

**HABITAT PREDICTORS OF A VERTEBRATE COMMUNITY IN A
FRAGMENTED NEOTROPICAL LANDSCAPE**

by

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Abstract

Habitat is an area that allows a species to survive and thrive. Habitat loss and habitat modification are considered two major threats to species persistence. Habitat predictors are environmental conditions which dictate patterns in species occupancy and thereby community distribution. Understanding habitat predictors at multiple spatial scales can aid managers in directing conservation measures, predicting effects of habitat modification and advancing theoretical knowledge about the effects of habitat fragmentation. Habitat predictors of ground-dwelling Neotropical vertebrates at multiple spatial scales, especially landscape scales, are often poorly known. To fill this knowledge gap, I conducted a study in a fragmented forest landscape in Guanacaste Province, Costa Rica. In the 1960s, continuous tropical wet forests in my study area were burnt to clear land for cattle ranching. This process modified swathes of wet forests into smaller fragments surrounded by human-use areas. I chose 19 forests in this landscape situated in and around the Área de Conservación Guanacaste (ACG), a UNESCO World Heritage Site, documented vertebrates using camera traps and calculated habitat variables at the three spatial scales of camera trap point, forest and landscape using field measurements and remote sensing imagery. We documented 32 species of ground-dwelling vertebrates and calculated 13 aspects of the vertebrate community as response variables. We tested the ability of 12 habitat variables to explain variation in the community response variables using linear mixed effect modelling in an AIC-based model averaging framework. Our results show that different scales of habitat affect different aspects of the vertebrate community, highlighting a need for examination of multi-scale habitat variables. Habitat predictors at landscape scales were important to the widest range of vertebrate response variables. Our key results highlight that threatened species associated with areas of continuous forests and species richness were highest in forests surrounded by plantation matrix as opposed to pasture. Detections of species at higher trophic levels (e.g. large carnivores) increased with the amount of forested area within 2km of camera traps. Our study thus highlights the need to examine various aspects of a vertebrate community, not just species richness, in order to understand in-depth, the effects of habitat change.

Lay Summary

Large tracts of continuous forests in Guanacaste province, Costa Rica were burned and cleared in 1960s for make way for cattle pastures. This burning converted continuous forests to smaller fragments surrounded by agricultural areas. Forest fragmentation is a major threat to the survival of many species. Ecological theory suggests that larger forest areas will contain more species and that intervening human-use areas deter dispersal. We tested these hypotheses by using camera traps to survey the animals on the forest floor and then related the animals we observed to aspects of the habitat and surrounding landscape that we had quantified with measurements of ground-based vegetation and satellite images. Our results suggest that the type of human-use area between forests can affect different types of animal groups and the total number of species, and that large-bodied species of conservation concern prefer continuous (unfragmented) forests.

Preface

Keerthikrutha Seetharaman conducted the study, analysed the data and wrote the thesis with edits and comments from Diane Srivastava, Jill Jankowski and Cole Burton. Field work was conducted with permission from the Ministry of Environment and Energy of Costa Rica (MINAE), Del Oro Pvt. Ltd. and Novelteak Costa Rica S.A. Camera trapping was conducted in compliance with University of British Columbia's Animal Ethics Committee permit A18-0327. Chapter 2 is presently being prepared as a manuscript for submission with Keerthikrutha Seetharaman and Diane Srivastava as authors.

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Abbreviations

ACG	Área de Conservación Guanacaste / Area of Conservation Guanacaste
AIC	Akaike's Information Criterion
AMSL	Above Mean Sea Level
EN	Endangered
GPS	Geopositioning System
HML	Human Modified Landscape User
IUCN	International Union for Conservation of Nature
IBT	Island Biogeography theory
LC	Least Concern
MINAE	Ministry of Environment and Energy of Costa Rica
NS	Not selected
NT	Near Threatened
QGIS	Quantum Geographic Information System
S1	Side 1
S2	Side 2
S3	Side 3
S4	Side 4
SLOSS	Single large or Several Small
TEAM	Tropical Ecology Assessment Monitoring
VIF	Variance Inflation Factors
VU	Vulnerable

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CHAPTER 1

General Introduction

Biodiversity effects of habitat modification

Deforestation and fragmentation of forests have occurred since the time humans turned from hunter-gatherers into agriculturists (Bhagwat et al. 2014). Humans have worshipped and protected fragments of forests, interspersed in human-modified landscapes, even before the advent of the Industrial Revolution (Aerts et al. 2006, Ormsby and Bhagwat 2010). The Industrial Revolution, however, resulted in large-scale deforestation to support intensive cultivation and urbanisation (Watson et al. 2014). The large-scale deforestation, along with increasing species extinctions and the need to conserve unique and culturally valued ecosystems, led to the promotion of environmental conservation as a worldwide concept (Chape et al. 2008). This concept in turn led to the creation and expansion of ‘protected areas’, primarily in the form of national parks, wildlife sanctuaries and biosphere reserves (Chape et al. 2008, Watson et al. 2014). The theoretical basis for the creation and maintenance of ‘protected areas’ originated in part from applying island biogeography theory (IBT) to mainland terrestrial contexts, equating fragments of undisturbed habitat to ‘islands’ and the intervening human-modified areas as a ‘sea’ of inhospitable matrix (Diamond et al. 1976). IBT provided a mathematically rigorous explanation for why larger and more connected areas are expected to have higher species richness (MacArthur and Wilson 1967). As a consequence, large forest areas and forest fragments were forcibly protected as ‘islands’ along with a technocratic management agenda (Chape et al. 2008). Due to this protection, communities who had used forest lands for millennia, much before the Industrial Era, were prevented from extracting forest produce, which could endanger their livelihoods and survival (Barrow & Fabricius 2002, Sekhar 2003, Brockington & Igoe 2006, Okech 2011). This application of IBT concepts to terrestrial habitats also influenced much of the research in the 1990s and 2000s on the effects of forest fragmentation (Laurance 2008). Results from these studies often contradicted the predictions of IBT. For example, several studies found that even small forest fragments and the supposedly ‘inhospitable’ matrix (i.e., intervening human-use areas, such as intensively cultivated agricultural lands) harbored a similar number of species as a large forest area, in part because these habitats were used by species previously thought to be restricted to large forests (Daily et al. 2001, Mendenhall et al. 2013).

These scientific findings, coupled with recognition of the alienation of human communities from ancestral forest land, resulted in the need for new conceptual frameworks in both applied and theoretical aspects of land use. In the applied aspect of land use, two debates emerged. The “land sharing vs. land sparing debate” was centered on the allocation of land for meeting the needs of both biodiversity conservation and agriculture (Fischer et al. 2014). The other debate which emerged was on decisions surrounding the size of protected areas (Fischer et al. 2014). This is known as the “Single Large (SL) or Several Small (SS)” or the “SLOSS” debate (Tjørve 2010, Fischer et al. 2014). In terms of the theory underlying land use effects, a revised IBT framework to study terrestrial ecosystems emerged, this was termed “countryside biogeography” (Daily et al. 2001). Along with this revised framework was the emergence of “landscape ecology” which represented a shift in focus from studying species only within the confines of a forest to the whole landscape in which the forest was situated (Daily et al. 2001, Fahrig 2003).

Rationale for the “land sharing vs. land sparing” debate has important implications for understanding the conservation implications of forest fragmentation. The ‘land sharing’ aspect of the debate proposes that the needs of biodiversity conservation and food production be met on the same piece of land through methods such as organic farming, whereas ‘land sparing’ proposes that these needs compete and so must be met on two different pieces of land, such as separating land used for intensive farming and protected areas (Phalan et al. 2014, Kremen 2015). Synthesis of the available literature on agricultural productivity so far supports ‘land sparing’ over ‘land sharing’, although members of the scientific community suggest that no one point of view is completely correct (Phalan et al. 2011, Kremen 2015). Although ‘land sharing’ might aid in resolving two conflicting needs, ‘land sparing’, with separate areas allotted for conservation and intensive agriculture, might be better for species-focussed conservation - especially of animals requiring large continuous forests (Grau et al. 2013). This debate, then, leads to further questions about how large and how continuous a forest should be to meet the conservation needs of a species, and where in the landscape should we “spare” or “share” lands. Such questions draw from the much earlier “SLOSS” debate.

The Single Large or Several Small (SLOSS) debate began when studies showed that two smaller pieces of forest with different species could result in protecting a greater number of different

species than a single large forest (Simberloff and Abele 1982, Wilcox and Murphy 1985, Baz and Garcia-Boyero 1995, Ovaskainen 2002, Tjørve 2010). As an outcome, this debate moved the focus from the number of species in a forest fragment to the total number of species in an entire fragmented landscape, although, still often not including the role of the matrix (Tjørve 2010). Additionally, this debate highlighted the need to understand the response of a species to its physical environment or habitat to decide on the size of the forest to be protected (Tjørve 2010). Ultimately, this debate informed a recent and controversial synthesis by Farhig et al. (2017) on the effects of ‘habitat fragmentation *per se*’. According to Farhig (2003), ‘habitat fragmentation *per se*’ is the difference in configuration (or spatial pattern) between habitat patches when controlled for the effects of habitat loss. These effects of fragmentation include the decrease in size of habitat patches, formation of a greater number of habitat patches and escalation in isolation distance between patches (Farhig 2003). Her synthesis of studies measuring only the effects of habitat fragmentation *per se* on the biodiversity metric of species richness concluded that there is either no effect or a positive effect of habitat fragmentation *per se* on species richness (Farhig 2017). However, her synthesis did not distinguish between invasive and non-native species or provide information about the geographical locations of the areas where these studies have been conducted (Farhig 2017, Fletcher et al. 2018a, Farhig et al. 2019). A more species-centered framework for fragmented landscapes is instead provided by ‘countryside biogeography’.

‘Countryside biogeography’ is a conceptual framework proposed by Daily et al. (2001) as a result of their studies in both forest and agricultural landscapes in Costa Rica. In a seminal study, Daily et al. (2001) assessed bird species richness in horticultural plantations and native forest of the Coto Brus area in Puntarenas province, in Southern Costa Rica. Their results showed that nearly 96% of the species occurred in both areas (Daily et al. 2001, Mendenhall et al. 2013). This finding led to investigations of other taxa in the same region, which found similar patterns (Mendenhall et al. 2013). These multi-taxa studies in Coto Brus, agreed with studies conducted in various other regions, such as Australia, Mexico, and India, in showing that agricultural landscapes can contain species previously thought to be solely forest dwelling (Mendenhall et al. 2013). The resultant “countryside biogeography” framework recommends that species conservation must be based on an understanding of how the physical environment determines an organism’s persistence and

dispersal, coupled with knowledge of the functional role of an organism within the ecological community (Mendenhall et al. 2013).

The ideas within ‘countryside biogeography’ are influenced by those of metapopulation theory and metacommunity theory (Hanski and Ovaskainen 2003, Leibold and Chase 2018). Both these theories highlight the importance of dispersal in linking populations and communities, and thus indirectly consider the role of the matrix in influencing colonization and extinction rates. (Leibold and Chase 2018). Dispersal is defined as a once-in-a-lifetime movement of organisms or propagules (Guzman et al. 2019). It often stabilizes populations through rescue effects or by resulting in spatiotemporal refuges from predation and can aid in maintenance of genetic diversity (Guzman et al. 2019). Matrix habitats and level of connectivity between habitats determine the extent to which dispersal is facilitated (Leibold and Chase 2018). Dispersal is distinguished from other types of movement such as foraging (much more frequent timescales) and migration (seasonal movements to and from different localities) (Guzman et al. 2019).

In summary, the major theoretical frameworks about the effects of land use on biodiversity highlight the need to empirically understand the environmental requirements of organisms, to consider the environment at multiple scales, especially the landscape scale, and to base studies within the context of managerial decisions.

History of forest fragmentation and recent forest conservation in Costa Rica

In the 1960s, the Costa Rican Government incentivised cattle ranching to support the beef processing industry in the United States (Arroyo-Mora et al. 2005, Stan and Sanchez-Azofeifa 2019). Large swathes of forest were burnt to create space for grass pastures (Arroyo-Mora et al. 2005, Stan and Sanchez-Azofeifa 2019). This resulted in Costa Rica having one of the highest deforestation rates in the world at the time (Kappelle et al. 2016, Stan and Sanchez-Azofeifa 2019). The province of Guanacaste was the main centre of this cattle-related deforestation, contributing to over 40% of Costa Rica's cattle production at the expense of high levels of deforestation in this province (Stan and Sanchez-Azofeifa 2019). A quantitative analysis of forest cover of Costa Rica from 1986-1991 found that there were only 80 forest fragments with an area greater than 5 sq. km, as compared to 7134 forest fragments within the sizes of 0.03 sq. km and 0.5 sq. km (Sanchez-Azofeifa et al. 2001).

In the 1980s, however, beef prices dropped, leading to a decrease in cattle demand (Stan and Sanchez-Azofeifa 2019). Additionally, the Costa Rican Government recognised the need for environmental conservation and adopted measures to initiate reforestation and payment for ecosystem services (Aichilex 1996, Stan and Sanchez-Azofeifa 2019). Some of these measures include tax deductions for reforestation, 2% interest commercial loans or funds for reforestation, permission for trees to be used as collateral and provision of certificates for forest protection and management (Aichilex 1996, Stan and Sanchez-Azofeifa 2019). Today, with these measures in place, Costa Rica has formally designated protected status to 27.6% of its forest cover, comparable to levels of forest protection of its immediate neighbours Nicaragua (37.2%) and Panama (20.9%), and substantially above many other countries (Worldbank 2018).

As part of these measures provided by the Costa Rican Government, a large portion of the province of Guanacaste is part of an *Área de Conservación* (Janzen 2018). Costa Rica has eleven conservation areas, each of which consists of a mixture of protected and human-use areas that collectively advance conservation and sustainable use goals through co-operative agreements between government, NGOs and private companies. As such, this system has elements of both land sharing and land sparing. The *Área de Conservación Guanacaste* (ACG) is a 163,000-ha conservation zone and an UNESCO World heritage site located near the Costa Rica-Nicaragua

border. It comprises of both terrestrial and marine zones which fall within various categories of protected areas as established by the IUCN (Janzen 2018). The terrestrial conservation area comprises three main forest types: the unique and threatened dry forests, wet forests, and cloud forests (Pringle 2017). Many wet forest areas of Guanacaste are mostly remnants formed as a result of forest conversion to pastures. They remain discontinuous with matrices of agricultural fields, settlements and roads separating them (Fig. 1.1).

Rationale for present study and rationale for choice of study area

The effects of forest fragmentation have been studied across the Neotropics. Vetter et al. (2010), in a quantitative synthesis of 30 studies conducted in the Neotropics, stated that fragmentation *per se* never occurs in the Neotropics and fragmentation always results in habitat loss, implying the effect of habitat loss cannot be excluded, contrary to the recommendations by Farhig et al. (2003). Their synthesis reported that species differentiated based on feeding guilds, and on body sizes, respond both positively and negatively to forest fragmentation (Vetter et al. 2011). For example, in the dry forests of Guanacaste Province in north-west Costa Rica, Barrantes et al. (2016) found bird species richness was unaffected by both forest size and distance between forests, but both species assemblages and changed in a nested structure, that is with the composition in small fragments being a subset of that in larger fragments. Such results speak to the need to examine if species in a fragmented landscape differ in their responses to fragmentation and to study aspects of species composition, rather than richness alone. These empirical results complement the recommendation by Vetter et al. (2010) that studies in the Neotropics be conducted in the regional scale due to differences in forest types and vegetation structure, and suggest that theoretical frameworks for understanding forest fragmentation must consider differences between species in their use of the environment and should be multi-scale in nature, forming the conceptual basis of this study.

My study determines the relative importance of habitat characteristics at different spatial scales (i.e extent in terms of area) that best predict the attributes of a Neotropical vertebrate community. I conducted my study in the wet forests covering the north and north-eastern slopes of Volcan Orosi, Área de Conservación (ACG). This is the first study using extensive camera trap captures of ground-dwelling vertebrates in the wet forests of this famous conservation area. We define habitat predictors as environmental conditions which reflect species preferences for using an area and thereby community distribution patterns. We use camera traps (Fig. 1.4-1.5) to document ground-dwelling vertebrates (restricted here to mammals and birds). This method is both non-invasive and is capable of collecting a large, standardized number of observations throughout both day and the night (Burton et al. 2015). We evaluate the importance of habitat characteristics measured at three spatial scales, at the level of a camera trap point (defined in chapter 2, but within 3m of the camera trap, in all directions; Fig. 1.2-1.3), forest (defined in chapter 2, but essentially

the forest fragment or equivalent subset of intact forest) and landscape scales (up to 2km from the camera trap, Fig. 1.1).

Our rationale in examining habitat predictors at multiple spatial scales is as follows. Habitat at large spatial scales affects population-scale mechanisms such as carrying capacity, dispersal and rescue effects, whereas habitat at smaller spatial scales affects individual-scale behavioural decisions about habitat selection for activities such as foraging, sleeping, basking, resource acquisition and predator avoidance (D.H. Johnson 1980, Fisher et al. 2011, Toews et al. 2017, Guzman et al. 2019). All of these processes may be relevant in determining the number of individuals and species that pass in front of a camera trap (Hofmeester et al. 2018).

We relate our methods to theories about the effects of habitat fragmentation as follows. The main predictions of island biogeography theory are that larger and more connected areas will have higher species richness than smaller and more isolated areas. We test this by relating community species richness, as well as the richness within specific feeding guilds, to habitat characteristics of forest size, total forest area and proximity index (as measure of isolation between forest fragments). Metacommunity theory highlights that different components of the community can differ in the relative sensitivity to regional dispersal and local processes (e.g. predator avoidance, resource availability) (Leibold and Chase 2018). We test this by relating differences between feeding guilds to proximity index and matrix type, and also three predictors related to predator avoidance: distance of forest from road (which is a covariate of human hunting pressure) (Prokopenko et al. 2017), extent of visibility (Hannon et al. 2006) and undergrowth density around a camera trap point. Finally, ‘countryside biogeography’ highlights the importance of the matrix in promoting safe dispersal to a new habitat forest, in migration and acting as alternate habitats for foraging ecological communities, through providing alternate food resources such as fruits in orange and coffee plantations (Daily et al. 2001). This theory led us to consider whether plantations and pasture differed in their impact on the species in adjacent forest fragments.

