillage)])
VILL <- (distVillage-mean.vill)/sd.vill
VILL[is.na(VILL)] <- 0
mean.edge <- mean(distEdge, na.rm = TRUE)
sd.edge <- sd(distEdge[!is.na(distEdge)])
EDGE <- (distEdge - mean.edge)/sd.edge
EDGE[is.na(EDGE)] <- 0

# Define location of site inside/outside patch as vector PATCH
PATCH <- data1$Patch

# Assign route identity to each site and define vector routes1 (for random effect)
routes1 <- as.numeric(data1$route)
length(routes1) # Check there is a route number for each record

# Assign year identity to each occasion/site and define vector years1 (for random effect)
years1 <- as.numeric(data1$year)
length(years1) # Check that there is a year number for each record

# Define observation matrix ysum
ysum <- as.matrix(data1[,2:38])
ysum # Check that only species detection frequency columns are included

# Define number of sites etc. for use in model
nsite <- nrow(ysum) # site (i)
nspec <- ncol(ysum) # species (k)
nyear <- 4 # year (t)
nroute <- max(routes1) # route (r)
```

```
nocc <- 6 # no. occasions


# Bundle and summarize data set

str( win.data <- list(ysum = ysum, nsite = nsite, J = rep(nocc, nsite), nspec = nspec, BRIGHT =
BRIGHT, GREEN = GREEN, ROAD = ROAD, VILL = VILL, EDGE = EDGE, PATCH = PATCH, nroute
= nroute, routes = routes1, nyear = nyear, years = years1, e = 0.00001))


# Specify model in BUGS language

sink("model1.txt")

cat("

   model {


          # Define priors for occupancy and detection

          for(k in 1:nspec){ # Loop over species (k)

                    lpsi[k] ~ dnorm(alpha.lpsi,tau.lpsi) # Occupancy (psi)

                     lp[k] ~ dnorm(alpha.lp,tau.lp) # Detection (p)

          }


          # Hyperpriors for occupancy

          alpha.lpsi ~ dnorm(0,0.01)


          # Hyperpriors for detection

          alpha.lp ~ dnorm(0,0.01)


          # Priors for site covariates

          for(k in 1:nspec){

                    beta1.psi[k] ~ dnorm(alpha.beta1.psi,tau.beta1.psi) # Greenness

                    beta2.psi[k] ~ dnorm(alpha.beta2.psi,tau.beta2.psi) # Brightness

                    theta1.psi[k] ~ dnorm (alpha.theta1.psi, tau.theta1.psi) # Road

                    theta2.psi[k] ~ dnorm (alpha.theta2.psi, tau.theta2.psi) # Settlement

                    theta3.psi[k] ~ dnorm (alpha.theta3.psi, tau.theta3.psi) # Edge

                    theta4.psi[k] ~ dnorm (alpha.theta4.psi, tau.theta4.psi) # Patch

                    theta5.psi[k] ~ dnorm (alpha.theta5.psi, tau.theta5.psi) # Patch*edge

          }


          # Hyperpriors for site covariates

          alpha.beta1.psi ~ dnorm(0, 0.01) # Greenness
```

```
tau.beta1.psi <- pow(sigma.beta1.psi,-2)
sigma.beta1.psi ~ dunif(0,5)
alpha.beta2.psi ~ dnorm(0, 0.01) # Brightness
tau.beta2.psi <- pow(sigma.beta2.psi,-2)
sigma.beta2.psi ~ dunif(0,5)
alpha.theta1.psi ~ dnorm(0, 0.01) # Distance to road
tau.theta1.psi <- pow(sigma.theta1.psi,-2)
sigma.theta1.psi ~ dunif(0,5)
alpha.theta2.psi ~ dnorm(0, 0.01) # Distance to settlement
tau.theta2.psi <- pow(sigma.theta2.psi,-2)
sigma.theta2.psi ~ dunif(0,5)
alpha.theta3.psi ~ dnorm(0, 0.01) # Distance to patch edge
tau.theta3.psi <- pow(sigma.theta3.psi,-2)
sigma.theta3.psi ~ dunif(0,5)
alpha.theta4.psi ~ dnorm(0, 0.01) # Location inside/outside patch
tau.theta4.psi <- pow(sigma.theta4.psi,-2)
sigma.theta4.psi ~ dunif(0,5)
alpha.theta5.psi ~ dnorm(0, 0.01) # Patch*edge interaction
tau.theta5.psi <- pow(sigma.theta5.psi,-2)
sigma.theta5.psi ~ dunif(0,5)

