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MONITORING MAMMALS AT MULTIPLE SCALES: CASE STUDIES FROM CARNIVORE COMMUNITIES

Kadambari Devarajan
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**MONITORING MAMMALS AT MULTIPLE SCALES:
CASE STUDIES FROM
CARNIVORE COMMUNITIES**

A Dissertation Presented

by

Kadambari Devarajan

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

September 2021

Organismic and Evolutionary Biology

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Kadambari Devarajan

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Toni Lyn Morelli, Chair

Paige Warren, Member

Jason Kamilar, Member

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DEDICATION

To Bhagya *paati*, grandma extraordinaire, for teaching me a great many things - hopscotch, pickling, and the grounding philosophy that *katradhu kaimanalavu*, *kalladhadhu ulagalavu* (*Tamil* for: what we have learned amounts to a fistful of sand, what we have yet to learn encompasses the whole world.)

And to *Carnivoro extinctus*, the mythical megacarnivore standing in for all the carnivores lost forever from this pale blue dot.

“Every thing must have a beginning. . . and that beginning must be linked to something that went before. . . Invention, it must be humbly admitted, does not consist in creating out of void, but out of chaos; the materials must, in the first place, be afforded: it can give form to dark, shapeless substances, but cannot bring into being the substance itself.”

– Mary Wollstonecraft Shelley, *Frankenstein*

“Know the ways of the ones who take care of you, so that you may take care of them. Introduce yourself. Be accountable as the one who comes asking for life. Ask permission before taking. Abide by the answer. Never take the first. Never take the last. Take only what you need. Take only that which is given. Never take more than half. Leave some for others. Harvest in a way that minimizes harm. Use it respectfully. Never waste what you have taken. Share. Give thanks for what you have been given. Give a gift, in reciprocity for what you have taken. Sustain the ones who sustain you and the earth will last forever.”

“The land is the real teacher. All we need as students is mindfulness.”

– Robin Wall Kimmerer, *Braiding Sweetgrass: Indigenous Wisdom, Scientific Knowledge, and the Teachings of Plants*

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ABSTRACT

MONITORING MAMMALS AT MULTIPLE SCALES: CASE STUDIES FROM CARNIVORE COMMUNITIES

SEPTEMBER 2021

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M.Sc., NATIONAL CENTRE FOR BIOLOGICAL SCIENCES - TATA

INSTITUTE OF FUNDAMENTAL RESEARCH

Ph.D., UNIVERSITY OF MASSACHUSETTS AMHERST

Directed by: Professor Toni Lyn Morelli

Carnivores are distributed widely and threatened by habitat loss, poaching, climate change, and disease. They are considered integral to ecosystem function through their direct and indirect interactions with species at different trophic levels. Given the importance of carnivores, it is of high conservation priority to understand the processes driving carnivore assemblages in different systems. It is thus essential to determine the abiotic and biotic drivers of carnivore community composition at different spatial scales and address the following questions: (i) What factors influence carnivore community composition and diversity? (ii) How do the factors influencing carnivore communities vary across spatial and temporal scales? (iii) At local scales, what are the roles of within- and between- guild interactions in structuring carnivore communities? I use carnivore distribution data from protected areas across the global

tropics to understand how multiple biodiversity metrics track one another at the regional scale. At the landscape scale, I apply carnivore community data from India to understand how spatiotemporal interactions at the local scale influence carnivore distribution patterns at larger scales. Lastly, at the local scale, I implement a field study of carnivore community occupancy at Kasanka National Park in Zambia using camera traps to understand spatiotemporal patterns of distribution. I employ these studies to delineate the importance of scale in developing a theoretical and applied understanding of community ecology, monitoring mammals at the community level, and conserving carnivore communities. This research shows that carnivore conservation and biodiversity monitoring at the community level is both context-specific and scale dependent.