Our response variables were also informed by three competing rationales for vertebrate conservation: to maximize representation of biodiversity, to conserve particular species at risk, or to ensure a broad range of ecological functional groups. Humans value biodiversity for its value as biological heritage, and many vertebrates are perceived to be highly charismatic (Albert et al.

2018). Such values provide a rationale for conservation. Here we examined overall species richness, as well as species richness partitioned by taxonomy and body size. Alternatively, conservation can prioritize providing habitat for species at risk. Local extinctions of vertebrate species can lead to changes in the rest of food webs (Crooks and Soule 1999, Buchmann et al. 2013, Jorge et al. 2013, Tee et al. 2018), and loss of key sources of food and income for local people (Robinson 2000, Suarez and Zapata-Ríos 2019, Wilkie et al. 2019). Here we examined IUCN threat status of species to relate to this objective. Finally, vertebrates perform important ecological functions in communities, such as herbivore control (Ahumada et al. 2011, Rees et al. 2017) and seed dispersal (Şekercioğlu et al. 2004, Ahumada et al. 2011, Lacher et al. 2019). Here we represent the functional role of species by classifying them based on feeding guilds, such as omnivores, carnivores and herbivores. In recognition of the role of species in higher trophic levels, we also include the highest trophic levels as a response variable.

Fig. 1.1 Study area with study forests in red and other fragments included in calculating various landscape metrics in blue. Large green area with clouds is forest around the Volcan Orosi, Área de Conservación Guanacaste (ACG), Guanacaste Province, Costa Rica (Inset map).

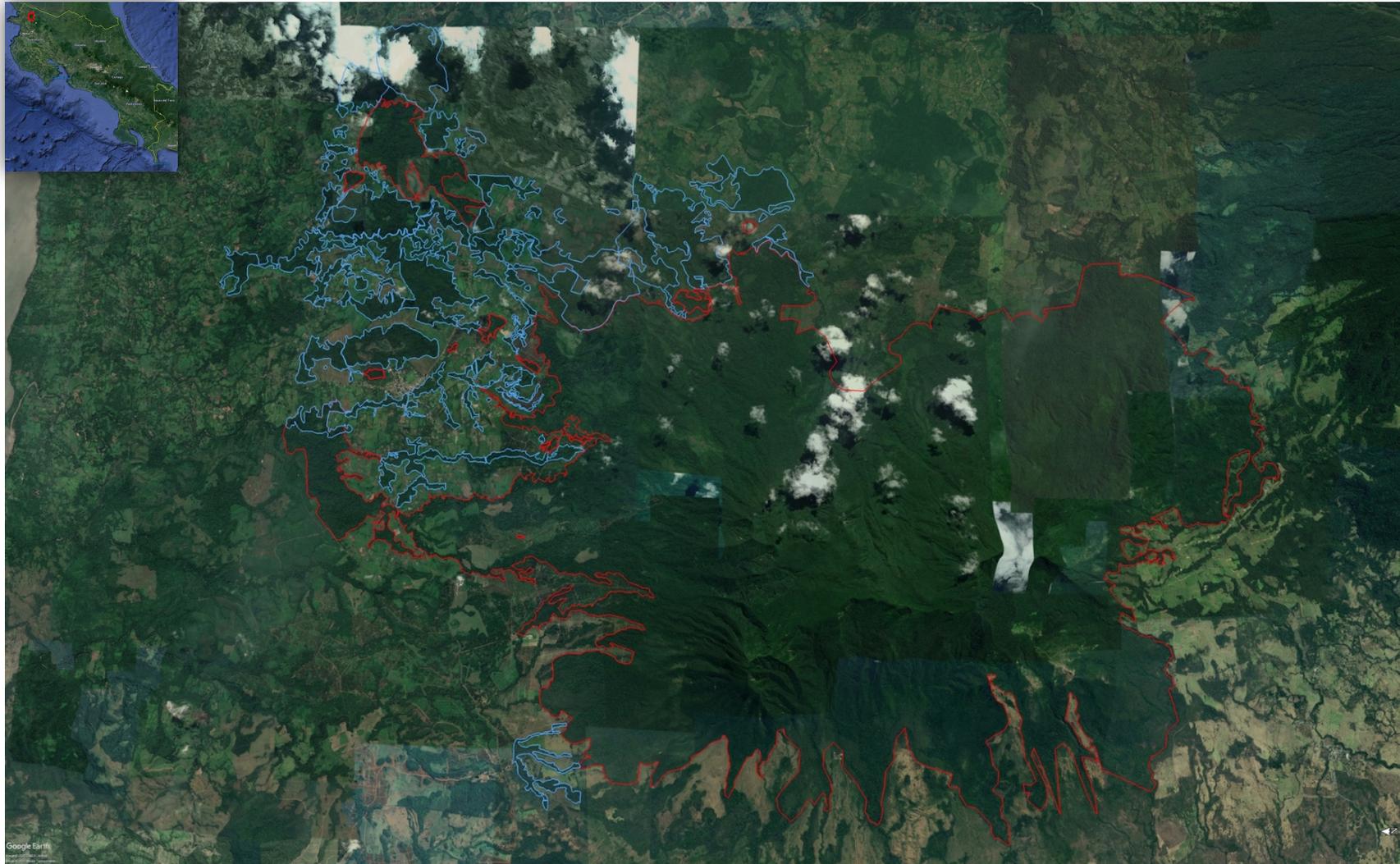


Fig. 1.2. Images of vegetation within study forests used in quantifying point-scale variables of extent of visibility, understory density and number of big trees around a camera trap point. Top left: Small fragment with liana growth and dense understory; Top Right: Large fragment, dense understory. Bottom Left: Large fragment, medium understory. Bottom Right: Continuous forest, open understory.



Fig. 1.3. An image showing a photograph of canopy cover, another variable measured at the scale of the camera trap point.



Fig. 1.4. Photograph of researcher standing at 2m distance from camera trap collecting vegetation data with 3m area in front of camera trap cleared. This camera trap was placed in a large fragment.



Fig. 1.5. Tapir recorded at the same trap as above image. This was the only record of a tapir using a fragment in the period of our study.



CHAPTER 2

Habitat predictors of vertebrate community in a fragmented neotropical forest landscape.

Introduction

The transformation of a continuous forest landscape into one with smaller, discontinuous patches of forest surrounded by a matrix is ‘forest fragmentation’ (Fahrig 2003, Wade et al. 2003, Haddad et al. 2015). Forest fragmentation is always a by-product of forest loss (Fahrig 2003). The effects of fragmentation *per se*, however, are independent of loss (Fahrig 2003, Wade et al. 2003, Haddad et al. 2015). Forest loss and fragmentation threaten many species with extinction (Vetter et al. 2011, Fahrig 2017, Pfeifer et al. 2017, Fletcher et al. 2018b, Zungu et al. 2020). Extinction or population extirpation of some vertebrates may be brought about by such landscape changes (Zamzow et al. 2018), specifically by negatively affecting various biological processes such as energy acquisition, predator avoidance, mating and dispersal (Peacock and Smith 1997, Smith et al. 2017c, Wang et al. 2017, Tucker et al. 2018) or by simply isolating and removing suitable habitat and reducing animal populations to such low numbers that they are highly sensitive to stochastic effects and local extinction (Burbidge and McKenzie 1989). These negative effects of fragmentation have previously been linked to the concomitant reductions in habitat area, increases in the distance between fragments, increases in amount of impenetrable edges and increases in exposure to human activities such as hunting and farming (Fuentes-Montemayor et al. 2009, Tucker et al. 2018, Zamzow et al. 2018). For example, the extirpation of forest birds and mammals from small, isolated fragments is in part due to the behavioural reluctance of these species to travel across deforested or disturbed areas (Laurance et al. 2002, Zamzow et al. 2018). Other forest species are more tolerant of open areas and human-modified landscapes; such species may be less affected by fragmentation (Vetter et al. 2011).

Currently, 70% of Earth’s forests are within 1km of a forest edge (Haddad et al. 2015). Forests in the tropics are expected to undergo high levels of deforestation and land-use change in the coming century (Laurance et al. 2014). It has been argued that species in the tropics are particularly sensitive to such anthropogenic disturbances as compared to temperate species (Vetter et al. 2011, Betts et al. 2019). The rationale here is that the sensitivity of species to large-scale disturbances (e.g., wildfires or glaciation) reflects the historical (evolutionary) exposure of those species to such

disturbances, and the tropical species pool has been less filtered by such effects (Vetter et al. 2011, Betts et al. 2019).

The effects of forest fragmentation on vertebrate populations may extend beyond the direct loss of biodiversity. In tropical forests, not unlike forests globally, vertebrates occupy multiple trophic levels and perform essential ecosystem functions (Ahumada et al. 2011). For example, apex predators play significant roles in herbivore control (Ahumada et al. 2011, Rees et al. 2017) and many other mesopredator and herbivore species act as seed dispersers (Şekercioğlu et al. 2004, Ahumada et al. 2011, Lacher et al. 2019). Loss of vertebrates can lead to cascading effects through food webs (Crooks and Soule 1999, Buchmann et al. 2013, Jorge et al. 2013, Tee et al. 2018), and reductions in ecosystem functioning (Lacher et al. 2019). Furthermore, loss of certain vertebrate species can lead to losses in cultural value, as many humans find certain species to be highly charismatic (Albert et al. 2018). Additionally, there is an economic value to this biodiversity, as vertebrates are key sources of food for sustenance and income for many communities (Robinson 2000, Suarez and Zapata-Ríos 2019, Wilkie et al. 2019). The ecological functions that species perform, and the values placed on them by humans, provide differing rationales to conserve vertebrates. Therefore, different aspects of the vertebrate community (e.g., species richness, threat status, ecological function) may be prioritized when considering the effects of forest fragmentation.

Vertebrate species have different habitat resource requirements, predation vulnerabilities and dispersal capabilities (Ahumada et al. 2011). Also, species in a vertebrate community can be characterized and grouped in terms of trophic functions and structure, significance to conservation and biodiversity, and community composition in terms of body mass and taxonomy. We would therefore expect that species, with the different functions they perform and biological groupings they belong to, may differ in how they respond to changes in habitat at different spatial scales (Johnson 1980, Fahrig 2017, Smith et al. 2017a). In general, spatial variation in the habitat at large scales, i.e., at the landscape scale, should affect the vertebrate community through metapopulation processes, such as dispersal (Guzman et al. 2019), whereas smaller-scale habitat structure should affect animals through individual behaviours (e.g., foraging and movement; Guzman et al. 2019).

Thus, in an ~17000 ha (170 sq. km.) area composed of forest remnants separated by human-use areas, we identify habitat characteristics acting as predictors for patterns in vertebrate community. The remnants in our study area were created as a result of burning and clearing tropical wet forests between 300-400m AMSL for cattle farming in the 1960s in Costa Rica (Kappelle 2016, Holdridge 1947). We expect animal responses to vary depending on the ability of the animal to move, forage, detect predators, disperse and survive. We expect these responses to vary at three spatial scales of habitat structure, i.e., point, forest and landscape. At the “point” scale, the habitat is as an area of up to 9m from a camera trap with a horizontal and vertical field of view of 90 and 70 degrees respectively, measured using photographs; at the “forest” scale, it is both field and satellite-imagery based measures of the forest in which the camera is embedded with sampled forest areas ranging between 0.5-27ha and at the “landscape” scale, it only satellite based measures of both forest and matrix habitats covering an area of 78-1256ha.

At the landscape scale, species persistence is predicted by theory to be related to the area of available habitat, the level of connectivity between habitat forests and the ability of matrix habitat to provide resources (Kupfer et al. 2006). For example, species richness generally increases with the size and connectedness of fragments, as predicted by island biogeography theory (Kupfer et al. 2006, Mendenhall et al. 2014). Island biogeography theory is a seminal theory in landscape ecology that assumes species richness in an island or forest is a dynamic equilibrium between species colonisation and species extinction (MacArthur and Wilson 1967). Metapopulation theory uses similar logic to predict that species with high energetic requirements (e.g. large apex predators) can only persist in either large patches or by foraging over multiple highly-connected patches. However, such theory does not account for matrix quality between fragments, which can increase occupancy through the provision of resources or increasing the effective connectedness of populations (Prugh et al. 2009). The concept of countryside biogeography argues that matrix quality can play a key role in determining species presence even within small forest fragments (Mendenhall et al. 2013). In our study, plantation is structurally more similar to native forests than is pasture, and is therefore likely a higher quality matrix. According to metacommunity theory, the level of habitat connectivity in combination with species interactions determine community diversity and structure (Chisholm et al. 2011, Leibold and Chase 2018). Community structure refers to composition of species in terms of the trophic levels they represent and the functions they

perform (Raffaelli and Hall 1996). Specifically, dispersal between patches can help maintain the interacting populations that compose communities due to gene flow, rescue effects and source-sink dynamics, although in theory too much dispersal could remove the spatiotemporal refuges that can stabilize both predator-prey and competitive dynamics (Leibold and Chase 2018). At the landscape scale, therefore, food web complexity tends to increase with observed levels of connectivity (LeCraw et al. 2014).

At the forest scale, the abundance of a species is affected by area of the forest, forest quality including habitat type and resource availability, and proximity of the forest to human activity such as distance to a road (Nelson et al. 2012, Matthews et al. 2014). Reductions in forest area can result in bottom-up effects on food webs through reduced availability of specific resources and therefore fewer specialized consumers within the forest (Cagnolo et al. 2009, Matthews et al. 2014). Reductions in forest area can also result in top-down effects when apex predators are unable to maintain viable populations because of large home range requirements (Sreekar et al. 2015). The decline of apex predators may subsequently lead to increases in mesopredators or herbivores (Crooks and Soule 1999, Duca et al. 2006). Forest characteristics, such as the proximity to roads, affect the accessibility for hunters – who often target apex predators and large-bodied prey, again perturbing the food web (Michalski and Peres 2007, Suarez and Zapata-Ríos 2019).

At the scale of a camera trap point, the distribution of ground-dwelling vertebrates is affected by habitat structure, more specifically the response of individual animals to spatial heterogeneity in habitat structural features such as understory density, extent of visibility, number of large trees within the forest and canopy cover. These habitat variables can aid in determining individual preferences for forest use (Laurance 2008). Dense understory cover can prevent large animals from moving effectively within the forest, reducing predation pressure from large-bodied predators and aiding persistence of smaller animals within the forest. By contrast, predators can often see further and move more freely in forests with many large trees and higher visibility in the understory, because of the gaps between trees (Laurance 2008, Smith et al. 2017b).

Few studies of Neotropical vertebrates have included both forest- and landscape-scale predictors (Vetter et al. 2011). Some of the landscape-scale studies include those testing countryside

biogeography theory from the Coto Brus region of Puntarenas Province in Southern Costa Rica (Daily et al. 2010, Mendenhall et al. 2013). However, to our knowledge, there are presently no studies examining the effect of fragmentation on the ground-dwelling vertebrate communities of the wet forests in and around ACG, and only one study has examined bird communities in the dry forests of this region (Barrantes et al. 2016). This data gap, as well as understanding if we observe similar patterns as those documented in other parts of Costa Rica, provide part of our rationale to conduct this study. The other aspect lies in the choice of study area. Costa Rica is considered to contain 4% of the world's biodiversity (Kohlmann et al. 2007). With 27% of its land area under protection, it is also considered a country which has successfully mainstreamed biodiversity conservation through various economic incentives (Huntley 2014, Whitehorn et al. 2019). Still, much of its forests remain fragmented as a result of converting forests into cattle pastures in the 1960s, existing as disconnected forests surrounded by matrix habitat with various types and levels of human-activity (Barrantes et al. 2016). In the 1960s, Guanacaste province represented 40% of Costa Rica's cattle industry while experiencing high levels of deforestation within its dry and wet forests (Stan and Sanchez-Azofeifa 2019). However, a few decades later Costa Rica created one of the most lauded conservation areas in the world in this province, the Área de Conservación Guanacaste (ACG) (Pringle 2017, Janzen 2018). This conservation area presently protects a substantial portion of the forests in Guanacaste, although swathes of its wet forests still remain in discontinuous fragments (Barrantes et al. 2016, Pringle 2017, Janzen 2018). In order to inform vertebrate conservation action in this fragmented landscape, it is essential to understand if and how the change in habitat structure due to fragmentation affects the vertebrate community. Thus, conducting this study in the Guanacaste province of Costa Rica can provide baseline data to support long-term monitoring and on-the-ground conservation and offer comparisons to other regions of the country.

We predict that habitat characteristics at all three spatial scales (landscape, forest, point) will be important determinants of the vertebrate community, as at each scale we have hypotheses based in ecological theory that link specific habitat characteristics with specific aspects of the vertebrate community. In particular, we tested the following hypotheses, proceeding from the landscape to forest to point scale:

- (1) Based on metacommunity theory, we would expect connectivity measures to affect the number of species and trophic levels. Specifically, we hypothesise that landscape scale measures of connectivity (proximity of neighbouring forests, matrix permeability) can affect the dispersal of species and therefore metacommunity persistence. We predict that highly-connected forests and forests surrounded by a tree-like matrix to have greater species richness and more species occurring in higher trophic levels as these two conditions will facilitate dispersal through provision of resources and refuge. We also predict that species which have higher tolerance for human activity and human-modified areas will be unaffected by measures of connectivity as their dependence on specialised forest habitats or resources will be lower.
- (2) Based on island biogeography theory, we hypothesise that landscape and forest scale measures of forest area and connectivity affect species richness through altering colonization (both area and connectivity) and extinction (just area) rates. We expect species richness to be higher in larger and more connected forest remnants.
- (3) Metapopulation theory suggests that the amount of forest area, both of the forest remnant (forest scale) as well as in the surrounding landscape (landscape scale) will particularly limit the presence of large, high trophic level species as such species energetically require a greater prey base and therefore often have large home ranges. We also predict that species with traits associated with extinction risk (categorised within the IUCN threatened categories) will be restricted to larger forest areas as these species are often forest specialists with low tolerance of human activity.
- (4) At the forest scale, the proximity of the forests to roads can affect the presence of large-bodied species as it increases access for human hunters. As hunters focus on large species (e.g. deer), including those at risk (e.g. tapir, currasow), we would expect such species to be fewer in forests closer to roads.
- (5) At the forest and point scale, the size and density of trees has the potential to affect species through impacts on herbaceous food resources. Higher tree density can increase shade cover, lowering amount of available sunlight to support understory food sources, thereby lowering the number of herbivores species which occur within such forests.