# Priors for random effects
for(r in 1:nroute){ # Spatial random effect - sites grouped into routes
        alpha.routes[r] ~ dnorm(0, tau.routes)
}
for(t in 1:nyear){ # Temporal random effect - occasions grouped into years
        alpha.years[t] ~ dnorm(0, tau.years)
}
# Hyperpriors for random effects
tau.routes <- pow(sd.routes,-2) # spatial hyperprior
sd.routes ~ dunif(0, 3)
tau.years <- pow(sd.years,-2) # year hyperprior
sd.years ~ dunif(0, 1)

# Ecological model for latent occurrence z
for(k in 1:nspec){ # Loop over species
```

```
    for (i in 1:nsite) { # Loop over sites
    # Occupancy probability differs between species and sites
    logit(psi[i,k]) <- lpsi[k]+ beta1.psi[k] * BRIGHT[i] +
    beta2.psi[k] * GREEN[i] + theta1.psi[k] * ROAD[i] +
    theta2.psi[k] * VILL[i] + theta3.psi[k] * EDGE[i] +
    theta4.psi[k] * PATCH[i] + theta5.psi[k] * EDGE[i] * PATCH[i] +
    alpha.routes[routes[i]] + alpha.years[years[i]]
     # Bernoulli distribution for occurrence frequencies
    z[i,k] ~ dbern(psi[i,k])
    }
}

# Observation model for observed data ysum
for(k in 1:nspec){ # Loop over species
    # Detection probability differs between species but not sites
    logit(p[k]) <- lp[k]
    for (i in 1:nsite) {
        mup[i,k] <- z[i,k] * p[k]
        # Binomial distribution for detection (detected/not detected)
        ysum[i,k] ~ dbin(mup[i,k], J[i])
    }
}

# Derived quantities
for(k in 1:nspec){ # Loop over species
    MeanSpecPsi[k] <- mean(psi[,k]) # Mean occupancy prob per species
}
MeanP <- mean(p[]) # Mean detection probability
MeanB1 <- mean(beta1.psi[]) # Mean effect of greenness on species occupancy
MeanB2 <- mean(beta2.psi[]) # Mean effect of brightness
MeanT1 <- mean(theta1.psi[]) # Mean effect of road dist
MeanT2 <- mean(theta2.psi[]) # Mean effect of settlement
MeanT3 <- mean(theta3.psi[]) # Mean effect of distance to edge of forest
MeanT4 <- mean(theta4.psi[]) # Mean effect of being inside/outside a patch

for (i in 1:nsite) { # Loop over sites
```

```
        NSpec[i] <- sum(z[i,])   # Number of species occurring at each site
        MeanSitePsi[i] <- mean(psi[i,]) # Mean occupancy per site
    }

    # Calculate Pearson chi-squared residuals to assess goodness-of-fit
    for(k in 1:nspec){ # Loop over species
        for (i in 1:nsite) { # Loop over sites
            ynew[i,k] ~ dbin(mup[i,k], J[i]) # Simulate an ‘ideal’ dataset
            d[i,k]<- (ysum[i,k] - mup[i,k]*J[i])/sqrt((mup[i,k]+e)*J[i]*
            (1-mup[i,k]-e)) # A small value, e, prevents division by zero)
            d2[i,k]<- pow(d[i,k],2) # observed
            dnew[i,k]<- (ynew[i,k]-up[i,k]*J[i])/sqrt((mup[i,k]+e)*J[i]*
            (1-mup[i,k]-e))
            dnew2[i,k]<- pow(dnew[i,k],2) # expected
        }
    }

    #Calculate the Pearson chi-squared discrepancy measure
    p.fit<-sum(d2[,]) # observed
    p.fitnew<-sum(dnew2[,]) # expected

  }
   ",fill = TRUE)
sink()

# Initial values
zst <- apply(ysum, c(1,2), max) # Observed occurrence as inits for z
zst[zst>1] <- 1
inits <- function() list(z = zst, lpsi = rnorm(n=nspec), lp = rnorm(n=nspec))

# Parameters monitored
params1 <- c("p", "psi", "beta1.psi", "beta2.psi", "theta1.psi", "theta2.psi", "theta3.psi", "theta4.psi")
params2 <- c("MeanSpecPsi", "NSpec", "MeanSitePsi", "MeanP", "MeanB1", "MeanB2", "MeanT1",
"MeanT2", "MeanT3", "MeanT4")
params3 <- c("p.fit", "p.fitnew")
```

```
# MCMC settings
ni <- 600000   ;   nt <- 110   ;   nb <- 20000   ;   nc <- 3


# Call JAGS from R for each set of parameters
out1 <- jags(win.data, inits, params1, "model1.txt", n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel = TRUE)


# Export derived estimates
print(out1, dig = 3)
out1exp <- out1$summary
write.csv(x=out1exp, "out1 params1.csv")


# Check for autocorrelation among chains and that parameter priors are not
# constraining distributions
acf(out1.2$sims.list$psi[,1,1])
hist(out1.2$sims.list$alpha.routes)