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OVERVIEW

... the problem is not to choose the correct scale of description, but rather to recognize that change is taking place on many scales at the same time, and that it is the interaction among phenomena on different scales that must occupy our attention. –Simon Levin (*The Robert H. MacArthur Award Lecture - 1989*)

The distribution, regulation, and maintenance of biodiversity are considered fundamental to ecology (Lawton, 1999; Peterson *et al.*, 1998; Sexton *et al.*, 2009). While they have been studied at different scales, there has been a bias towards small-scale experimental studies and large-scale meta-analyses for various reasons, including feasibility, access to resources, species and landscape characteristics, and the availability of tools to researchers (Levin, 1992; Schneider, 2001; Mayor *et al.*, 2009; McGill, 2010; McGarigal *et al.*, 2016). As a result of this, the proximate causes of local dynamics and the mechanisms behind interactions have been well-studied for certain taxa disproportionately over others. At larger scales, studies have tended to focus on pattern rather than process (Figures 0.1–0.4). The notions of pattern and scale are considered tightly interconnected, where pattern is a surrogate for variation, the measurement of which hinges on the scale being considered (Levin, 1992; Schneider, 2001; McGill, 2010; Peters *et al.*, 2007).

Considerations of pattern and scale are, indubitably, central to ecology and biogeography (Levin, 1992; Schneider, 2001; McGill, 2010). These are intricately related to the objectives of the study. Increasingly, ecological research seems to involve data collected at different spatial, temporal, and organizational scales (Figures 0.1, 0.2).

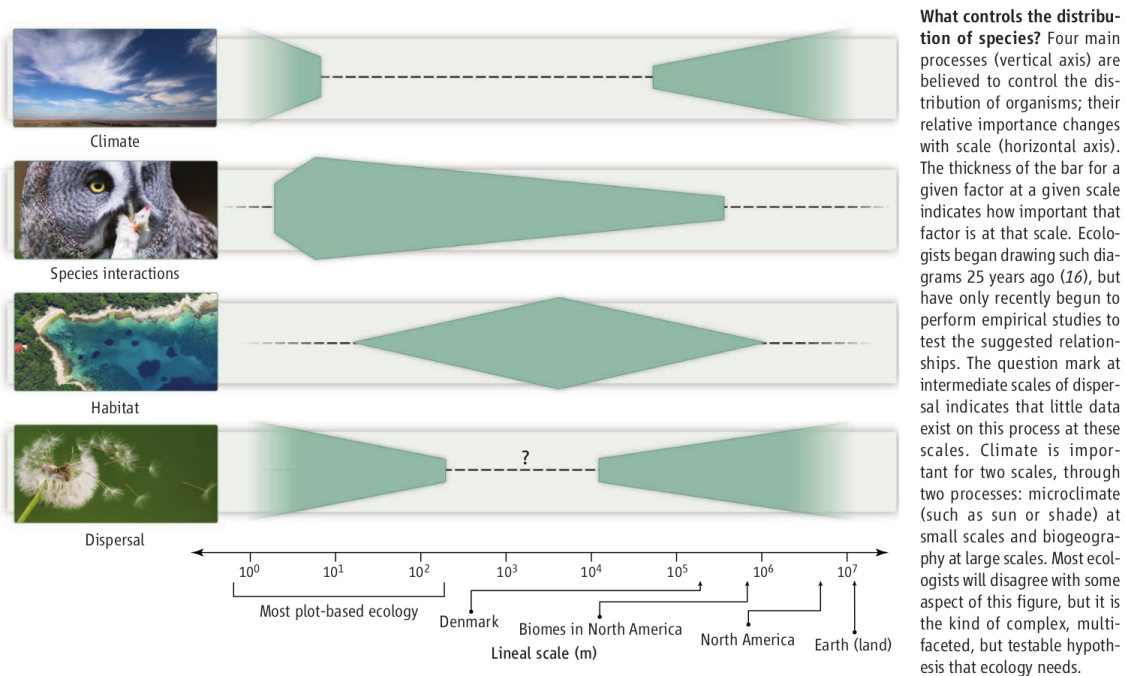


Figure 0.2. Diagrammatic representation of the processes driving species distributions at different spatial scales. This differs from (Figure 0.1) since it depicts how some factors could emerge as important drivers at multiple scales (eg. climate and dispersal). [Source: (McGill, 2010)]

tion and abundance of species from a single season or at best a few seasons of data. Long-term datasets from the wild or multi-year enclosure experiments are countably rare, primarily due to logistical and methodological constraints. In order to make robust inferences, the spatial and temporal scales chosen should be relevant to the level of organization the study species fall under.

Monitoring Carnivore Communities

Carnivores are distributed widely, and considered to be important in the structure and functioning of species assemblages and communities through their direct and indirect interactions with other species at different trophic levels (Jiménez *et al.*, 2017; Gompper *et al.*, 2016; Schuette *et al.*, 2013). Given their importance, and the enormous pressure that vertebrate carnivores are experiencing from global change (Linnell

& Strand, 2000; Linnell *et al.*, 2001; Gittleman *et al.*, 2001; McKenna & Bell, 1997), it is of high conservation priority to understand the factors driving carnivore community assemblages in different systems.