- (6) At the point scale, the vegetation in the immediate vicinity of the camera trap point can affect the ability of species to move, hunt or hide. We predict denser vegetation (both understory and trees) near a camera trap to negatively affect larger-bodied species whose maneuverability within the forest will be hampered. By contrast, smaller mammals may seek denser vegetation to provide refugia from predators and to forage.

Methods

Study Area and Forests

We collected data on vertebrates using camera traps from the end of October 2018 to April 2019 in forests within and around the Área de Conservación Guanacaste (ACG) in north-west Costa Rica (Fig. 2.1). Our 170 km² study area also incorporates the town of Santa Cecilia, Guanacaste (Fig. 2.1). This study area is presently composed of unmanaged forests of different sizes, commercial orange and teak plantations, subsistence cultivation, human settlements and ACG (Fig. 2.1). The forests in this study area are classified in the Holdridge life zone system (Holdridge 1947) as tropical wet forest transitioning to premontane wet forest. We chose 19 forests within the study area to represent both continuous forests (eight forest areas >350ha) and fragments (large fragments (seven forests of 5-27ha) and small fragments (four forests of 0.5-3ha)) (Fig. 2.1, Table 2.1). These forests were chosen from a pool of potential sites such that the range of elevations (constrained to 300–400 m) was balanced across forest categories and there was minimal correlation between forest category and either latitude or longitude (Cuke and Srivastava 2016) (Fig. 2.1, Table 2.1). Human pressure on the landscape has increased significantly over the last thirty years, including the development of both industrial and subsistence agriculture, road-building and increases in resident and migrant populations (D. Srivastava pers. comm.). Within each forest we established a smaller ‘sample area’, defined as the area within the forest available to setup the camera traps. In forest fragments, the sample area was the area of the fragment with an 8m inner buffer from the forest edge, as these first few meters were typically impenetrable with liana growth. In continuous forests, the sample area was 150m from the nearest road to avoid edge effects (Laurance 2000, Laurance et al. 2002), and 4.38 ha in extent to approximate the sample area of an intermediate-sized fragment. This enabled us to ensure that any difference between intact forest and fragmented forest in the number of species recorded was due to differences in the forest rather than in the distance between camera traps. We chose to only use an 8m inner buffer for fragments as opposed to 150m used in continuous forests due to size constraints posed by fragments.

To account for seasonal variability in our sampling, our camera traps were active during both the dry and wet seasons as well as the transition between them (Janzen 2018). Our first sampling period (43-day duration, wet season) began at the end of October and lasted until mid-December, the second sampling period (50-day duration, transition to dry season) started at mid-December

and lasted until mid-February and the third sampling period (53-day duration, dry season) started in mid-February and lasted until mid-April.

Field Methods

We collected information on terrestrial vertebrates within each of the 19 forests using Reconyx HC500 camera traps installed at ~50cm from the ground level. We deployed two camera traps at each site per each sampling period. We standardised the internal camera settings following the protocol of the Tropical Ecology Monitoring (TEAM) network (Motion sensor-ON, Sensitivity-high, No. of photos per trigger-3, Date/time-Current data/time, temperature in °C, resolution- high, user label – “First three letters of sampling month-Site ID-Camera No.”). We followed the deployment procedure of the Tropical Ecology Assessment and Monitoring network (Team Network 2011, Ahumada et al. 2011, 2013, Beaudrot et al. 2016, Rovero and Ahumada 2017) with a few modifications. We used a stratified random sampling approach in which we sampled in two opposite sections of the study forest. This procedure ensured that camera traps were not spatially clustered. To ensure spread of sampling locations, we generated sixteen random points with a minimum of 10m distance between two points in each forest using QGIS (v3.14. Madeira). We chose the minimum distance of 10m due to the size constraint posed by the smallest fragment which has a size of 0.5ha. We chose two points per sampling period such that both of them were on opposite sides and opposite quadrants of the sampling areas; these two points ended up being at least 30m apart. Measurements of distances between the two points in each forest in all the sampling periods is provided in Appendix Table A.7. We manually transferred chosen points into the GPS prior to fieldwork. Within 20m of each random point, we selected a tree with at least two meters of unobstructed ground in front of it and at least 5m from a stream or river. Cameras were placed in theftproof metal cases, then attached to trees with rope ~50 cm above the ground, and secured with a cable lock. We used lithium-ion batteries in all camera traps to ensure durability. We retrieved and changed the location of camera traps at the end of each sampling period. This design allowed us to sample six different locations within each forest, ensuring better spatial coverage than two fixed camera traps. As this necessarily confounds season and camera trap point, we included season as a random effect (i.e. a temporal block) in our models. Of the total 114 deployments of camera traps, 104 deployments successfully captured images for the entire sampling period. In the remaining 10 deployments there was a malfunction in the camera traps,

which resulted in little information being collected, and these are not included in the analysis. The number of trap nights for each camera trap was trimmed from the beginning of the deployment so that exactly 43, 50 and 53 trap nights were obtained from each camera trap for the first, second and third sampling periods, respectively. We chose to trim the data rather than account for variation in the model as we used Chao estimates of species richness as a response variable which requires equal sampling in one period. In terms of total sample effort, our study collected data for 5053 trap-nights (1548, 1650, 1855 trap nights in 36, 33 and 35 camera traps for first, second and third sampling periods respectively). Detailed information on camera trap setup, retrieval and data processing is provided in Appendix 1.1 and 1.2. We conducted all spatial analysis using Google Earth v7.3.2.5776 Satellite Imagery (Gorelick et al. 2017) and QGIS (v3.14. Madeira).

In addition to deploying camera traps, we also collected habitat information, at both the point and forest scale, to act as predictors for understanding spatial variation in the vertebrate community. At the point scale, this information included photographs of the canopy directly overhead (for quantifying canopy cover) as well as the forest in four orthogonal directions (for metrics of vegetation structure) (Appendix Fig. A.1) (Cruz et al. 2018). Both canopy and vegetation photographs were collected using a Mi Xiaomi phone (Model No. Redmi 4-MAI132) at a distance of 2m from the camera trap (Appendix Fig. A. 1). We shot all the canopy photographs by holding the phone parallel to the ground at a height of ~180cm and forest photographs by holding the phone at an angle which allowed for capturing 50% ground and 50% vegetation at a height of ~170cm (Appendix. Fig. A. 1). At the level of sample area within a forest (Fig. 2.1), we measured tree density by ordered distance sampling (Krebs 2014), recording the distance from a point to the third closest tree for each of ten random points along a 200m transect. We also recorded the diameters of the three closest trees at each of these ten random points.

Response variables and predictors

Our camera traps recorded photographs of mammals and birds during both the day (natural light) and night (infrared flash). Mammals and birds were identified based on descriptions and checklists (Wainwright and Arias 2007, Garrigues & Dean 2014, Janzen 2018). When identification was difficult, we sought advice from naturalists knowledgeable on the fauna of this region or the animal was only classified at the genus level. Rats, most likely of the genus *Proechimys* or *Hoplomys*,

were grouped as ‘large rats’ as even genus level identification was not possible from photographs. Among the birds detected, we only included curassows (*Crax rubra*), crested guans (*Penelope purpurascens*) and tinamous (*Tinamus major* and *Crypturellus boucardi*) in our analysis, as these are either ground-dwelling species or larger sized birds which are reliably recorded with a camera trap (Garrigues & Dean 2014). Photographic captures of humans, dogs, one species of reptile and birds other than ground-dwelling birds were discarded prior to calculations. Two types of mammals, one resembling an agouti (three captures) and the other a squirrel (one capture), were unidentifiable and were excluded from the analysis; this exclusion is insignificant compared with the thousands of captures for each camera trap.

We calculated 13 descriptors of vertebrate community structure based on the vertebrate species captured by each camera trap (Appendix Table A.2.). All the 13 response variables were calculated at the level of a single camera trap point deployed within one sample period. The response variables were selected to act as measures of trophic structure, community composition and conservation significance. Measures of trophic structure included the maximum trophic level of any species captured (Appendix Fig. A.6) and Chao estimates (Colwell and Elsensohn 2014) of herbivore, carnivore and omnivore richness. Measures of community composition included total number of encounters as well as number of encounters of large vs. medium vs. small mammals and ground-dwelling birds. We calculated the five measures of community composition based on the assumption that detectability is similar across species/groups and that the number of encounters is directly proportional to density. We define an encounter as a continuous (<2 minutes apart) photographic capture of a species. We defined large mammals as those with average body length > 100cm, medium 60-99cm, and small <60 cm (Appendix Table A.1 and Table A.8). Measures of conservation significance included Chao estimates of total species richness, highest IUCN Red List category (EN-Endangered, VU-Vulnerable and NT-Near Threatened) and maximum body length. We included species richness as a measure of conservation significance as local biodiversity is often used as a proxy for conservation value (Hillebrand et al. 2018). We also included body length as a measure relevant to conservation as large-bodied species are known to be more prone to extinction (Cardillo et al. 2000) and may be prioritized by the public as “charismatic megafauna”. Also relevant to conservation was the percentage of species that are classified as human-modified landscape (HML) users, which should be least vulnerable to

anthropogenic activity. We classified species as HML users when ‘Artificial/Terrestrial’ was included in the ‘Habitat/Ecology’ section of the IUCN Redlist for the species. Further explanation of methods for calculation of each response variable and sources for species attributes are provided in Appendix 2 & Appendix Table A. 1-2, 8-10.

Also, we classified predators as animals with a trophic value greater than or equal to 3.6 (Appendix Table A.1). Therefore, predatory carnivores in our study include tayra (*Eira Barbara*), great grison (*Galictis vittata*), jaguarundi (*Herpailurus jaguarundi*), ocelot (*Leopardus pardalis*), margay (*Leopardus weidii*), jaguar (*Panthera onca*) and puma (*Puma concolor*) while predatory omnivores in our study include coyote (*Canis latrans*), capuchin monkey (*Cebus capucinus*), striped hog nosed skunk (*Conepatus semistriatus*), currasow (*Crax rubra*), common opossum (*Didelphis marsupialis*), brown four-eyed opossum (*Metachirus nudicaudatus*), gray four-eyed opossum (*Philander opossum*), white-nosed coati (*Nasua narica*), raccoon (*Procyon lotor*) and crested guan (*Penelopina purpurescens*). Lower trophic level omnivores include white-lipped peccary (*Tayassu pecari*) and collared peccary (*Pecari tajacu*) (Appendix Table A. 1). Small mammals detected in our study included several omnivores (striped hog-nosed skunk, three species of opossums), as well as large rats (*Hoplomys* sp. and *Proechimys* sp.), small rats (*Heteromys* sp.), rabbits (*Sylvilagus* sp.) and squirrels (*Sciurus granatensis* and *S. variegatoides*) (Appendix Table A. 1).

We calculated 12 predictors, comprising four variables at each of the three spatial scales: camera trap points, forests and surrounding landscape (Fig. 2.1.). Point-scale variables are based on photographs taken at the camera trap, and provide perspective on an animal’s immediate ability to move, see, hide and forage. These included canopy cover above a camera trap point and average understory cover, average extent of visibility and number of big trees around a camera trap point. Details on calculation of each of these variables along with figures is provided in Appendix Table A. 3 and Appendix Fig. A. 1-3.

We chose forest-scale variables that we assumed to be relevant to habitat use for most of the detected species: tree density, tree diameter distribution, forest area and distance to nearest road from forest. We estimated tree density using ordered distance methods (Krebs 2014). We

summarized the distribution of tree diameters with the exponential rate parameter; high rate values indicate a dominance of small diameter trees whereas low rate values indicate an increase in the representation of large diameter trees (Augusto et al. 2014). We measured forest area and distance to nearest road using Google Earth v7.3.2.5776 (Gorelick et al. 2017). For our purpose of using this as a measure of human activity, we only considered roads that were passable by a truck, were at least 3m in width and were frequently used based on our prior field knowledge. We calculated the shortest Euclidean distance from the study forest edge to the road, using the ruler tool in Google Earth v7.3.2.5776 (Gorelick et al. 2017).

We chose landscape-scale variables assumed to be relevant to dispersal ability and large-scale habitat availability for the sampled species. These were calculated entirely from satellite imagery viewed using Google Earth v7.3.2.5776. For each study forest, we calculated a proximity index (Gustafson and Parker 1994) which collates the inverse distance of neighbouring forests, weighted by their area, reasoning that functional connectivity increases the closer and larger that potential source forests are. We also scored the adjacent anthropogenic matrix using satellite imagery from Google Earth as either plantation (score = 1), mixed plantation-pasture (0.5) or pasture (0), representing a transition from a more closed tree-based matrix to a more open grass or crop-based matrix. We chose to model this variable as continuous as it follows an order and provides distinct information about the type of vegetation immediately (that is in a distance of 1m from the boundary) surrounding a forest. In the case of sites in continuous forest, we scored the matrix immediately outside of the boundary of the entire continuous forest using satellite imagery from Google Earth. We also calculated the total forest area within both a 500m and 2km radius of each camera trap point (Appendix Fig. A. 2).

Statistical Analyses

All analyses were carried out in R v3.6.3 (R Core Team 2020). To understand the effect of the various habitat variables on the terrestrial vertebrate community we tested the effect of the 12 predictors on each of the 13 response variables using linear mixed effects models (lmer function in lme4 and lmerTest packages in R) with forest identity ('Forest ID' in Table 2.1) and sampling period as random effects (i.e. different random intercepts for each forest and each sampling period). By including forest identity as a random effect, we could control for the spatial non-

independence of camera traps located in the same forest. By including sampling period as a random effect, we could control for differences between sampling periods in duration and time of year. Overall, the random effect of forest ID was associated with 0.62-46.73% of variance in null models, whereas the temporal block was only associated with 0-2.82% variance. Predictors were all scaled and centered to enable comparability, and to prevent artefactual results originating from differently scaled variables. To reduce skew in the distribution of predictors, we needed to first log-transform all forest-scale and three of the four landscape-scale variables prior to scaling and centering (Appendix Table A. 4). We checked the extent of correlation between predictors using variance inflation factors (VIF) in the `usdm` package in R (Craney and Surlles 2002, Naimi et al. 2014). Forest area and proximity index had very high variance inflation factors (VIF = 12). We therefore corrected proximity index for the effects of forest area by extracting the residuals from a regression of area on proximity index, and then used the detrended value in model selection (Appendix Table A. 5). For all models, we used residual plots to ensure that residuals were normally distributed. We often needed to transform the response variables using either root transformations or inverse transformations to meet model assumptions (Appendix 2 & Appendix Table A. 5).

We conducted our model building in two steps. First, we asked which spatial scale, i.e., landscape, forest or point, best explained variation in each response variable by creating eight models for each, representing the predictors collected at each of the three spatial scales as well as all combinations of the three spatial scales and a null model (Table 2. 2). We compared these eight models with the second order Akaike's Information Criterion i.e., AICc, selecting those models within $\Delta\text{AICc} < 2$ of the best model (Burnham and Anderson 2001). We then examined parameter estimates based on weighted model averaging of the selected model set (Barton 2014), and considered significant those variables whose model-averaged 95% confidence interval did not contain the value zero. Note that because the model selection procedure and the predictor confidence intervals address subtly different questions, they can sometimes give opposite results (e.g. even if the null model is within 2 AIC of the best model, significant predictors can emerge following model averaging, or vice versa). This is in part due to the fact that model selection is based on models including all variables at a particular spatial scale, so that the importance of specific variables within a scale can be masked by the inclusion of unimportant variables.

Results

Species and Encounter Information

The camera traps recorded a total of 32 identifiable vertebrate species, represented in 3101 independent encounters in 5053 camera trap nights (i.e. a mean of 30 encounters per camera trap deployment). In addition, we recorded 15 human encounters, 18 domestic dog encounters and 398 encounters of birds other than ground-dwelling birds, but did not include these in our analysis. The total number of species encountered was still increasing at the end of the study, even after the 5053 camera trap nights, indicating that there are likely more species to be recorded from this study area (Appendix Fig. A. 4, A.5).

According to the IUCN Red List, three out of the 32 species are in a threatened category: Baird's Tapir (*Tapirus biardii*) is endangered; white lipped peccary (*Tayassu pecari*) and great curassow (*Crax rubra*) are vulnerable. An additional three species are categorized as near threatened (Appendix Table A. 1). Out of the 28 species of mammals and four species of birds, four species are primarily arboreal-dwelling white-faced capuchin (*Cebus capucinus*), two squirrel species (*Sciurus granatensis* and *Sciurus variegatoides*) and the primarily-arboreal crested guan (*Penelopina nigra*). Fifteen species of animals were recorded in all of continuous, large fragment and small fragments (Fig. 2), twelve were found only in fragmented forests, and eleven only in continuous forests (Fig. 2.2, Appendix. Table 6). Out of the total encounters, 602 were of large mammals, 443 of medium-sized mammals, 1676 of small mammals and 366 of ground-dwelling birds.

Predictors

Overall, the most important spatial scale in terms of predicting the vertebrate community appeared to be landscape; the top models for all 13 response variables included landscape-scale predictors (Table 2.3, Fig. 2.3). Forest-scale predictors affected eight response variables, whereas only four response variables were affected by point-scale predictors (Table 2.3, Fig. 2.3). We now examine, in detail, the direction and magnitude of significant predictors at each scale.