# Goodness-of-fit summary
# Plot ratio of posterior dists of p.fit (obs): p.fitnew (exp)
par(mfrow = c(1, 2), mar = c(5,5,3,2), cex.lab = 1.5, cex.axis = 1.5)
plot(out1.2.2$sims.list$p.fit, out1.2.2$sims.list$p.fitnew, xlim = c(200, 1000), ylim =c(200, 1000), main = "", xlab = "Discrepancy observed data", ylab = "Discrepancy expected data", frame.plot = F, cex = 1.5)
abline(0,1, lwd = 2)
# Bayesian p-value
(bpv <- mean(out1.2.2$sims.list$p.fitnew > out1.2.2$sims.list$p.fit))
```

APPENDIX 2.

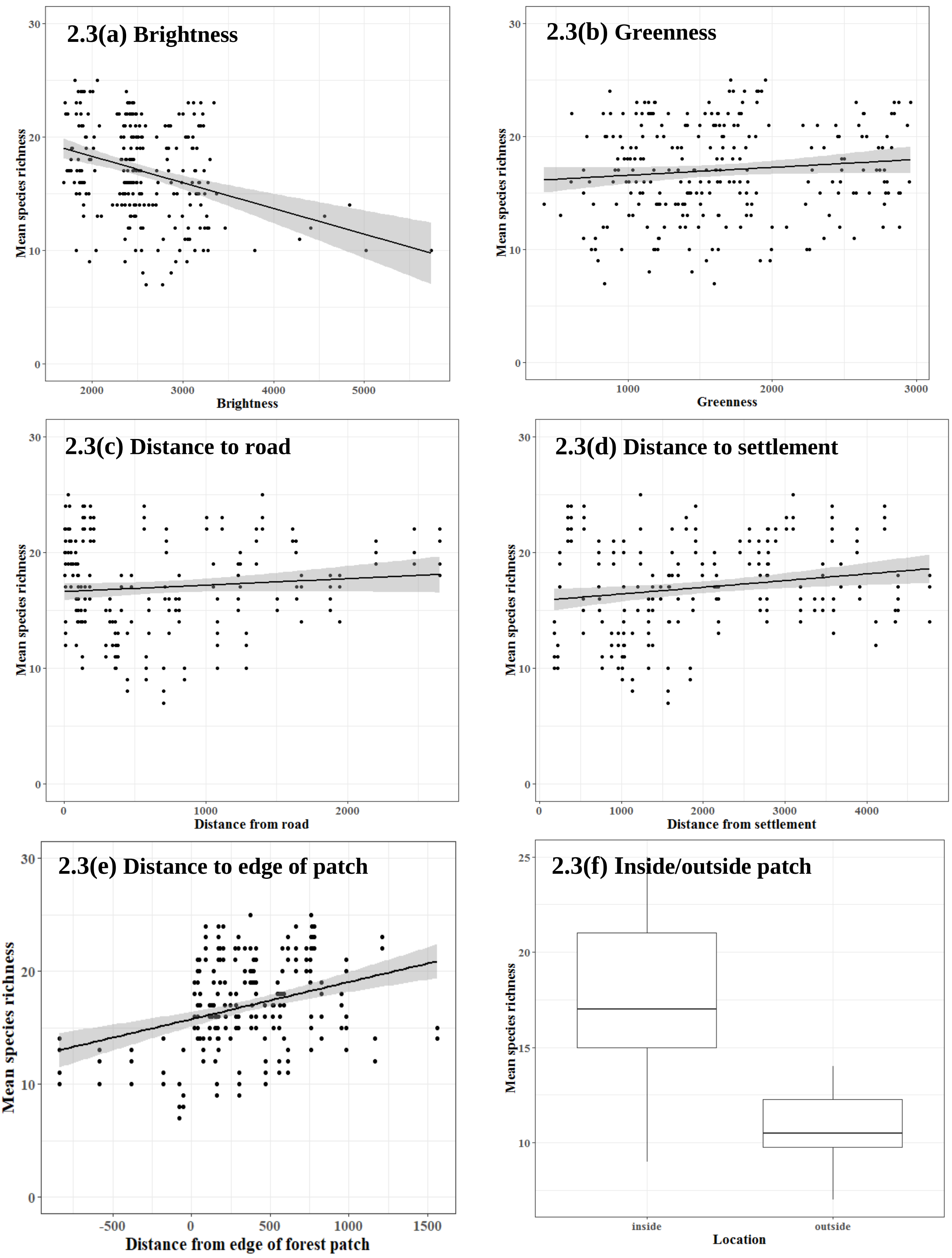


Figure 2.3. Effects of soil reflectance (a), vegetation greenness (b), and distances to the nearest road (c), settlement (d) and edge of the occupied vegetation patch (e) on species richness, as well as mean species richness inside and outside of a forest patch (f), and associated 95% credible intervals.