Monitoring wildlife populations has been an essential component of ecological studies and conservation strategies. While classical methods such as those involving point counts, transects, mist nets, cover boards, and pitfall traps continue to be in use for studying populations of birds, reptiles, and amphibians, tools like camera traps and drones are gaining traction for monitoring mammals (Devarajan *et al.*, 2020). Advances in technology and increased access by researchers, wildlife managers, policy makers, and citizen scientists have resulted in a dramatic increase in methods involving camera traps, aerial surveys, drones, and GPS loggers for wildlife monitoring in the past decade. Interest in studying entire communities simultaneously is growing, paving the way for multi-species or community models in ecological research (Devarajan *et al.*, 2020). However, incorporating species interactions into these models is considered challenging and hence remains an underutilized, if important, aspect of wildlife monitoring (Waddle *et al.*, 2010; Rota *et al.*, 2016).

Hierarchical modeling approaches such as occupancy modeling (MacKenzie *et al.*, 2002) and spatial capture-recapture (Royle & Young, 2008; Royle *et al.*, 2009) are emerging as the *de facto* statistical methods for studying species occurrence, distributions, and abundance (Figure 1.3). The most commonly used methods for estimating occupancy involve detection/non-detection data, while count data is used for estimating the abundance of species. Until recently, monitoring studies have focused on single species, although the tools used for wildlife monitoring frequently result in the detection of several species that can be thought of as ‘monitoring by-catch’.

A study that has been designed for a guild of large and meso-carnivores will differ in both field implementation and statistical modeling compared to one that aims to understand species richness across a community or one involving specific prey and predator species. Interactions such as competition (or niche partitioning), mutualisms and other associations, herbivory and predation play an important role in structuring communities. Failing to incorporate and account for these in studies will result in a loss of ecological-realism as well as a flawed and incomplete representation of complex systems.

It is important to include biotic interactions while designing community studies depending on the scale of the study. The degree and nature of the interactions between species needs to be incorporated; if this is not possible, the consequences of not including biotic interactions should be stated (Devarajan *et al.*, 2020). For instance, the modeling framework as well as the study design of a multi-species study will change based on whether the species of interest are all carnivores, herbivores, or a mix. The framing of the model will change based on whether it involves, for instance, a prey-predator interaction or a size-based interaction with dominant and subordinate species. Furthermore, this is something that needs to be kept in mind during the design phase for a multi-species study.

While habitat characteristics and other abiotic factors are almost always considered in estimating species presence, species traits and interactions are frequently disregarded. This is in part due to the complexity involved in modeling species interactions (Waddle *et al.*, 2010; Rota *et al.*, 2016). It is computationally and statistically difficult to disentangle species interactions, which ends up adding another level of uncertainty to an already complex and challenging problem. This is amplified in systems with rare and elusive species, dynamic landscapes, and disturbances (anthropogenic

and otherwise) (Sollmann *et al.*, 2011). Community-level studies are also resource intensive, need a lot of planning, and frequently have complicated project logistics.

Given the practical importance of such multi-species models, it is crucial to determine which species characteristics or traits (such as detectability, body size, home range, and behavior) are most influential in multi-species datasets. It is also essential to understand how sensitive statistical inference is to study design, especially when studies are designed for a focal species but can give insights about a community landscape. The role of biogeographic barriers, current and historical environment, physiological and ecological species traits or environmental filtering, and biotic interactions in determining community composition is a fundamental line of inquiry in ecological research (Webb *et al.*, 2002).

In this dissertation, I address the following questions:

- What factors influence community composition and dynamics?
- How do the factors influencing communities vary across spatial and temporal scales?
- At local scales, what are the roles of within- and between- guild interactions in structuring communities?

These questions are crucial in developing a theoretical and applied understanding of community ecology, and for monitoring biodiversity at the community-level.

To understand community composition and infer interactions a multi-pronged approach involving camera traps for spatio-temporal interactions and available dietary data or scat analysis for dietary preferences is often necessary. A multi-method approach to estimating species occurrence involving camera traps, hair snares, and

track plots is useful in maximizing coverage for carnivore communities. In addition to providing insights into the spatial distribution and density patterns of mammalian species, time-activity data can be obtained based on camera timestamps. For carnivores, camera traps, in combination with geospatial and bioclimatic data, can facilitate understanding spatial and temporal patterns, as well as habitat use. An important benefit of camera traps, scat collection, and hair snares is that they are non-invasive, and can be used to study rare, elusive, and nocturnal species, and several of them at once.