Landscape-scale predictors

Most response variables were well predicted by models including landscape-scale variables. We had predicted that landscape variables of total forested area, proximity index and matrix type would primarily affect the trophic structure and species richness of the vertebrate community (Table 2.3a, Fig. 2.3). This prediction was partially supported. Specifically, we found higher richness of carnivore and omnivore species and a higher maximum trophic level in forests surrounded by more tree plantations than pasture (Table 2.3a, Fig. 2.3). Contrary to our predictions, the proximity of neighbouring forests had no effects on these particular variables (Table 2.3a, Fig. 2.3). Both the maximum trophic level and carnivore richness increased with total forest area within 2km, but decreased with total forest area within 500m (Table 2.3a, Fig. 2.3). These patterns were mirrored by the medium-sized mammal encounters, whereas large mammal encounters were negatively correlated with forest area within 2km. Large-bodied animals were also negatively correlated with proximity to neighbouring forests (Table 2.3a, Fig. 2.3). Ground-dwelling bird encounters increased with forest area within 500m (Table 2.3a, Fig. 2.3). Finally, we had also predicted that small and medium-sized prey would be sensitive to open pasture matrix, but not species associated with human-modified landscapes. Encounters of small, but not medium, mammals were lower in forests surrounded by open matrix, as were encounters of large mammals and all animals (Table 2.3a, Fig. 2.3). Encounters of HML users were unrelated to plantation matrix, and also unrelated to any predictor variables (Table 2.3a, Fig. 2.3).

Forest-scale predictors

Forest-scale variables were part of the selected models predicting maximum body length, highest IUCN status, percentage of HML users, total number of encounters of all animals, ground-dwelling birds and large mammal encounters (Table 2.3, Fig. 2.3). We had predicted that the amount of forested area, either at forest or landscape scales, would affect the large-bodied, highest trophic level, and IUCN-listed species. Indeed, camera traps in larger forests recorded species in higher IUCN categories (Table 2.3b, Fig. 2.3). However, this was not driven by effects of forest area on maximum body length encountered, nor by numbers of large mammals encountered, as neither variable was affected by forest area. Instead, the result was due to positive effects of forest area on ground-dwelling birds, including two IUCN-listed species (Table 2.3b, Fig. 2.3, Appendix Table A.1). We had predicted that the distance of a road from a forest would negatively affect species

vulnerable to hunting, such as deer and tapirs. We found no support for our prediction, as large mammal encounters were unrelated to distance from road. Instead, we found herbivore richness to be higher in sites closer to roads, perhaps due to the dominance of small herbivores like agoutis which often forage in undergrowth (Table 2.3b, Fig. 2.3). Finally, we had predicted that tree density and diameter would affect trophic groups differentially, but the best models for trophic structure responses did not include forest variables. Instead, forests with dense trees had fewer overall encounters, notably of large mammals, yet such forests recorded higher maximum body lengths (Table 2.3b, Fig. 2.3).

Point-scale predictors

Point-scale variables were only included in top models for two response variables related to body size: maximum body length of observed animals and medium-sized mammal encounters (Table 2.3c, Fig. 2.3). Both variables were negatively correlated with the number of large trees around camera traps (Table 2.3c, Fig. 2.3). We had predicted that visibility and understory cover would affect the types of species captured by camera traps, but we found no evidence for such effects.

Discussion

Our study had two fundamental objectives. The first objective of this study was to identify the relative importance of habitat at landscape, forest and point spatial scales for the ground-dwelling vertebrate community in a fragmented landscape. The second major objective was to determine which aspects of the vertebrate community were affected by these habitat variables. With regard to the first objective, we found that habitat variables associated with landscape scales affected almost all modelled aspects of the vertebrate community, whereas forest-scale habitat variables affected just half of our response variables (including IUCN Red List species and large mammals), and the point-scale microhabitat around camera traps affected only two response variables (medium-sized mammals and maximum body length). Important habitat predictors included matrix type and total forest area within 500m or 2km (all landscape variables), forest area and tree density (both forest variables) and the number of large trees near the camera trap (a point variable). With regards to our second objective, the strongest effects of habitat structure were seen in higher, carnivorous trophic levels, large and medium sized mammals, and ground-dwelling birds.

Elucidating our first conclusion, one of the most consistent landscape predictors of the vertebrate community was matrix type. In fragmented landscapes, matrix quality can play a critical role in determining the strength of edge effects as well as the permeability of the matrix to animal movement (Gascon et al. 1999, Daily et al. 2001, Pfeifer et al. 2014). As tree plantations are more similar in vegetative structure to a natural forest than pastures, they may be more permeable to forest animals. Matrix type was classified into three categories, as plantation, a matrix with trees of ~9m height, or open pasture, i.e. grazed pasture or areas with vegetable cultivation with nearly no trees, or mixed, with both open pasture and plantations at forest boundaries. In forests adjacent to plantation matrix, we recorded more species (especially carnivores and omnivores), higher trophic levels and more overall encounters, especially of large and small mammals.

Small mammals in particular may be reluctant to cross an exposed, open matrix due to the lack of cover and exposure to avian predators (Kennedy and Marra 2010, Haapakoski et al. 2013). The plantations in our study were primarily commercial orange trees and, in only one case, teak. These orange plantations contain evenly spaced trees with grass understory and frequent human activity during the day. The presence of human activity during the day could deter diurnal predators,

benefiting smaller animals. By contrast, the even spacing between the trees, the roads within the plantations and the lack of human activity in the night could favor crepuscular or nocturnal predators by providing access to higher prey abundance (which is evident with higher encounters of small mammals) and easier routes to travel from one forest to another. Orange fruits provide easy access to food of high sugar content (Lucier et al. 2006), and may attract small mammals and opportunistic feeders such as omnivores which in our study generally consume fruits and insects. For example, during field work we witnessed coatis feeding on oranges on trees. Coatis are found in large social groups and so are other omnivores such as peccaries. We think coatis drove some of the positive correlation between the total number of encounters, large mammal encounters and a plantation matrix (Fig. 2.3). We think that coatis also drove the result behind higher encounters of large-bodied animals in forests with lower proximity to other nearby forests.

We had expected HML users to be relatively insensitive to the level of connectivity characterised by either matrix type or the proximity of neighbouring forests. Indeed, these 18 species were unaffected by these variables, and unaffected by any habitat variable examined in this study. Most of the HML using species are herbivores or omnivores, with relatively generalized diets, potentially permitting them to exist in a wide range of habitats, including forests and matrix.

Island biogeography theory predicts that species richness should be higher in larger forest areas and metacommunity theory suggests that species and trophic diversity should both increase with the total area of forest in the surrounding landscape. However, in our study, species richness was unaffected by the area of a forest or the total forest area at either 500m or 2km scales. This also contrasts with the effects of total forest area on several response variables linked to trophic structure and community composition, suggesting that total forest area increased the prevalence of certain types of species while concomitantly reducing the prevalence of other types of species – resulting in no net change in species number but a change in the food web, highlighting that application of island biogeography theory to this landscape might be inappropriate. Specifically, the highest trophic level observed, the number of medium-sized mammals encountered and carnivore richness were positively correlated with the total amount of forest area within 2km of the camera trap, but herbivore and omnivore richness were not correlated with forested area. Such results are consistent with theoretical predictions that large total amounts of habitat are needed to

provide enough prey resources to support top trophic levels (Robinson and Redford 1986, LeCraw et al. 2014). The 2-km radius circle contains 12.5 km² in area, larger than many of the home ranges of animals in the higher trophic levels (i.e., trophic value >4, *Galictis vittata*, *Herpailurus yaguarundi*, *Panthera onca*, *Leopardus pardalis*, *Puma concolor*, *Leopardus weidii*, *Philander opossum*, *Metachirus nudicaudatus*, *Eira barbara*, *Canis latrans*) in our study area, with species-specific estimates of home ranges between 1.5 to 25 km² (Schweinsburg 1971, Gehrt and Fritzell 1997, Fragoso 1998, Bond et al. 2000, Presley 2000, Grinder and Krausman 2001, Yensen and Tarifa 2003, Dillon and Kelly 2008, Giordano 2016). By contrast, encounters of large mammals decreased as total forest area in 2km increased. This trend was largely driven by coatis, which forage opportunistically on a range of food items in both forests and matrix habitats. Ground-dwelling birds were affected more by total forest area within 500m than 2km, which may reflect the short flight distances of some of these species (Garrigues & Dean 2014). Finally, positive effects of forest area within 2km were often accompanied by negative effects of forest area within 500m. This pattern suggests that while forest area at large scales (2km) may increase population densities of ground vertebrates, at smaller scales (i.e. 500m) highly fragmented forest will cause animals to congregate in the few small areas of forest where the camera traps are located (leading to a negative effect of forest area on encounter rates at this scale). This pattern also provides evidence against the “several small” perspective of the SLOSS debate.

The vertebrate community was not only affected by total forest area but also the size of individual forests. We found that the species most at risk (highest IUCN Red List category) were recorded by camera traps located in larger forests. In our study, Baird’s tapir (*Tapirus bairdii*) is IUCN endangered, white lipped peccaries (*Tayassu pecari*) and currasows (*Crax rubra*) are IUCN vulnerable, and margays (*Leopardus weidii*), jaguars (*Panthera onca*), and some tinamou species (*Tinamus major*) belong to the IUCN near-threatened category (Appendix Table A. 1). Except for currasows, our camera traps recorded these at-risk species in higher frequencies in large fragments and/or continuous forest (Fig 2.2). The higher frequency of currasows in small fragments, contrary to the pattern reported in a previous study (Pardo et al. 2017), is attributed to frequent usage of a single fragment (forest no. 10, Fig. 2.1) by a family consisting of two adults and two juveniles. Although a tapir was encountered in a large fragment (Fig. 2.1, Forest no. 13) rather than intact

forest, this tapir was only one encounter out of the total 17 encounters in our study and was just outside a protected area boundary which encompassed the largest continuous forest in our study.

There are several possible explanations for the general pattern of IUCN red listed species being associated with larger or continuous forests. First, many of these species are threatened because of hunting pressure (e.g. tapirs, peccaries, currasows), and hunters have less access to the interiors of large continuous tracts of forest. Until recently, park guards frequently patrolled those continuous forested areas contained within the Parque Nacional Guanacaste; now, anecdotal evidence of park guards and biologists suggests that hunting pressure may be increasing. Second, some of these threatened species, such as jaguars (24.7-1268.8 km²), have large home ranges in comparison to the other species in our study (Morato et al. 2016), and if this was coupled with a preference for forests or an aversion to human activity, this would restrict them to large or intact forests.

Interestingly, we also found herbivore richness to be higher in forests closer to roads. Herbivores in our study were dominated by small mammals (agoutis, small rats, large rats, squirrels, pacas) and a species of bird, the Great Tinamou (*Tinamus major*). Only two herbivore species in our study, white-tailed deer (*Odocoileus virginianus*) and Baird's Tapir (*Tapirus bairdii*), were large mammals and these were rarely observed in our study. If predators tend to avoid these areas, it may be that proximity to roads can effectively reduce predation risk. Such an effect is documented in temperate North America, where preference of elk for areas closer to human activity is attributed to lower predation risk (Hebblewhite et al. 2005, Nelson et al. 2012).

Vegetation structure also affected encounter rates, at both forest and point scales. Forests in our study included different successional stages, from secondary forest with dense but small diameter trees to primary forest with more large trees. There was a greater number of encounters of species in forests with lower tree density, suggesting higher animal density in more mature forests. This pattern was particularly pronounced for large mammals, although maximum body length per camera trap point showed a paradoxical trend by being lower in areas with fewer trees. We also found evidence that the prevalence of large trees immediately around the trap was influential. For example, both medium mammals and those with the greatest body length were encountered more in areas of the forest with few large trees – presumably because in such microhabitats it is easier

to move or detect predators. This illustrates the need to account for fine-scale habitat selection in camera trap studies, a point also evident in previous studies such as the role of exotic cover on mesopredators occurrence = in southern California and dense bush on native forest mammal assemblages in South Africa (Crooks 2002, Smith et al. 2017b).

It is important to address the limitations of our study. First, we obtained and report data on the vertebrate community at the scale of camera traps placed within forests only. As we do not have community data for multiple, replicated landscapes or in the matrix habitat, we are not able to test hypotheses related to the landscape-scale responses to fragmentation (Fahrig 2017). We suspect that some of the eleven species that we only found in continuous forest, for example, may have occasionally used the matrix for foraging and dispersal. Nor can our design detect lag effects of habitat change, such as extinction debts. Therefore, instead of testing the effect of fragmentation *per se*, we restrict the scope of our study to understanding the habitat-predictors of a vertebrate community sampled inside forests in at multiple-scales. Second, although sampling effort was consistent between traps, it was not exhaustive: species were still accumulating by the end of the study (Appendix Fig. A. 4, Appendix Fig. A.5). Thus, any difference between vertebrate groups or habitat types in the rate of species accumulation has the potential to influence the results. For example, detection probability influences species accumulation as well as the number of encounters, and is known to differ between mammalian trophic levels (Rovero et al. 2014). However, by using the Chao estimate of species richness, we do attempt to estimate asymptotic species richness. Third, we were not able to include additional predictors such as road density, night-light intensity, forest composition, vehicular movement, noise or edge density, which may have shed more light on the community structure in our study area. However, our study does include many of the predictors most frequently identified in the literature as important for vertebrate occupancy (Watling and Donnelly 2006, Vetter et al. 2011).

The conclusions of our study imply that a tree-plantation matrix is superior to pasture matrix in supporting a diverse vertebrate food web in fragmented forests, as is maintaining a high percentage of total forest area in the landscape. However, the size of individual forest remnants is also important, affecting species of conservation concern. Further loss and fragmentation of continuous forests in this and similar regions with similar elevations may result in population reductions or extirpations of threatened species in the Neotropics.

Fig. 2. 1. Study design including location and landcover of study area (main panel, shown as an inset from the map of Costa Rica), and the spatial scale of all predictors (three bottom panels, illustrated for a focal camera trap in forest 14). In the main panel, each study forest is identified by a red number (see Table 2.1) beside the six red dots indicating each of the camera trap points for that forest. Forests 3–8 are within continuous forest protected as part of the Area de Conservación Guanacaste UNESCO World heritage site.

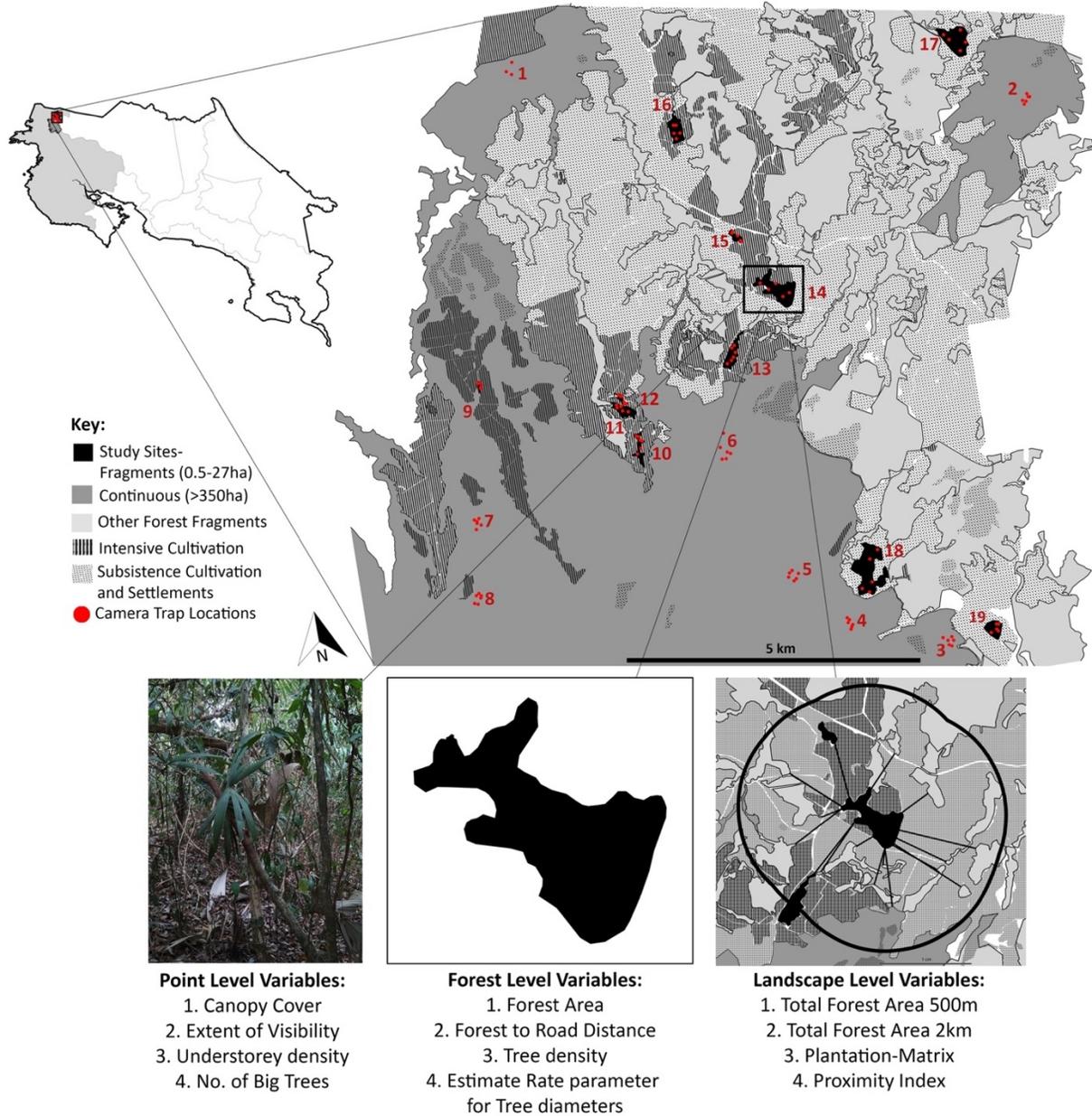


Fig. 2. 2.a. Average daily encounter rate per site (six camera traps per site) in continuous forest and small and large forest fragments for 32 species within 30 families and 19 orders. Species are organised from high to low encounter rate within order and family. Orders are divided by thick grey lines and families by dashed black lines. Families: F1- Dasyproctidae, F2- Cuniculidae, F3- Echimyidae, F4- Heteromyidae, F5- Sciuridae, F6- Procyonidae, F7- Felidae, F8- Mustelidae, F9- Mephitidae, F10- Canidae, F11- Didelphidae, F12- Leporidae, F13- Dasypodidae, F14- Tayassuidae, F15- Cervidae, F16- Tapiridae, F17- Myrmecophagidae, F18- Cebidae, F19- Cracidae, F20- Tinamidae. Orders: 1- Rodentia, 2- Carnivora, 3- Didelphimorphia, 4- Lagomorpha, 5- Cingulata, 6- Cetartiodactyla, 7- Perissodactyla, 8- Pilosa, 9- Primates, 10- Galliformes, 11- Tinamiformes.

b. Foodweb of all species recorded in camera trap study created using literature reviews. All abbreviations correspond to names in 2b. Species excluded from analysis (in blue): BP- *Buteo platypterus*, Ss- *Setophaga* sp., Cs- *Chordeiles* sp., PC- *Piaya cayana*, PN- *Parkesia noveboracensis*, Cs- *Catharus* sp., Ms- *Melospiza* sp., Ls- *Leptotila* sp., CA- *Cathartus aura*, Gs- *Geotrygon* sp. 's' added to species name whenever only Genus is known but not the species.

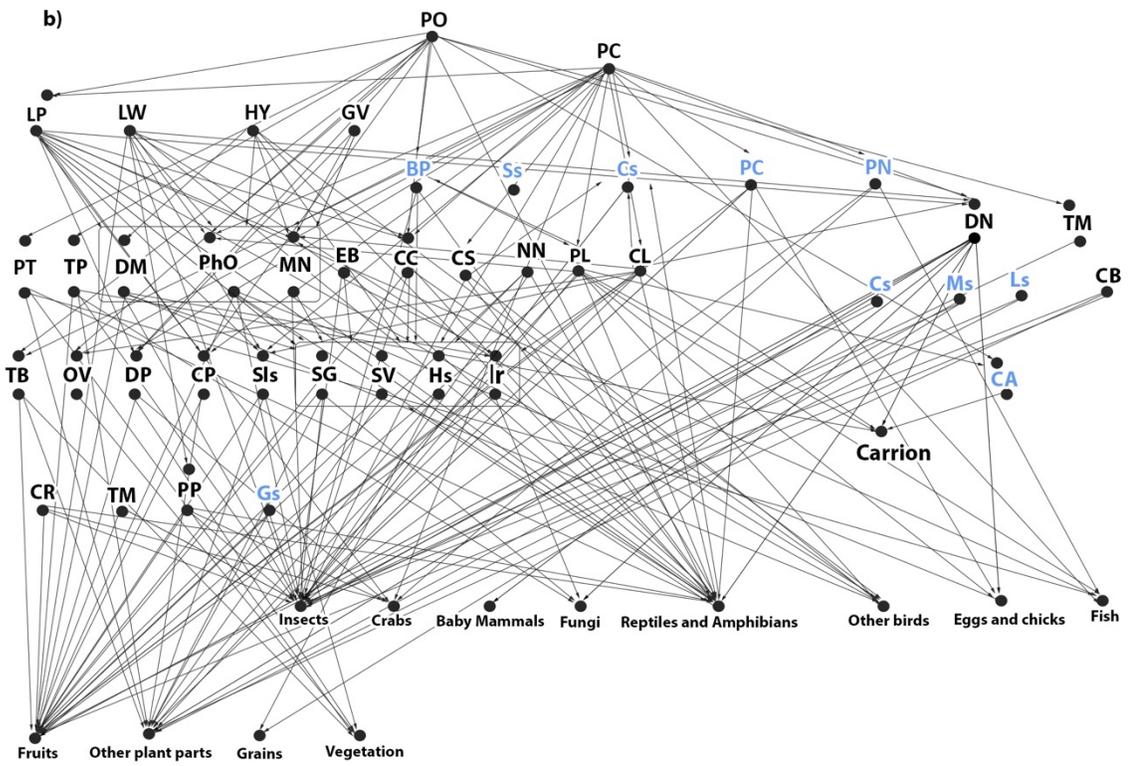
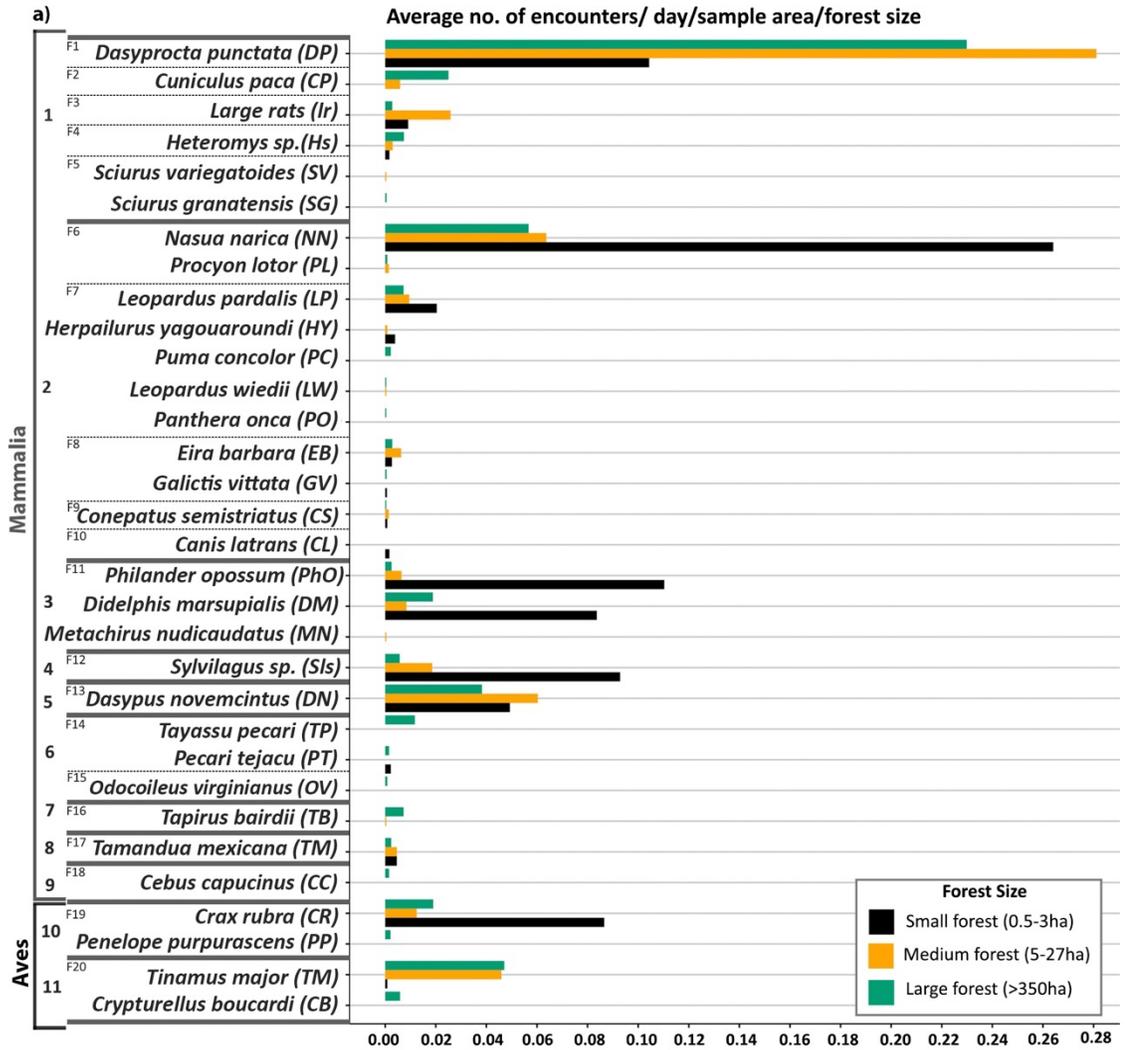
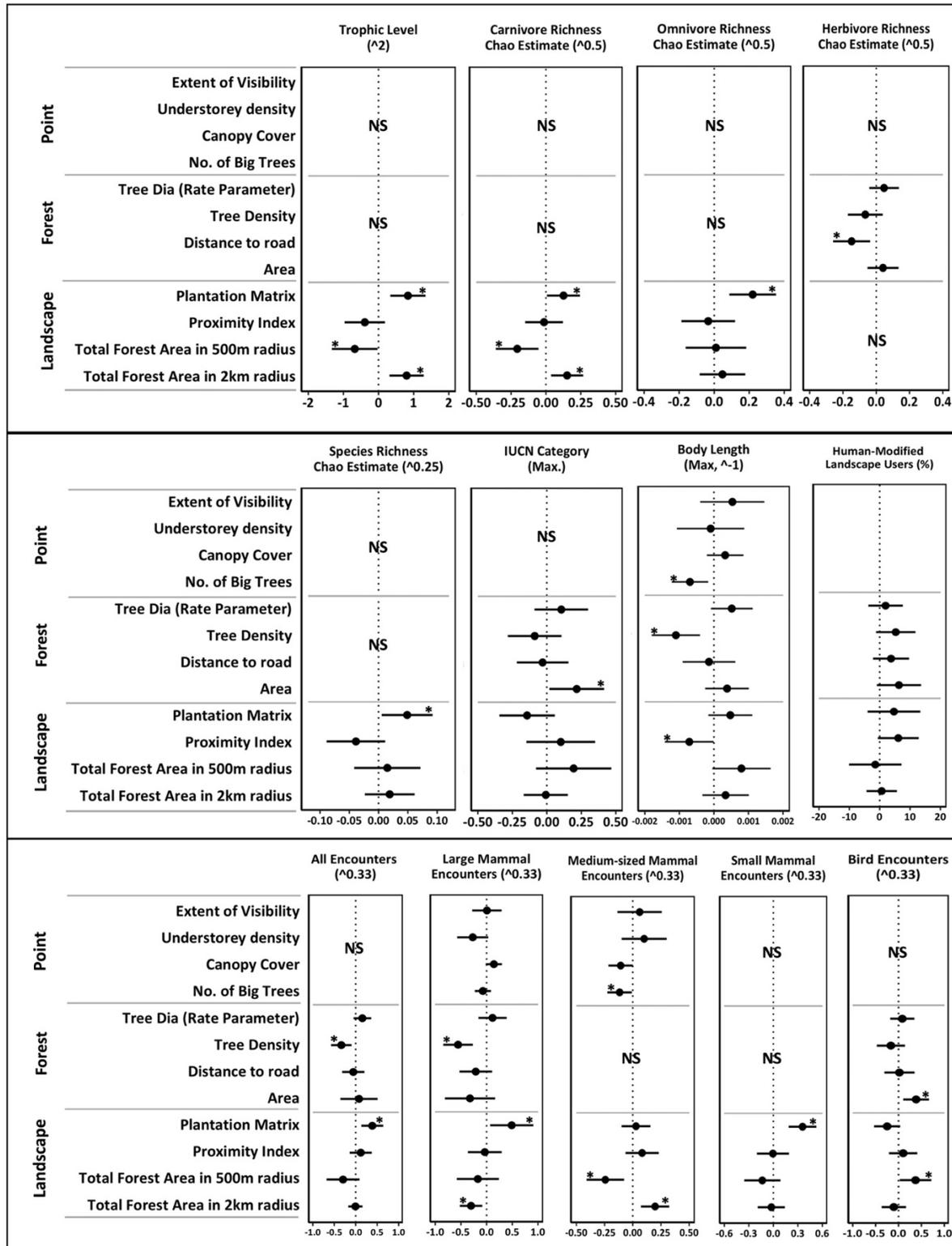


Fig. 2. 3. Parameter estimates averaged over top models ($\Delta AIC_c < 2$) for response variables representing trophic structure, conservation significance and community composition. Horizontal grey lines separate the predictors into three different spatial scales (point, forest, landscape) as defined in the Methods. Because all response variables are centered and standardized, these parameter estimates are directly comparable. NS = Scale and the variables in that scale are 'Not Selected' as best model.



TROPHIC FUNCTIONS

CONSERVATION SIGNIFICANCE

COMMUNITY COMPOSITION

Table 2.1. Information on all study forests. ‘Forest No.’ corresponds to numbers provided beside camera trap locations in Fig. 2.1. Forest Category was defined as: Continuous = Forest size >350ha, Large fragment = 5-27ha, Small fragment = 0.5-3ha. ‘Plantation Matrix’ was scored as: 0 = pasture, 0.5= mixed plantation and pasture, 1 = plantation. The rate parameter for tree density refers to that estimated from an exponential distribution. Details on calculations of the habitat variables are provided in Appendix Table A.3.

Forest No.	Sample Area Latitude (°N)	Sample Area Longitude (°E)	Forest Area (in ha)	Forest Category	Plantation Matrix	Tree Density No. of Trees ^{-ha}	Tree Diameter (Rate Parameter)	Forest to Road Distance (in m)	Road Width (in m)	Proximity Index (log)
1	11.082	-85.436	461.0	Continuous	0.5	74.0 x 10 ²	0.172	1.92	9.62	13.3
2	11.065	-85.356	398.0	Continuous	0.5	142.0 x 10 ²	0.654	1.46	6.62	9.20
3	10.981	-85.381	19091.0	Continuous	0.5	78.0 x 10 ²	0.317	1.92	9.62	13.2
4	10.995	-85.404	19091.0	Continuous	0.5	75.0 x 10 ²	0.358	1.92	9.62	13.2
5	10.986	-85.397	19091.0	Continuous	0.5	84.0 x 10 ²	0.184	1.92	9.62	13.2
6	11.016	-85.412	19091.0	Continuous	0.5	74.0 x 10 ²	0.214	1.92	9.62	13.2
7	11.011	-85.453	19091.0	Continuous	0.5	86.0 x 10 ²	0.205	1.92	9.62	13.2
8	10.999	-85.455	19091.0	Continuous	0.5	93.0 x 10 ²	0.440	1.92	9.62	13.2
9	11.033	-85.449	0.5	Small Fragment	1	46.0 x 10 ²	0.234	116	8.89	8.65
10	11.019	-85.425	3.0	Small Fragment	1	56.0 x 10 ²	0.310	18.0	3.43	10.0
11	11.025	-85.427	5.0	Large Fragment	1	88.0 x 10 ²	0.289	3.87	6.89	10.2
12	11.027	-85.427	1.0	Small Fragment	1	56.0 x 10 ²	0.175	1.00	19.5	9.23
13	11.032	-85.408	6.0	Large Fragment	1	65.0 x 10 ²	0.447	2.69	7.00	8.89
14	11.041	-85.400	19.0	Large Fragment	0.5	108.0 x 10 ²	0.252	3.76	4.89	7.19
15	11.050	-85.405	2.0	Small Fragment	0.5	86.0 x 10 ²	0.415	6.12	5.98	3.87
16	11.068	-85.411	8	Large Fragment	0.5	14.0 x 10 ²	0.415	1.00	9.32	7.73
17	11.075	-85.365	18	Large Fragment	0.5	77.0 x 10 ²	0.251	8.32	8.29	7.15
18	10.995	-85.392	27	Large Fragment	0.5	89.0 x 10 ²	0.109	3.17	5.19	13.4
19	10.982	-85.374	6	Large Fragment	0	61.0 x 10 ²	0.164	185	4.52	7.12

Table 2.2. List of Models included in study.

Name of Model	Model.
Null	1 + (1 Site ID) + (1 Sampling Season/Period)
Point scale	Extent of visibility + Understory density + No. of Big Trees + Canopy Cover + (1 Site ID) + (1 Sampling Season/Period)
Forest scale	Forest Area + Distance from Forest to nearest road + Tree density within forest + Tree diameters within forest + (1 Site ID) + (1 Sampling Season/Period)
Landscape scale	Total forest area in 2km of camera trap point + Total forest area in 500m of camera trap point + Proximity index of forest + Type of matrix around forest + (1 Site ID) + (1 Sampling Season/Period)
Point + Forest scale	Extent of visibility + Understory density + No. of Big Trees + Canopy Cover + Extent of visibility + Understory density + No. of Big Trees + Canopy Cover + Forest Area + Distance from Forest to nearest road + Tree density within forest + Tree diameters within forest + (1 Site ID) + (1 Sampling Season/Period)
Point + Landscape scale	Extent of visibility + Understory density + No. of Big Trees + Canopy Cover + Total forest area in 500m of camera trap point + Proximity index of forest + Extent of plantation type matrix around forest + (1 Site ID) + (1 Sampling Season/Period)
Forest + Landscape scale	Forest Area + Distance from Forest to nearest road + Tree density within forest + Tree diameters within forest + Total forest area in 2km of camera trap point + Total forest area in 500m of camera trap point + Proximity index of forest + Type of matrix around forest + (1 Site ID) + (1 Sampling Season/Period)
Point + Forest + Landscape scale	Extent of visibility + Understory density + No. of Big Trees + Canopy Cover + Forest Area + Distance from Forest to nearest road + Tree density within forest + Tree diameters within forest + Total forest area in 2km of camera trap point + Total forest area in 500m of camera trap point + Proximity index of forest + Type of matrix around forest + (1 Site ID) + (1 Sampling Season/Period)

Table 2.3a.: Top models and model-averaged estimates of parameters for variables representing ‘Trophic Structure’ retained in the confidence set ($\Delta AIC < 2$). Standard errors are given in parentheses, and parameter estimates significantly greater than zero are in bold.

Response Variable	Top models (AICc <2)	Extent of Visi-bility	Understorey Density	Plant Cover	No. of Big Trees	Tree Diameter	Tree Density	Forest to Road Distance	Forest Area	Type of Matrix around forest	Proximity Index	Forest Area in 2km radius	Forest Area in 500m radius
Trophic Level (Max, ^2)	Landscape	NA	NA	NA	NA	NA	NA	NA	NA	0.840 (0.253)	-0.392 (0.291)	0.80 (0.247)	-0.677 (0.329)
Carnivore Richness (Chao Estimate, ^0.5)	Landscape, Null	NA	NA	NA	NA	NA	NA	NA	NA	0.126 (0.060)	-0.013 (0.068)	0.152 (0.058)	-0.206 (0.077)
Omnivore Richness (Chao Estimate, ^0.5)	Landscape	NA	NA	NA	NA	NA	NA	NA	NA	0.220 (0.067)	-0.034 (0.077)	0.047 (0.066)	0.010 (0.087)
Herbivore Richness (Chao Estimate, ^0.5)	Forest, Null	NA	NA	NA	NA	0.050 (0.045)	-0.066 (0.053)	-0.150 (0.060)	0.040 (0.047)	NA	NA	NA	NA

Table 2. 3b.: Top models and model-averaged estimates of parameters for variables representing ‘Conservation Significance’ retained in the confidence set ($\Delta AIC < 2$). Standard errors are given in parentheses, and parameter estimates significantly greater than zero are in bold.