In this dissertation, I review the community modeling literature to evaluate current best practices for focal-species and community-focused monitoring study design (Chapter 1). I also design and conduct a field study (Chapter 4), and use existing data sets to understand the drivers of carnivore community composition and dynamics at different scales (Chapters 2 and 3).

My broad hypotheses are that at regional scales, habitat features and climate are likely to be more important than interactions between species. Biotic interactions, anthropogenic influences, and land cover/habitat characteristics are likely to be more important at local and landscape scales. For a regional scale study on carnivore communities, I implemented a study of biodiversity metrics relevant to carnivore communities in the global tropics and sub-tropics (Chapter 2). At the landscape scale, I used existing data from a study designed for a guild of carnivores to identify the abiotic and biotic drivers of multi-species distribution patterns (Chapter 3). Lastly, at the local scale, I conducted a field study of carnivore community occupancy at Kasanka National Park in Zambia using camera traps to understand spatiotemporal patterns of distribution (Chapter 4). The latter two chapters build on the literature review of multi-species occupancy studies (Chapter 1).

Chapters

Chapter 1: Multi-species Occupancy Models: Review, Roadmap, and Recommendations

Recent technological and methodological advances have revolutionized the monitoring of wildlife. Although most biodiversity monitoring initiatives are geared towards focal species of conservation concern, focus has increasingly shifted to the study of entire communities, specifically the spatiotemporal drivers of community size and structure and interactions among species. This has resulted in the emergence of multi-species occupancy models (MSOMs) as a promising and efficient approach for the study of community ecology. Given the potential of MSOMs for conservation and management action, it is critical to know how sensitive inferences are to study design and assumption violations. This is especially true for studies that are designed for a focal species but can give insights about a community.

In this chapter, I implement a systematic review of the recent literature on MSOMs, identify areas of improvement in the multi-species study workflow, and provide a reference model for best practices for focal-species and community-focused monitoring study design (Devarajan *et al.*, 2020). This was done by finding literature related to community or multi-species models through the Web of Science portal, and from the resulting journal articles, using the software package ViXen (Ramachandran & Devarajan, 2018) for extracting information such as the taxa being studied, study design and methods, detectors used, spatial and temporal scales, and study area. The review focused on 92 studies published between 2009 and early 2018, spanning 27 countries and a variety of taxa.

This literature review was used to inform a roadmap with best practices for MSOM studies, from simulations to design considerations and reporting, for the collection of new data as well as those involving existing datasets. This review highlights a consistent under-reporting of details that are central to determining the adequacy of designs for generating data that can be used to make inferences about community level patterns of occupancy, including the spatial and temporal extent, types of detectors used, covariates considered, and choice of field and statistical tools. This reporting bias could consequently result in skewed estimates, affecting conservation actions and management plans. On the other hand, comprehensive reporting is likely to help researchers working on MSOMs assess the robustness of inferences, in addition to making strides in terms of reproducibility and reusability of data.

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Chapter 2: Drivers of Carnivore Community Composition, Diversity, and Distribution at the Regional Scale

At large scales, the differential rates of speciation, extinction, and dispersal are thought to influence species distributions and abundances (Barnosky, 2001; Sexton *et al.*, 2009). Geographical area as well isolation, evolutionary history, and climate are considered to be important factors influencing global trends in species diversity, composition, distribution, and abundance (Brown, 1971; Colwell *et al.*, 2004; Fleagle & Gilbert, 2006; Gaston, 2009; Mayor *et al.*, 2009; McCain & King, 2014; Pearson & Dawson, 2003; Svenning *et al.*, 2015).

Vicariance events and disturbance can also be considered important across scales, depending on the nature and intensity of the event. Regional cycles such as glaciation and the prehistoric ranges of organisms are considered important factors that help explain why there are no lizards in Massachusetts or why several plant species are shifting northwards (Fleagle & Gilbert, 2006; Sexton *et al.*, 2009; Svenning *et al.*, 2015). Thus the drivers of the distribution and abundance of species are multifarious with interactions between the factors either damping or amplifying certain effects. There are a number of hypotheses that attempt explaining how fitness varies across species ranges, such as range limit theory, lower fitness at range margins, and the abundance center hypothesis (Colwell *et al.*, 2004; Gaston, 2009; Sexton *et al.*, 2009) (although there is some contradictory evidence from invasion ecology).

The regional scale is one of the larger spatial scales where there is not much variation in the climatic layer and there is a dispersal limitation that is a barrier to species distributions. Area and isolation, which determine the rates of colonization or immigration and extinction, are considered determinants of species distribution and abundance at the regional level (Pearson & Dawson, 2003; Sexton *et al.*, 2009; McCain & King, 2014). All the species occurring in the region, taken together, are indicative of the gamma diversity of the area. The landscape scale, which is a rung below the regional scale in the hierarchy, in terms of extent, is linked with the regional scale through the turnover of species (Peters *et al.*, 2007). This is the change in species composition between communities across a landscape, and is measured through the beta diversity which is the variation in species diversity.

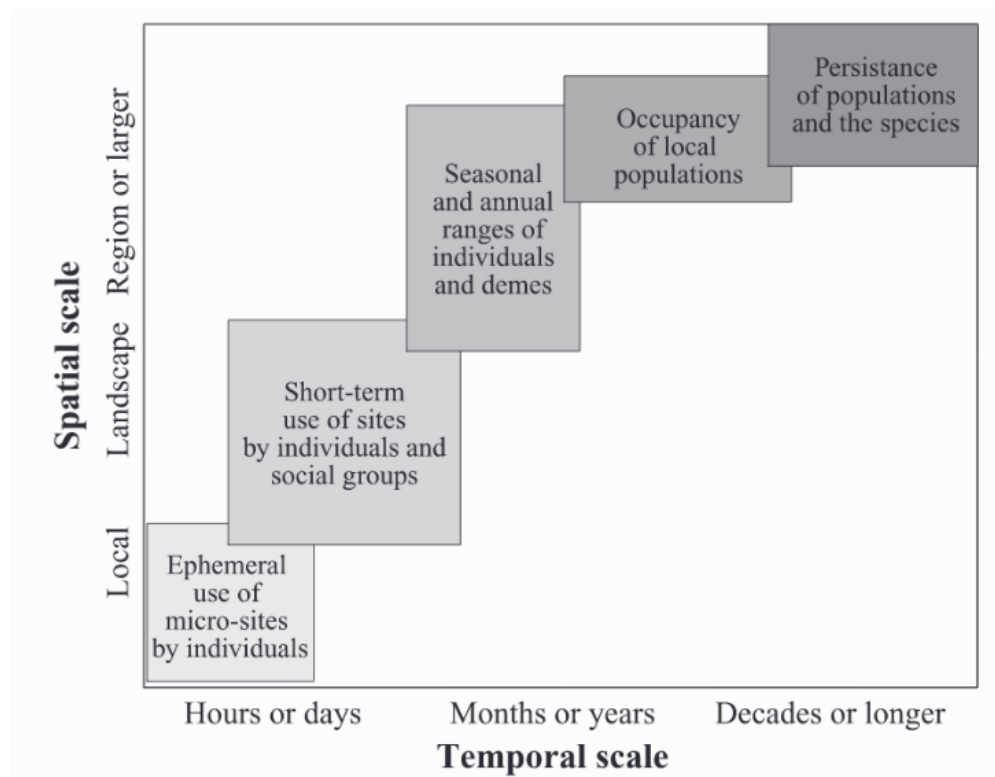


Figure 0.3. Diagrammatic representation of the relationship between spatial and temporal scales. This is particularly relevant for long-lived and wide-ranging species such as ungulates. [Source: (Mayor *et al.*, 2009)]

The smallest spatial scale in the hierarchy is the local scale, which is at the community-level and indicative of how suitable the habitat is in terms of both biotic and abiotic conditions. The species diversity at this scale is termed as alpha diversity. Species characteristics, such as physiology, along with biotic interactions emerge as important drivers of species distribution and abundance at the local scale (Barnosky, 2001; Brown, 1971; Mccain & King, 2014; Cunningham *et al.*, 2021).