Response Variable	Top models (AICc <2)	Extent of Visibility	Under-storey Density	Plant Cover	No. of Big Trees	Tree Diameter	Tree Density	Forest to Road Distance	Forest Area	Type of Matrix	Proximity Index	Forest Area in 2km radius	Forest Area in 500m radius
Species Richness (Chao Estimate, $\wedge 0.25$)	Null, Landscape	NA	NA	NA	NA	NA	NA	NA	NA	0.050 (0.022)	-0.040 (0.025)	0.020 (0.021)	-0.015 (0.030)
Body Length (Max, $\wedge -1$)	Point+landscape, Point, Point+forest	0.0005 (0.0005)	-0.0001 (0.0005)	0.0003 (0.0003)	-0.0007 (0.0003)	0.0005 (0.0003)	0.001 (0.0003)	0.0001 (0.0004)	0.0004 (0.0003)	0.0005 (0.0003)	-0.0007 (0.0003)	0.0003 (0.0003)	0.0008 (0.0004)
IUCN Category (Max)	Forest, Landscape, Forest+landscape, Null	NA	NA	NA	NA	0.105 (0.098)	-0.090 (0.010)	-0.030 (0.094)	0.216 (0.10)	-0.143 (0.101)	0.101 (0.130)	-0.008 (0.080)	0.194 (0.140)
Human Modified Landscape User (HML User)	Null, Forest+Landscape, Landscape	NA	NA	NA	NA	1.93 (2.86)	5.27 (3.25)	3.73 (2.99)	6.33 (3.70)	4.68 (4.39)	6.12 (3.39)	0.66 (2.52)	-1.45 (4.36)

Table 2. 3c.: Top models and model-averaged estimates of parameters for variables representing ‘Community Composition’ retained in the confidence set ($\Delta AIC < 2$). Standard errors are given in parentheses, and parameter estimates significantly greater than zero are in bold.

Response Variable	Top models (AICc <2)	Extent of Visibility	Under-storey Density	Plant Cover	No. of Big Trees	Tree Diameter	Tree Density	Forest to Road Distance	Forest Area	Type of matrix	Proximity Index	Forest Area in 2km	Forest Area in 500m
Total encounters (^0.33)	Forest + landscape, Landscape, Forest	NA	NA	NA	NA	0.154 (0.104)	- 0.335 (0.120)	-0.056 (0.131)	0.077 (0.220)	0.385 (0.129)	0.118 (0.130)	-0.006 (0.083)	-0.295 (0.194)
Large Mammal Encounters (^0.33)	Point+ forest, Forest+ landscape	0.006 (0.144)	-0.270 (0.152)	0.141 (0.079)	- 0.072 (0.080)	0.115 (0.138)	- 0.555 (0.144)	-0.211 (0.159)	-0.323 (0.250)	0.50 (0.211)	-0.040 (0.170)	-0.303 (0.110)	-0.171 (0.206)
Medium Mammal Encounters (^0.33)	Land-scape, Point, Null	0.060 (0.099)	0.101 (0.100)	-0.107 (0.054)	- 0.116 (0.055)	NA	NA	NA	NA	0.028 (0.064)	0.083 (0.074)	0.200 (0.063)	-0.243 (0.084)
Small Mammal Encounters (^0.33)	Landscape	NA	NA	NA	NA	NA	NA	NA	NA	0.357 (0.086)	-0.005 (0.099)	-0.025 (0.084)	-0.135 (0.112)
Ground Dwelling Bird Encounters (^0.33)	Null, Landscape, Forest	NA	NA	NA	NA	0.083 (0.133)	- 0.166 (0.155)	0.020 (0.166)	0.385 (0.141)	-0.247 (0.144)	0.102 (0.155)	-0.102 (0.133)	0.372 (0.174)

CHAPTER 3

General Conclusion

Summary of Study

We found that different landscape variables had different effects on various characteristics of the vertebrate community. The response variables of highest trophic level, carnivore richness and total number of large and medium mammal encounters showed the broadest range of response to the different habitat characteristics, significantly affected by at least three predictors. The predictor of plantation matrix affected the majority of response variables, whereas the total amount of forest area (both within 2km and 500m), density of trees within each forest remnant and number of big trees near a camera trap affected fewer response variables.

Although our study did not explicitly test any specific theory of community structure, our results do suggest that some theories may be better suited to our study area than others. For example, the theory of island biogeography predicts that larger and better-connected forests should contain a greater diversity of species. However, we obtained no support for any of the richness variables – at least at the camera trap scale - being affected by forest area. We did find, contrary to expectations of island biogeography theory, that species richness was significantly and positively affected by a plantation matrix, implying that forest fragments are not isolated islands in a sea of inhospitable matrix. We also found that forests surrounded by plantation matrix were more likely to contain species in higher trophic levels, and carnivores and omnivores. When forests were surrounded by a plantation matrix they also had higher numbers of small and large mammals and total number of animals encountered per camera trap. The importance of matrix quality is emphasized in both metacommunity theory and countryside biogeography, and we suggest that in our study area a likely mechanism may be the protective cover of the plantation trees, resource subsidies of oranges, and lower levels of human activities during evening and night. Both of these theories are also consistent with the importance of total amount of forest area in the form of disjointed forests at larger spatial scales (0.5 - 2km), rather than simply the continuous forest area of a single forest remnant, in affecting trophic level, carnivore richness and encounters of large and medium-sized mammals. Finally, one of the most important findings of our study was that the highest IUCN rank detected in a site increased with forest area. While our analysis was not fine-grained enough to isolate which particular species drove this result, we note that the species which are of conservation

concern, i.e., categorised within the threatened categories of the IUCN Red list, in our study area include several species of large and small mammals and ground-dwelling birds such as tapirs, margays and curassows. For this subset of the vertebrate community, the evidence favours the ‘Single Large’ part of the SLOSS debate, highlighting the need to preserve large continuous forests in the place of several small forests.

Recommendations for future research and conservation action in Study Area

Some of the main limitations of our study include the lack of camera traps in matrix habitat, limiting the full picture of the effects of forest fragmentation (Farhig 2017). We also could not provide measures of the effects of variables such as levels of human presence, human generated noise and light pollution and species-based information on the vegetation within the forests in which the study was conducted. Therefore, we recommend that future studies use a grid-based or transect-based landscape scale study with the areas within the matrix habitat included and the above predictors also be measured and included, this will allow to obtain a more comprehensive understanding of the effects of forest fragmentation (Farhig 2017). Also, the sampling effort in our study, even though it lasted for 5053 trap nights, could only document one instance of jaguars, the apex predator, and 17 instances of tapirs, a threatened large-bodied herbivore. We therefore recommend that future sampling effort be appreciably greater than in the current study in order to gain a better understanding of the usage of the landscape by these animals. Our study also documented activities of people with guns and dogs within forest fragments and the ACG. These are most likely hunters. We recommend camera traps or periodic patrols be conducted in these forests to prevent hunting of wildlife as hunting is a pervasive threat to many species (Harrison et al. 2016). In order to also prevent hunting and gain an understanding into the populations of threatened and near threatened species, we recommend species-specific population density studies similar to studies on jaguars and tapirs elsewhere (Silver et al. 2004, Gonzalez-Maya et al. 2012, Carbajal-Borges et al. 2014) to be conducted through collaborations with the local community, international camera trapping community and through indirect sign census methods (Munari et al. 2011, Sikes and Bryan 2016).

We also recommend that a study on primate landscape usage be undertaken in this study area as often primates are known to only use continuous forests/ large fragments and are affected by the lack of connectivity (Umapathy et al. 2011). If the results of such a study show that primates prefer to stay in one forest rather than move to other forests due to constraints posed by the matrix such as roads or plantations, then it is recommended that canopy rope bridges be provided as interventions for facilitating primate movement between these forests (Umapathy et al. 2011). So far, primate studies in Guanacaste are restricted to the dry forest. Arboreal camera trap studies should be undertaken. This area is known to be home to 64 species of mammals (Janzen 2018) but our study documented only 28, implying that many species were missed - perhaps because they are more arboreal-dwelling than ground-dwelling (Gregory et al. 2014).

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Appendix 1.

Methodology for Camera Trap Setup, Retrieval and Data processing

Camera Trap Setup and Retrieval

Electronic equipment included Reconyx HC500 camera traps, Sandisk Ultra (16GB) cards, Energizer Ultimate Lithium Batteries and Smart phone SD card reader with type B Micro USB cable. The smart phone and SD card reader were used for checking working conditions of camera traps.

At the chosen random point within the sampling area in the study forest we identified a suitable tree, henceforth camera-trap-tree, for setting-up the camera trap. We ensured that the camera-trap-tree was within 20m radius of the random point and was facing animal tracks or potential animal paths as recommended by the protocol provided by the Tropical Ecology Assessment and Monitoring (TEAM) network (Team Network 2011, Ahumada et al. 2011, 2013, Beaudrot et al. 2016, Rovero and Ahumada 2017). In addition to this, we also cleared an area of about 3m from the camera-trap-tree of small plants in order to obtain unobstructed pictures of the animals. In most cases, the camera traps were setup 50cm above the ground or at a height and angle which we estimated would capture a medium-sized animal moving 2 meters from the trap (through mimicking its movements and checking the resulting image with a SD card reader). We recorded on a whiteboard the start date of sampling, names of researchers, latitude & longitude of the sampling point and time of setting up the camera trap, and then photographed the whiteboard immediately prior to each deployment. We used Energizer Ultimate Lithium-ion batteries for the entire study period. We found that most batteries lasted for two sampling seasons (~80 days) continuously. However, as a precautionary measure, we added fresh batteries to at least 15 cameras at the start of the second and changed batteries in all cameras in the third sampling session. When fresh batteries were exhausted we, re-used batteries saved from previous sampling sessions. We tested used batteries prior to deployment in the field with an analog multimeter and used only those batteries with a voltage $>1.2V$. The usage of Lithium ion batteries avoided the hassle of having to periodically check batteries allowing for saving field-personnel hiring costs.

We retrieved cameras at least after 43 days in each period, after which we shifted the camera into another randomly chosen point within the same forest. During camera retrieval we recorded date, time and information of the researchers retrieving the trap. Each time a camera trap was deployed

at a new location we replaced it with a different set of SD cards. The photographs were backed-up onto two 1TB hard drives and uploaded into cloud each evening. As a precautionary measure the SD cards were not erased until the end of the study.

Data Processing

Of the total 114 camera traps that were setup, 104 camera traps had worked until the completion of the study. We attribute the failure of 10 camera traps to battery drain, internal defects in the camera-trap and in one instance large sized silica gel packets which perhaps interfered with circuitry within the trap. We classified images according to study forest, sampling location within forest and sampling period. We identified and counted the number of animals in each image in Wild ID v0.9.6 with a complete re-check after identifying it for the first time. To provide for speedier identification we set the time difference between a set of images at 1min on Wild ID and changed information on an image if the number of animals/ type of animals differed between two images within that minute. In cases when a continuous capture involved one animal followed by another, such as a mother Tapir (*Tapirus bairdii*) followed by a baby, and there was only one individual in each image in the continuous capture then the last photograph in the sequence was marked as 'two' instead of one so as to ensure that the maximum number of animals in that capture was correctly accounted for.

We identified mammals using the checklists provided in Janzen (2018) and Wainwright (2007) and birds using Garrigues and Dean (2014). In cases when the identification was difficult we sought advice from naturalists with knowledge of the fauna of this region. If the images remained difficult to identify, we classified the animal into the nearest genus or attributed it to the more common species rather than a specialist species i.e., two encounters of possibly *Didelphis virginiana* was attributed to *Didelphis marsupialis* and 153 encounters of members belonging to the genus *Sylvilagus* was classified only as '*Sylvilagus* sp.'. In the case of large-sized rats most likely of the genera, *Proechimys* or *Hoplomys*, we classified them as 'Large rats' (63 encounters) as distinguishing between the genera was difficult. The identified images were exported a .csv file and the data trimmed to the shortest time-period between setup and pickup at a camera trap point in a sampling period. We deleted all encounters of humans and dogs prior to data processing.

We defined an ‘encounter’ to be a continuous capture with the difference between two continuous captures being of no more than two minutes. We chose to use 2minutes as our threshold in order to account for different individuals of the same species moving in and out of a frame of a camera trap. We recognise that there is a possibility of overestimation of the number of individuals due to this procedure, however, it accounts for the possibility of the animal being an entirely different individual. We marked each encounter with a unique alphanumeric ID manually on MS excel. Using R v3.6.3 (R Core Team 2020) we counted the maximum number of individuals per encounter, totalled this as the total number of encounters for a species at a camera trap point and generated a matrix of camera trap point by species names. We generated another matrix with species characteristics (Appendix Table A. 1) and used matrix multiplication on these two matrices.

Appendix 2.

Calculation of Response Variables

Response variable transformation

We checked the distribution of residuals for each of the 13 response variables modelled with the global model containing all 12 predictors. Except for IUCN category and Human-modified landscape users (%), the residuals were not normally distributed for the response variables. Therefore, for these 11 variables we calculated the optimal exponential transformation based on Tukey's lambda using the 'transformtukey' function of the rcompanion package in R v3.6.3 (R Core Team 2020). In order to keep the transformation uniform within a category of response variables, we chose to transform with cube roots all the variables characterising community composition (Appendix Table A. 5.) and with square roots for all the Chao estimates characterising trophic structure (Appendix Table A. 5). However, we squared the maximum value of trophic level encountered at a camera trap, used a quartic root of the Chao estimate of total species richness as residuals of cube and square roots of these variables were not normally distributed. We used an inverse function of the Max. Body length as the Tukey's lambda value for this variable was -0.975. The final variable of Max. Body Length was calculated as $-1*((\text{Values of Maximum body length})^{-1})$. We used this value based on the formula provided in the rcompanion package.

Table A. 1. Species Information. IUCN Category: 0-Least Concern, 0.5-Near Threatened, 1-Vulnerable, 1.5- Endangered; HML User = Human Modified Landscape User. ABL = Average Body Length. R1- Reference no. in Table. A.8. Reference list for Diet and Body size from Animal Diversity Web., R2- Reference no. in Table A.9. Reference list for information from IUCN Red List Database, R3- Reference no. in Table. A.10. Reference list of other literature with information on diet.

Species	Family	Order	Class	Feeding Guild	ABL (in cm)	IUCN Category	Trophic Level	HML User	R1	R2	R3
<i>Canis latrans</i>	Canidae	Carnivora	Mammalia	Omnivore	87.5	0	3.96	Yes	2	2	NA
<i>Cebus capucinus</i>	Cebidae	Primates	Mammalia	Omnivore	21.75	0	4	No	3	5	NA
<i>Conepatus semistriatus</i>	Mephitidae	Carnivora	Mammalia	Omnivore	57	0	4.25	No	4	6	NA
<i>Crax rubra</i>	Cracidae	Galliformes	Aves	Omnivore	89	1	3.72	Yes	1	7	NA
<i>Crypturellus boucardi</i>	Tinamidae	Struthioniformes	Aves	Omnivore	28	0	2.75	Yes	1	8	3
<i>Cuniculus paca</i>	Cuniculidae	Rodentia	Mammalia	Herbivore	71	0	2	No	5	9	NA
<i>Dasyprocta punctata</i>	Dasyproctidae	Rodentia	Mammalia	Herbivore	51.75	0	2.67	Yes	6	10	NA
<i>Dasyopus novemcinctus</i>	Dasypodidae	Cingulata	Mammalia	Carnivore	70.75	0	3.47	Yes	7	11	NA
<i>Didelphis marsupialis</i>	Didelphidae	Didelphimorphia	Mammalia	Omnivore	34.75	0	3.8	Yes	8	12	NA
<i>Eira barbara</i>	Mustelidae	Carnivora	Mammalia	Omnivore	65	0	3.98	No	10	13	NA
<i>Galictis vittata</i>	Mustelidae	Carnivora	Mammalia	Carnivore	68	0	4.62	Yes	11	14	NA
<i>Heteromys</i> sp.	Heteromyidae	Rodentia	Mammalia	Herbivore	13.55	0	2.75	No	12	NA	NA
<i>Herpailurus yagouaroundi</i>	Felidae	Carnivora	Mammalia	Carnivore	63.75	0	4.45	No	25	30	NA

Table A. 1. Species Information. IUCN Category: 0-Least Concern, 0.5-Near Threatened, 1-Vulnerable, 1.5- Endangered; HML User = Human Modified Landscape User. ABL = Average Body Length. R1- Reference no. in Table. A.8. Reference list for Diet and Body size from Animal Diversity Web., R2- Reference no. in Table A.9. Reference list for information from IUCN Red List Database, R3- Reference no. in Table. A.10. Reference list of other literature with information on diet.