Climate is known to be a major driver of evolution in organisms, having impacts on their population dynamics as well as distributions, at large as well as small scales (Fleagle & Gilbert, 2006; Mccain & King, 2014; Pearson & Dawson, 2003; Sexton *et al.*, 2009; Svenning *et al.*, 2015). The distributions and geographic ranges of different species are influenced by environmental variation through impacts on energy acquisition and physiological tolerances. While populations respond to such changes in the physical environment through adaptations, the responses by individuals to these changes happens through acclimation. Responses to climate change can take the form of “local extirpations, range contractions and shifts, decreased abundance, phenological shifts, morphological or genetic changes” (Mccain & King, 2014).

In a review of studies on how mammals (typically homeothermic or heterothermic endotherms) respond to climate change involving 73 North American and 8 other species occurring elsewhere, body size and activity times were found to be the main drivers, when several behavioral, physiological, and biogeographic traits were considered (Mccain & King, 2014). Factors that could influence species response include species traits, biogeography, and phylogeny (Mccain & King, 2014; Fleagle & Gilbert, 2006; Sexton *et al.*, 2009; Svenning *et al.*, 2015). Of the traits examined, species distributions and ranges correlated with responses to climate change, i.e., the mammals occurring in higher latitudes and/or altitudes were more likely to respond to changes

in climate (McCain & King, 2014; Pearson & Dawson, 2003). Since traits such as hibernation, burrowing, and nesting were not found to be major factors, one possible conclusion is that some mammals can reduce the impacts of climate change through behavioral adjustments, while others cannot. Given this, it is necessary to examine physiological responses at the individual level to understand how body size and activity times, which are tightly coupled with the physiology of organisms, are affected by environmental variation.

There are several mechanisms that could result in non-random species assemblages at large geographical scales. Some drivers of community composition and richness include trait- or environment-associated speciation and extinction, density-dependent speciation and extinction, habitat filtering and geographical range limits, and inter-specific competition (Cardillo, 2011). There are several considerations when studying community composition: What kinds of organisms compete with each other? Is there scale-dependence in the relative importance of competition and habitat filtering? Is there variation in the impact of competition and habitat filtering based on the habitat type (extreme or resource-limited habitats such as deserts vs. less extreme habitats like grasslands and forests)? Which species traits are important in order to monitor communities? What if closely related species don't have similar biological traits?

The focus of this chapter is to compare species co-occurrences and community composition across the tropics and sub-tropics. I used a dataset of 515 mammal communities that was originally constructed for a study on the ecological and evolutionary drivers of mammal biodiversity (Rowan *et al.*, 2020) to understand how biodiversity metrics for carnivore communities track one another.

Chapter 3: Drivers of Carnivore Distribution at the Landscape Scale

For a species of interest, their distribution is given by the range of their occurrences, at a predetermined spatial and temporal scale (Figure 0.4). Similarly, their abundance is indicative of their population size. A number of analytical methods have come about to help understand why organisms are where they are and what causes them to vary in their abundance. For instance, occupancy analysis and species distribution models are often used to understand the distribution of species, while spatial capture-recapture is used to estimate abundances. These methods incorporate models comprising of different factors that could predict occurrence and density. These predictors include abiotic factors, biotic factors, dispersal, history, and evolution. Abiotic factors are climatic and environmental conditions including water, temperature, humidity, wind, altitude, and soil, while biotic factors include interactions among species.

The physiological and ecological characteristics of a species that influence their distribution and abundance are called environmental or habitat filtering. At large geographical scales, the mechanisms that produce non-random assemblages include trait- or environment-linked speciation and extinction, density-dependent speciation and extinction, habitat filtering and range limits, and interspecific interactions. Climate and physical features are important at the regional scale, while land cover and habitat type emerge as important drivers at smaller scales. However it is necessary to keep in mind that there are interactions and correlations between the factors themselves. For instance, the interactions between habitat and climate are well understood. Climate could also be related to species traits such as cold tolerance and physiological limits.

Anthropogenic change is also emerging as an important predictor of species distribution and relative abundance patterns, especially at local scales. Anthropogenic effects related to urbanization, roadways, land use, logging, pollution, hunting, over-harvesting, habitat fragmentation, and disease all have differential impacts on different organisms at different scales. For instance, among mammalian carnivores, certain species, including big cats such as leopards, are able to adapt to urbanization better than others. Human commensals such as rodents and dogs also impact other mammals through competition, predation, and disease transmission, affecting species distributions and abundances in complex ways.

This chapter will focus on carnivore community data from the Banni grasslands of northwestern India, from a study that was designed for canids. This dataset is from a field-based study of a guild of co-occurring, mammalian carnivores using camera traps in an arid ecosystem in India. In this chapter, I use this data to understand how spatiotemporal partitioning between the study species at local scales relates to their co-occurrence at larger spatial scales.