Species	Family	Order	Class	Feeding Guild	ABL (in cm)	IUCN Category	Trophic Level	HML User	R1	R2	R3
<i>Large Rats</i> (<i>Proechimys</i> sp./ <i>Hoplomys</i> sp.)	Echimyidae	Rodentia	Mammalia	Herbivore	22.75	0	2.58	No	14	NA	NA
<i>Leopardus pardalis</i>	Felidae	Carnivora	Mammalia	Carnivore	81	0	4.25	No	15	18	NA
<i>Leopardus wiedii</i>	Felidae	Carnivora	Mammalia	Carnivore	62.65	0.5	4.12	No	16	19	5
<i>Metachirus nudicaudatus</i>	Didelphidae	Didelphi- -morphia	Mammalia	Omnivore	54.25	0	4	Yes	17	20	NA
<i>Nasua narica</i>	Procyonidae	Carnivora	Mammalia	Omnivore	105	0	3.77	No	18	21	NA
<i>Odocoileus virginianus</i>	Cervidae	Cetartio- -dactyla	Mammalia	Herbivore	190	0	2	Yes	19	22	NA
<i>Panthera onca</i>	Felidae	Carnivora	Mammalia	Carnivore	167.5	0.5	4.33	Yes	20	23	NA
<i>Pecari tajacu</i>	Tayassuidae	Cetartio- -dactyla	Mammalia	Omnivore	90	0	3.52	Yes	21	25	NA
<i>Penelope purpurascens</i>	Cracidae	Galli- -formes	Aves	Omnivore	89	0	3.72	No	1	26	7
<i>Philander opossum</i>	Didelphidae	Didelphi- -morphia	Mammalia	Omnivore	54.05	0	4.03	Yes	22	27	NA
<i>Procyon lotor</i>	Procyonidae	Carnivora	Mammalia	Omnivore	77.65	0	3.81	Yes	23	28	NA
<i>Puma concolor</i>	Felidae	Carnivora	Mammalia	Carnivore	120	0	4.17	No	24	29	NA
<i>Sciurus granatensis</i>	Sciuridae	Rodentia	Mammalia	Herbivore	42.5	0	3.17	Yes	26	31	NA
<i>Sciurus variegatoides</i>	Sciuridae	Rodentia	Mammalia	Herbivore	27.85	0	3.05	Yes	27	32	NA

Table A. 1. Species Information. IUCN Category: 0-Least Concern, 0.5-Near Threatened, 1-Vulnerable, 1.5- Endangered; HML User = Human Modified Landscape User. ABL = Average Body Length. R1- Reference no. in Table. A.8. Reference list for Diet and Body size from Animal Diversity Web., R2- Reference no. in Table A.9. Reference list for information from IUCN Red List Database, R3- Reference no. in Table. A.10. Reference list of other literature with information on diet.

Species	Family	Order	Class	Feeding Guild	ABL (in cm)	IUCN Category	Trophic Level	HML User	R1	R2	R3
<i>Sylvilagus unknown</i>	Leporidae	Lagomorpha	Mammalia	Herbivore	43.6	0	2	Yes	28	NA	NA
<i>Tamandua mexicana</i>	Myrmeco- -phagidae	Pilosa	Mammalia	Carnivore	62	0	3.5	No	29	33	NA
<i>Tapirus bairdii</i>	Tapiridae	Perisso- -dactyla	Mammalia	Herbivore	215	1.5	2	No	30	34	NA
<i>Tayassu pecari</i>	Tayassuidae	Cetartio- -dactyla	Mammalia	Omnivore	87.5	1	3.43	No	31	35	NA
<i>Tinamus major</i>	Tinamidae	Struthioni- -formes	Aves	Herbivore	43	0.5	2	Yes	1	37	NA

Table A. 2. Calculation methodologies for 13 response variables in study.

Category	Variable	Definition/ Explanation	Calculation methodology
Trophic Function	Max. Trophic Level	The maximum value of trophic level of a species out of all the species recorded at a camera trap.	We calculated the trophic level for all the species by constructing an interaction matrix and calculating the trophic level of each species in our study using the Cheddar package of RStudio v1.2.5033 (R Development Core Team). We then selected the maximum trophic level represented at each camera trap point.
Trophic Function	Carnivore Richness (Chao Estimate)	Chao estimate of the sum total carnivore richness occurring at a single camera trap point.	We classified species as carnivore, herbivore, omnivore using the same interaction matrix used for calculating trophic level. We classified species as ‘carnivore’ if the diet was predominantly animal (including insects) and as ‘herbivore’ if the diet was predominantly plant (including vegetative parts, seeds, grains, fruit). We calculated the Chao estimate for the total number of carnivorous, herbivorous, or omnivorous species by applying the ‘estimateR’ function from the Vegan package of RStudio v1.2.5033 (R Development Core Team) for each camera trap point.
Trophic Function	Herbivore Richness (Chao Estimate)	Chao estimate of the sum total herbivore richness at a single camera trap point.	
Trophic Function	Omnivore Richness (Chao Estimate)	Chao estimate of the sum total omnivore richness at a single camera trap point.	
Conservation Significance	Total Species Richness (Chao Estimate)	Chao estimate of the sum total species richness of a camera trap point.	We (Appendix Table A. 3.) applied the ‘estimateR’ function of the vegan package to the species occurrence matrix (species x camera trap point) calculate the Chao estimate of species richness at each camera trap point
Conservation Significance	Max. IUCN Category	The IUCN category of the most threatened species out of all the species recorded at a camera trap.	From the IUCN Red list, we obtained IUCN categories for each species (Appendix Table A. 1), converted the categories into numerical values such that Least Concern (LC)= 0, Near Threatened (NT) =0.5, Vulnerable (VU) = 1 and Endangered (EN) = 1.5. We then selected the highest IUCN category occurring at a camera trap point.
Conservation Significance	Max. Body Length	The maximum body length of a species recorded at a single camera trap.	We obtained information on body length from Animal Diversity Web (https://animaldiversity.org/), Janzen et al. (1983) and Garrigues and Dean (2014) and calculated the average body length (ABL) for each species. We selected the species with the largest body length occurring at a camera trap point.

Table A. 2. Calculation methods of 13 response variable in study.

Category	Variable	Definition/ Explanation	Calculation methodology
Conservation Significance	Human-Modified Landscape Users (%)	Percentage of species which are recorded to use 'Human-modified' habitats out of all recorded species at a camera trap.	If the habitat type of a species contained the classification 'Artificial/Terrestrial' under the 'Habitat/Ecology' section in the IUCN Redlist assessment of a species then the species was categorised as a 'Human Modified Habitat Users' (HML users). We expressed the number of HML user species at a camera trap as a percentage of the total number of species recorded at the camera trap.
Community Composition	Total Encounters	Sum total encounters of all species per camera trap.	We defined an 'encounter' to be the maximum number of animals in a continuous capture of a single species such that the minimum difference between two unique captures is two minutes. The 'total encounters' at a camera trap point was the sum total of the encounters of all the species.
Community Composition	Total Large Mammal Encounters	Sum total encounters of mammals (ABL > 100cm) per camera trap, where ABL = average body length	We summed all encounters of mammals within the specified body length category for each camera trap point.
Community Composition	Total Medium-sized Mammal Encounters	Sum total encounters of mammals (ABL 60-99cm) per camera trap.	
Community Composition	Total Small Mammal Encounters	Sum total encounters of mammals (ABL <59cm) per camera trap.	
Community Composition	Only Bird encounters	Sum total encounters of tinamous, curassows and guans	We summed the total number of encounters of <i>Tinamus major</i> , <i>Crax rubra</i> , <i>Cryptellurus boucardi</i> and <i>Penelope purpurascens</i> .

Table A. 3. Calculation methodologies for 12 predictors in study. All point-scale variables were calculated using images captured in April 2019 using a Mi Xiaomi phone (Model No. Redmi 4-MAI132) and on a Lenovo Thinkpad X470.

Scale	Variable	Calculation Method
Point	Understory density	<p>We calculated ‘understory density’, ‘extent of visibility’ and ‘no. of big trees’ from photos obtained by standing 2m from the camera trap, at a height of 175cm and tilting the phone-camera to an angle such that ~50% of the image covered the ground and ~50% of the image covered the above-ground vegetation (Appendix Fig.A.1). There were four such images for each camera trap point, starting facing the camera and then tuning 90°, 180° and 270° (Appendix Fig. A.1). We selected three images to act as references for each of the below described qualitative measures. The researcher scored images blind to location.</p> <p>To measure understory density, we scored photographs as ‘no understory’, ‘medium understory’ and ‘dense understory’, corresponding to a score of 0, 0.5 and 1 respectively. To measure extent of visibility, we scored visibility as 3–6m, 6–9m or >9m.</p> <p>To count ‘the number of big trees’ in a 3m radius of a camera trap, we identified a tree with circumference $\geq 30\text{cm}$ using prior field knowledge. The circumference of this tree on 13.5cm height image was measured 1cm, and this 1cm was used as the size-reference for a ‘big tree’. Only those trees within $4.5\text{cm} \pm 0.5\text{cm}$ of the height of the photograph (i.e., within 3m of a camera trap) were counted. The total number of big trees in each camera trap point was calculated as a sum total of number of big trees in each of the four photographs in each camera trap point.</p>
Point	Extent of Visibility	
Point	No. of Big Trees	
Point	Canopy Cover	<p>We captured canopy cover by holding the camera at a height of ~180cm at an angle parallel to the ground. We calculated the canopy cover by converting images to black and white, noting the color of plant and sky with image numbers, generating a histogram, recording black and white values of the image in ImageJ and dividing black/white+black or white/black+white depending on which color plant and sky were converted to.</p>
Forest	Area (sq. m)	<p>Study forest boundaries were manually drawn on Google Earth v7.3.2.5776 (Gorelick et al. 2017) Pro up to the nearest 1m and areas recorded manually. Due to the large values, the variable was log-transformed prior to scaling and centering.</p>
Forest	Forest to Road Distance (m)	<p>We identified the point at which the forest boundary was closest to a motorable road (See Methods) using satellite imagery and prior field knowledge, drew straight lines using the ruler tool on Google Earth v7.3.2.5776 (Gorelick et al. 2017) and recorded the distances. Due to the large differences between values, the variable was log-transformed prior to scaling and centering.</p>

Table A. 3. Methods of calculating the 12 predictors in study. All point-scale variables were calculated using images captured in April 2019 using a Mi Xiaomi phone (Model No. Redmi 4-MAI132) and on a Lenovo Thinkpad X470.

Scale	Variable	Calculation Method
Forest	Tree density	We calculated tree density using the ordered distance sampling method following Krebs (2014) in April 2019. Trees were defined as rooted, free-standing woody plants above 1.5m height and 1cm circumference. A total of ten random points, one per 20m segment of a transect, were sampled at in each of the 19 study forests. To ensure normal distribution of the values, the variable was log-transformed prior to scaling and centering.
Forest	Tree diameter (Rate Parameter)	We measured circumference of the three closest trees to each of the 10 random points used in the ordered distance sampling. The tree diameters of thirty trees at all the forests followed a Poisson distribution which could not be corrected with a scale parameter, therefore we calculated a rate parameter for the tree diameters using the 'eexp' function in the EnvStats package in RStudio v1.2.5033 (R Development Core Team) following de Lima et al. (2019). To ensure normal distribution of the values, the variable was log-transformed prior to scaling and centering.
Landscape	Total Forest Area in 500m radius	We calculated the total forest area from each camera trap point by drawing a circle with 500m radius using Google Earth v7.3.2.5776 (Gorelick et al. 2017) (Appendix Fig. A.2) around each point, and recording the sum of all forested area within the circle. To ensure normal distribution of the values, the variable was log-transformed, prior to scaling and centering.
Landscape	Total Forest Area in 2km radius	We used the same method as above, but with a 2km radius circle.
Landscape	Proximity Index	We calculated proximity index following Gustafson & Parker (1994) by generating a 1km buffer around a study forest using QGIS v3.10, incorporating the buffer into Google Earth v7.3.2.5776 (Gorelick et al. 2017), manually drawing and measuring Euclidean distances using the ruler tool and manually measuring the area of each forest. The measurements were used to calculate the proximity index for each study forest. The proximity index for the study forests 3–8 was calculated for the entire continuous forest encompassing them. See Appendix Fig. A.3.
Landscape	Plantation Matrix	We define matrix to be the anthropogenic-activity in the area immediately (within 1m) outside the study forest. For the continuous forest containing study forests 3–8 (See Fig.2.1) we considered the whole area of continuous forest as the study forest. We identified the matrix using both Google Earth v7.3.2.5776 (Gorelick et al. 2017) imagery and prior field knowledge. We classified it as only crop, mixed (combination of crop/plantation/settlements/forest) and only plantation. We converted the qualitative measure into quantitative by assigning only crop = 0, Mixed = 0.5 and only plantations = 1.

Table A. 4. Predictors Summary

Spatial scale	Predictor	Mean	SD	Median	Min	Max	Source	Transformation	Variance Inflation Factor (VIF)
Point	Plant Cover	87.5	6.96	88.8	60.4	97.2	In Situ Photographs	Scaled	1.17
Point	Understory density	0.625	0.278	0.625	0.00	1.00	In Situ Photographs	Scaled	4.17
Point	Extent of Visibility	4.39	1.34	3.75	3.00	8.25	In Situ Photographs	Scaled	3.59
Point	No. of Big Trees	1.61	1.25	1.50	0.00	7.00	In Situ Photographs	Scaled	1.24
Forest	Area (ha)	665 x 10 ¹	910 x 10 ¹	18.6	0.53	191 x 10 ²	Google Earth	Log, Scaled	5.37
Forest	Forest to Road Distance (m)	17.9	44.9	1.92	1.00	185	Google Earth	Log, Scaled	3.28
Forest	Tree diameter (Rate Parameter)	0.299	0.132	0.252	0.109	0.654	In Situ	Log, Scaled	3.46
Forest	Tree Density (No. of trees/ha)	0.083	0.024	0.078	0.046	0.143	In Situ	Log, Scaled	4.37
Landscape	Total Forest Area in 2km radius (ha)	149 x 10 ²	661 x 10 ¹	178 x 10 ²	576	187 x 10 ²	Google Earth	Log, Scaled	2.01
Landscape	Total Forest Area in 500m radius (ha)	119 x 10 ²	831 x 10 ¹	177 x 10 ²	18.9	181 x 10 ²	Google Earth	Log, Scaled	6.87
Landscape	Proximity Index	232 x 10 ³	264 x 10 ³	227 x 10 ²	47.7	646 x 10 ³	Google Earth	Log, Scaled	4.30
Landscape	Plantation Matrix	0.615	0.263	0.500	0.000	1.000	Google Earth & In Situ	Scaled	6.88

Table A. 5. Response variables summary.

Response Variable	Mean	SD	Median	Min	Max	Transformation Used
Max. Trophic Level	3.98	0.304	4.03	2.75	4.62	Square
Carnivore Richness (Chao Estimate)	1.50	1.35	1.00	0.00	10.0	Square root
Herbivore Richness (Chao Estimate)	3.04	1.81	3.00	0.00	9.0	Square root
Omnivore Richness (Chao Estimate)	2.19	1.52	2.00	0.00	7.0	Square root
Total Encounters	33.6	29.7	25.5	1.00	151.0	Cube root
Total Large Mammal Encounters	5.79	12.4	1.00	0.00	96.0	Cube root
Total Medium-sized Mammal Encounters	4.26	3.70	3.00	0.00	20.0	Cube root
Total Small Mammal Encounters	16.1	15.7	11.0	0.00	72.0	Cube root
Total Large Sized Bird Encounters	3.58	7.54	1.0	0.00	60.0	Cube root
Total Small Bird Encounters	3.89	11.0	0.00	0.00	80.0	Cube root
Total Species Richness (Chao Estimate)	7.63	4.14	7.00	1.00	25.0	1/4th root
Max. IUCN Category	0.519	0.512	0.50	0.00	1.50	None
Max. Body Length	107.0	39.2	105.0	51.7	215.0	Inverse
Human-Modified Landscape Users (%)	69.6	17.4	68.3	20.0	100	None

Table A. 6. Average daily encounter rate per forest within each of three different forest size classes. Forest Type denotes which type of forest the species was observed in.

Species	Forest (>350ha) (Continuous)	Forest (5-27ha) (Large)	Forest (0.5-3ha) (Small)	Forest Type
<i>Canis latrans</i>	0.0000	0.0000	0.0017	Only Small
<i>Cebus capucinus</i>	0.0015	0.0000	0.0000	Only Continuous
<i>Conepatus semistriatus</i>	0.0004	0.0014	0.0008	All Forest sizes
<i>Crax rubra</i>	0.0190	0.0125	0.0866	All Forest sizes
<i>Crypturellus boucardi</i>	0.0059	0.0000	0.0000	Only Continuous
<i>Cuniculus paca</i>	0.0250	0.0059	0.0000	Large & Continuous
<i>Dasyprocta punctata</i>	0.2299	0.2811	0.1043	All Forest sizes
<i>Dasyopus novemcinctus</i>	0.0382	0.0603	0.0494	All Forest sizes
<i>Didelphis marsupialis</i>	0.0188	0.0084	0.0837	All Forest sizes
<i>Eira barbara</i>	0.0028	0.0062	0.0027	All Forest sizes
<i>Galictis vittata</i>	0.0005	0.0000	0.0007	Small & Continuous
<i>Heteromys sp.</i>	0.0074	0.0029	0.0017	All Forest sizes
<i>Holcosus quadrilineatus</i>	0.0000	0.0004	0.0000	Only Large
Large Rats (<i>Hoplomys sp./Proechimys sp.</i>)	0.0028	0.0259	0.0091	All Forest sizes
<i>Leopardus pardalis</i>	0.0073	0.0095	0.0205	All Forest sizes
<i>Leopardus wiedii</i>	0.0004	0.0005	0.0000	Large & Continuous
<i>Metachirus nudicaudatus</i>	0.0000	0.0004	0.0000	Only Large
<i>Nasua narica</i>	0.0567	0.0637	0.2641	All Forest sizes
<i>Odocoileus virginianus</i>	0.0008	0.0000	0.0000	Only Continuous
<i>Panthera onca</i>	0.0004	0.0000	0.0000	Only Continuous
<i>Pecari tajacu</i>	0.0015	0.0000	0.0022	Small & Continuous
<i>Penelope purpurescens</i>	0.0021	0.0000	0.0000	Only Continuous
<i>Philander opossum</i>	0.0025	0.0064	0.1104	All Forest sizes
<i>Piaya cayana</i>	0.0005	0.0000	0.0000	Only Continuous
<i>Procyon lotor</i>	0.0009	0.0015	0.0000	Large & Continuous
<i>Puma concolor</i>	0.0023	0.0000	0.0000	Only Continuous
<i>Herpailurus yagouaroundi</i>	0.0000	0.0009	0.0039	Large & Small
<i>Sciurus granatensis</i>	0.0005	0.0000	0.0000	Only Continuous
<i>Sciurus variegatoides</i>	0.0000	0.0004	0.0000	Only Large
<i>Sylvilagus sp.</i>	0.0057	0.0186	0.0929	All Forest sizes
<i>Tamandua mexicana</i>	0.0023	0.0046	0.0046	All Forest sizes
<i>Tapirus bairdii</i>	0.0073	0.0004	0.0000	Large & Continuous
<i>Tayassu pecari</i>	0.0118	0.0000	0.0000	Only Continuous
<i>Tinamus major</i>	0.0471	0.0460	0.0008	All Forest sizes

Table A. 7. Distance between camera traps that worked during the study according to sampling period and Site ID. Refer Fig.2.1 for location of Site ID.