I used a Bayesian hierarchical modeling approach using JAGS and involving MSOM best practices described in Chapter 1 to estimate the occupancy of the four canid species. I identified how different biotic and abiotic factors influenced the species distribution patterns and used a body size-based framework to incorporate biotic interactions between the species.

This manuscript based on this chapter is currently under revision for a journal. A preliminary version is available on bioRxiv (Devarajan & Vanak, 2020):

Devarajan, K. (2021). Spatiotemporal Partitioning at Local Scales Facilitates Carnivore Coexistence at the Landscape Level.

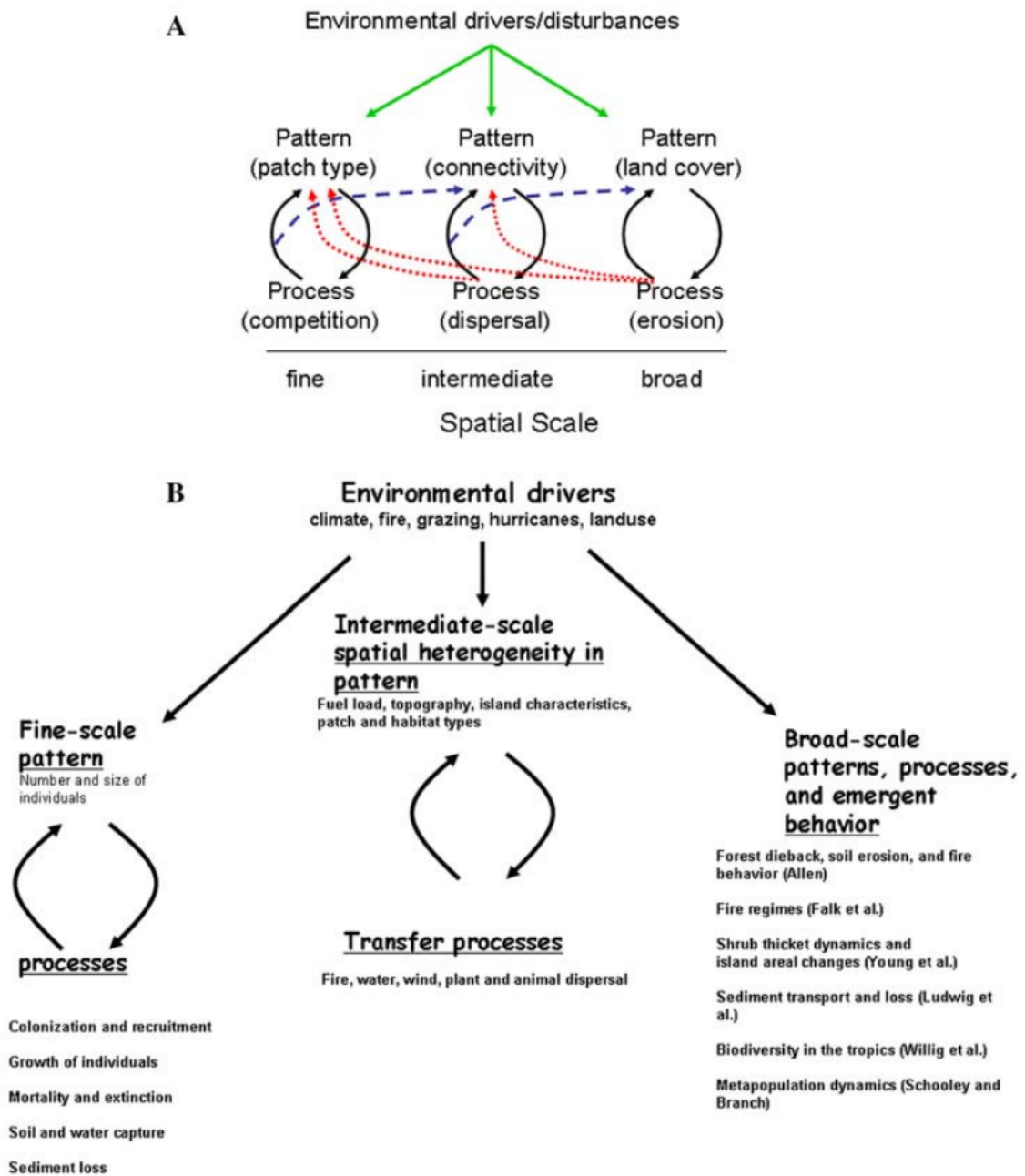


Figure 0.4. A diagrammatic representation of cross-scale interactions and pattern-process relationships. [Source: (Peters *et al.*, 2007)]