Site ID	Name of Site	Sampling Period	Distance (in m)
1	NIC	December	213
2	But	February	159
2	But	December	113
2	But	November	132
3	PIA	February	151.57
3	PIA	December	98.05
3	PIA	November	107
4	I5	February	213.44
4	I5	December	103.85
4	I5	November	100
5	PIB	February	186.56
5	PIB	December	138
5	PIB	November	154.84
6	I2N	December	263
6	I2N	February	120
6	I2N	October	156.09
7	PIC	December	30
7	PIC	february	120
7	PIC	November	170.59
8	PID	February	191
8	PID	December	177
8	PID	November	87
9	S6	February	92
9	S6	December	31.17
9	S6	November	78
10	S1	December	226.96

Site ID	Name of Site	Sampling Period	Distance (in m)
10	S1	November	62
11	L2	February	242
11	L2	December	148.97
11	L2	November	206
12	S2	December	106.38
12	S2	February	156
12	S2	November	195.47
13	PSP	December	86
13	PSP	February	284
13	PSP	October	270
14	L4	February	262
14	L4	December	254.33
14	L4	November	532
15	S4	December	94.15
15	S4	February	247
15	S4	November	214
16	L3	December	223
16	L3	November	176
17	L6	February	404
17	L6	November	363.3
18	PLA	December	480
18	PLA	February	540
18	PLA	November	765.6
19	PSA	December	116
19	PSA	February	193.57
19	PSA	November	125.5

Table A. 8. Reference list for Diet and Body Size from Animal Diversity Web and Bird Guide for Costa Rica – Garrigues & Dean (2007).

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Table A. 8. Reference list for Diet and Body Size from Animal Diversity Web and Bird Guide for Costa Rica – Garrigues and Dean (2007).

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Table A. 9. Reference list for information from IUCN Red List Database.

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Fig. A. 1. Methodology of information collection for point-scale predictors. S1, S2, S3, S4 are Side1, Side2, Side3 and Side4, the images at right angle to each other obtained from each side of a camera trap by standing at a distance of 2m from the camera trap, at a height of ~170 cm and placing the phone at an angle such that each image recorded 50% above ground vegetation and 50% ground.

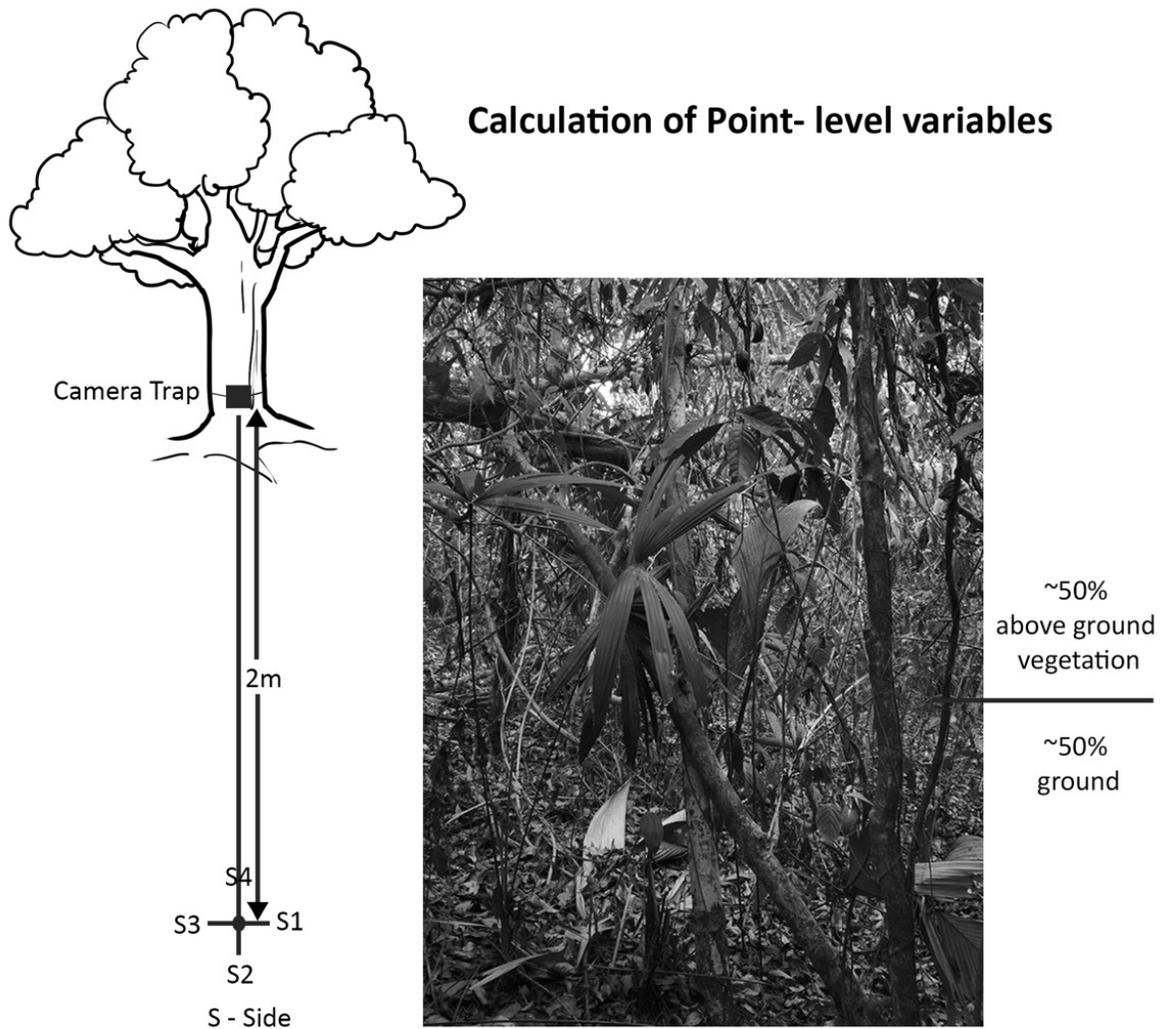


Fig. A. 2. Total Forest Area in 500m (a) 2km Panel (b): Calculated by drawing a circle of respective radii from a single camera trap point (focal point) using the circular ruler tool in Google Earth Pro v7.3.2.5776, measuring the area of forests (in grey) within circle and summing it on RStudio v1.2.5033. We acknowledge that spatial covariance is possible between nearby sites where circles partially overlap using this method.

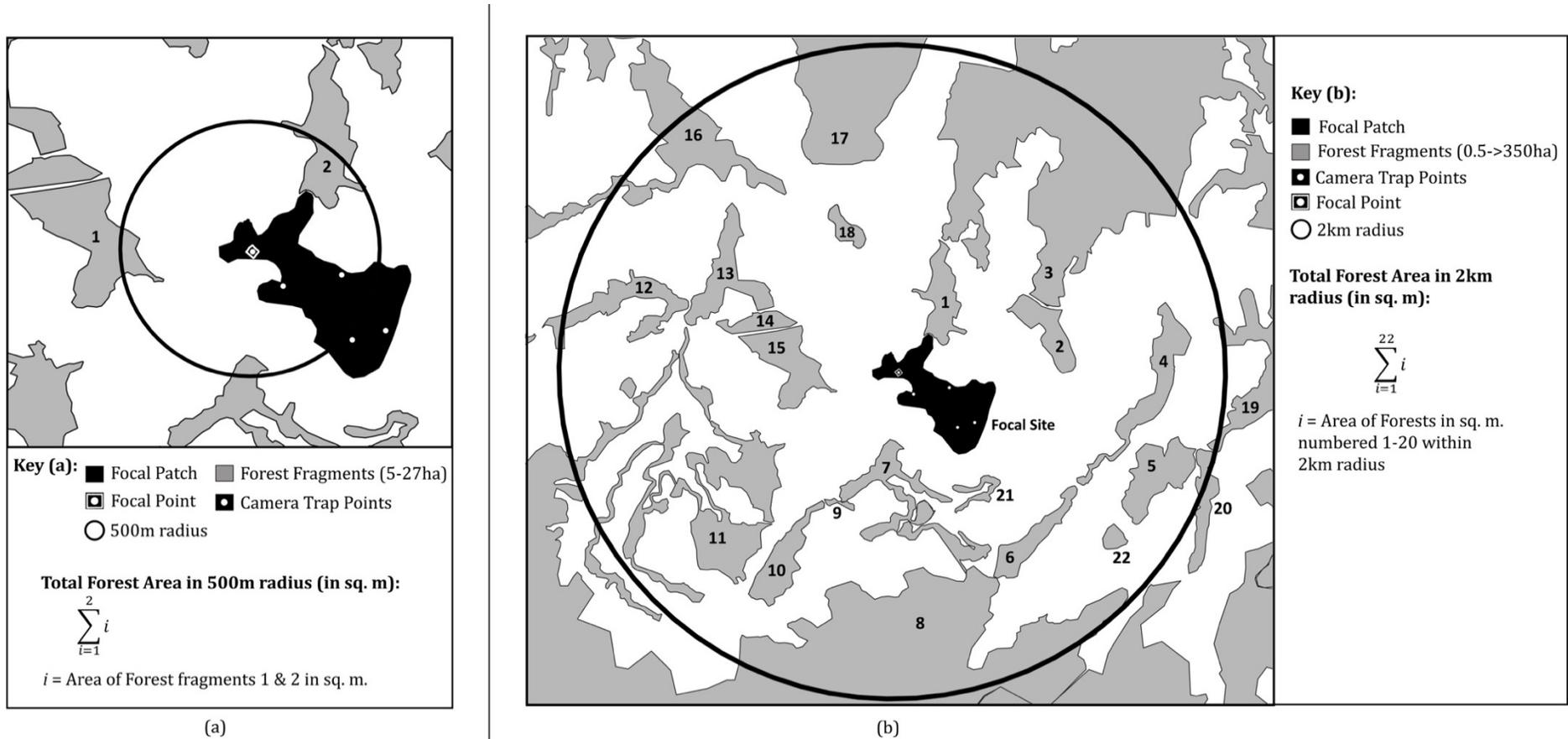


Fig. A. 3. Calculating Proximity Index for one study forest (Focal Forest). Forests which are within a 1km buffer of focal forest are numbered 1-18 and Euclidean distances from 'Focal forest' to other forests are denoted by letters a-r. The 1km buffer was generating using QGIS and Euclidean distances using ruler tool on Google Earth v7.3.2.5776 (Gorelick et al. 2017) Pro. The equation used to calculate the proximity index is displayed on the right.

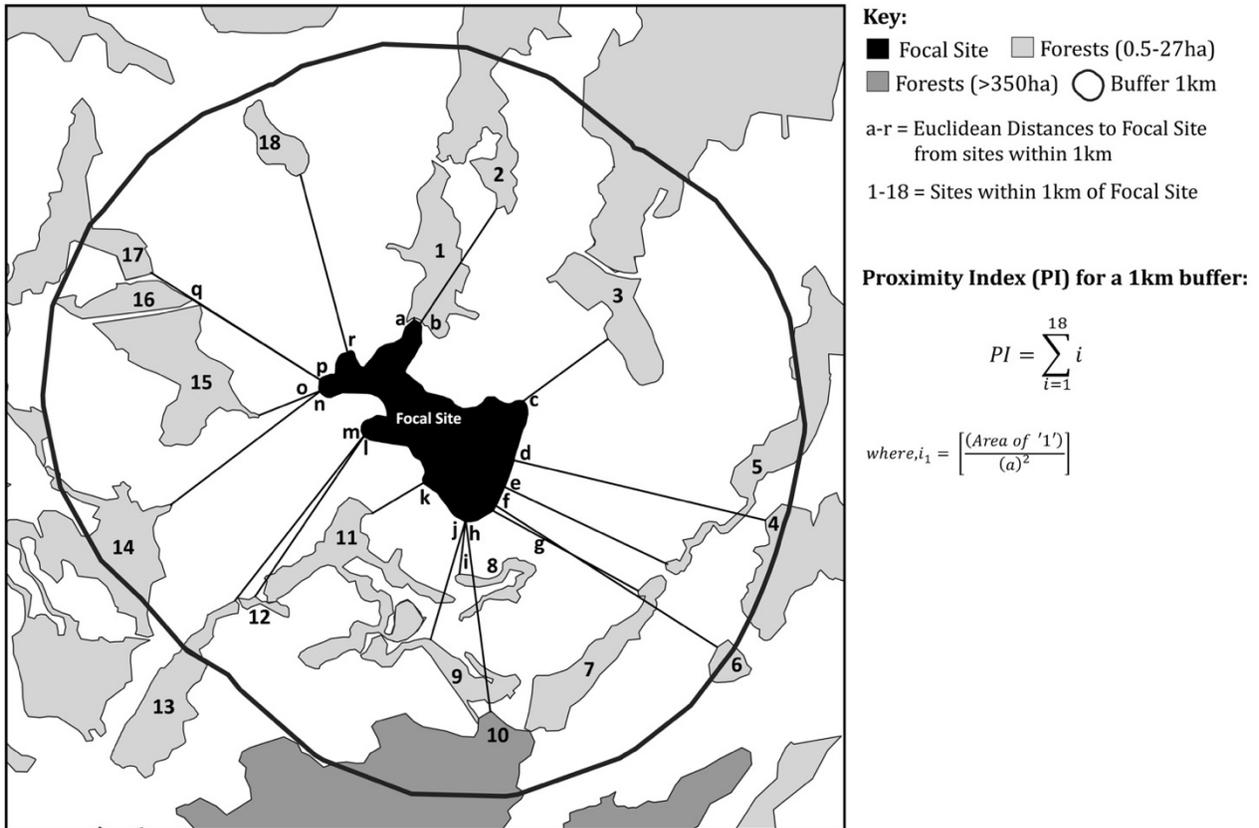


Fig. A. 4. Species accumulation curve for study area, with images pooled over the entire sampling period for each camera trap.

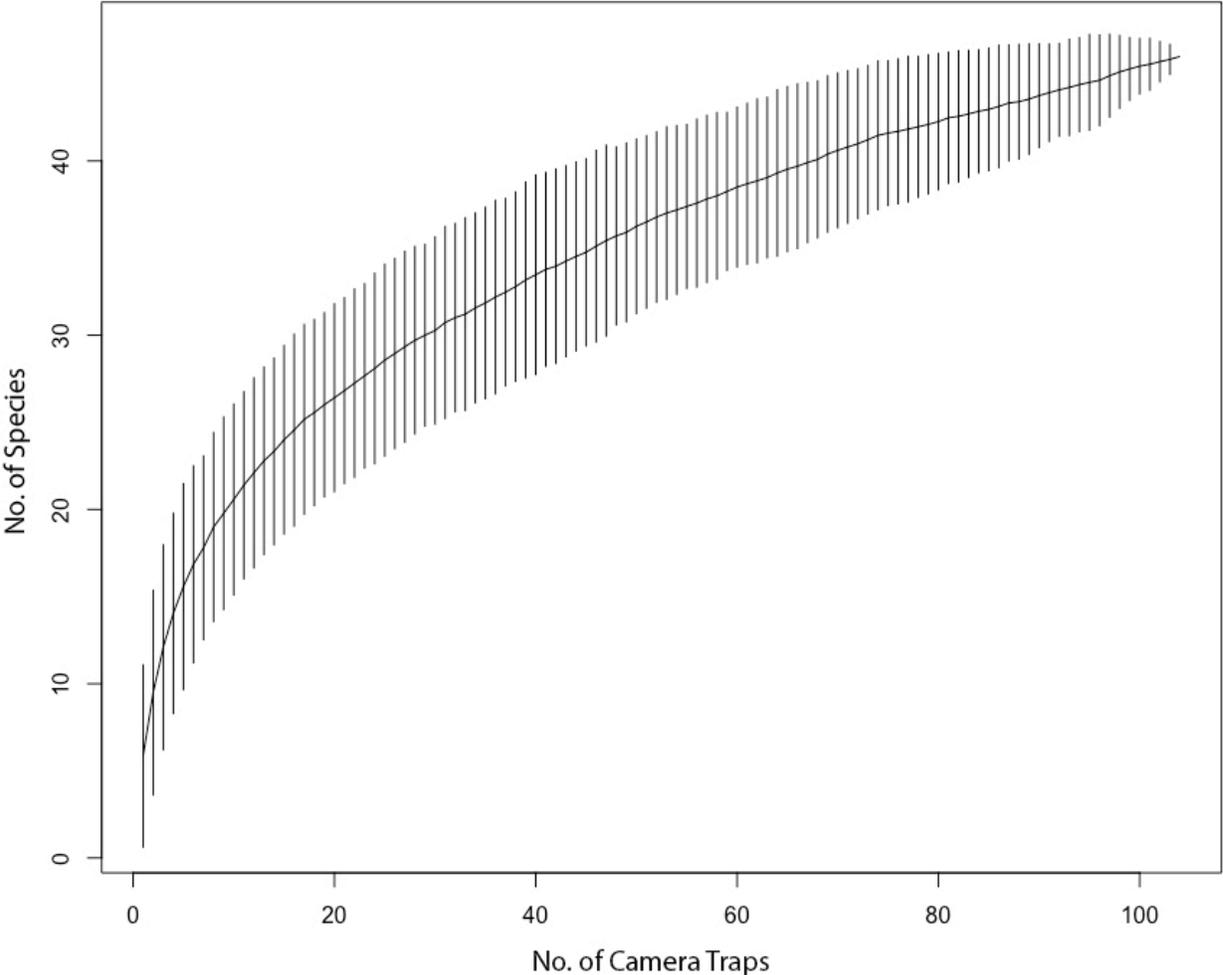


Fig. A. 5. Species accumulation curve for study area, with images pooled over the entire sampling period for each camera trap in black, for all forest fragments in red and forests sampled in continuous forests in blue.