Chapter 4: Drivers of Carnivore Distribution at the Local Scale

The mechanisms that drive the coexistence of species have been the focus of several studies, theoretical as well as experimental, in community ecology. The vast amount of research that has gone into understanding the coexistence of similar species in ecological communities has in turn helped advance the field of community ecology through the development of modeling tools, theoretical frameworks, and empirical data. However, despite being well-studied, the term ‘coexistence’ is often misunderstood and unclear in terms of the heterogeneity of definitions available. Furthermore, the problem of scale in ecology extends to species coexistence studies as well.

There are two broad frameworks that have been employed in studying species coexistence at different scales, namely, empirical and theoretical (May, 1974; Roughgarden, 1974; Paine, 1966; Holt *et al.*, 1994). The empirical approach has been characterized by resource partitioning studies, experimental or inferred, while the underlying basis for the theory behind coexistence has been the Lotka-Volterra model and its extensions. However, the Lotka-Volterra model has come under scrutiny for being more phenomenological as opposed to mechanistic, explaining patterns well but not sufficient to understand the processes driving species interactions and coexistence (Tilman, 1980, 1987).

Recent research in competitive coexistence has also been informed by the consumer-resource theory put forth by Tilman (Tilman, 1980). Tilman’s models differ from the Lotka-Volterra models by explicitly modeling the relationship between the consumer and resource without the consumer species partitioning or exploiting a resource implicitly through a mystery parameter. There are advantages and limits to using either of the frameworks and the models put forth under each. A disadvantage of Lotka-Volterra models has been reliance on analyses of behavior when the system is

at equilibrium, and relatively few studies under non-equilibrium conditions (Caswell, 1982). Another limitation is the assumption of similar resource utilization curves between interacting species by many researchers, despite evidence that shows facilitation of competitive coexistence when interacting species exhibit differently shaped resource utilization curves (Roughgarden, 1974).

The processes that are thought to influence species coexistence can broadly be categorized into biotic and abiotic. The biotic component is epitomized by interactions between species. While competition and predation have been the focal points of classical experiments, positive associations between species have also been considered. The abiotic axes have primarily comprised of resources such as habitat (involving resource selection, use, and limits), disturbance, and stress (such as the intermediate disturbance hypothesis). While this classification is more for convenience, research on coexistence typically builds on a mix of abiotic and biotic features. For instance, stress can be environmental or take the form of species interactions.

The interactions between species and among individuals of the same species have formed an integral component of species coexistence research. These interactions could be negative, such as competition, parasitism, and predation, or positive, like mutualistic complexes and commensalism, in nature.

- **Competition:** Competitive interactions have formed the basis for both empirical as well as theoretic research in species coexistence. Historically, Gause's experiment on competition between two species of paramecia, resulted in the definition of the 'competitive exclusion principle' (Gause *et al.*, 1934; Hardin, 1960), and spawned off the research on species coexistence. By the competitive exclusion principle, two species with identical niches cannot coexist and invariably result in one of the species outcompeting the other. Species coexistence

can thus be considered as an alternate outcome to competitive exclusion in competing species. The primary empirical methods for studying competition have involved resource partitioning and character displacement, while Lotka-Volterra models and their analogues have helped inform theoretical studies. Resource partitioning studies explore the limits placed by interspecific competition on the number and ability of species to coexist. Research on this was propelled by the Hutchinsonian niche concept, where a niche is thought of as a n-dimensional hypervolume, such that each dimension is a niche axis that corresponds to different biotic and abiotic factors that species differentially respond to (Whittaker *et al.*, 1973). Hutchinson also postulated, through observing the ‘paradox of the plankton’ (Hutchinson, 1961), that the time involved in the competitive exclusion of one species by another and the time taken by environmental variation to affect the population dynamics of the competing species interact to determine species coexistence. A disadvantage of resource partitioning studies is that not all factors or niche axes can be measured, only variation along a subset of the environmental and biological factors can be measured (the proportion of axes that are a subset of the n-dimensions is unknowable). Furthermore, the organisms and study systems chosen for these studies are non-random, and biased towards certain organisms and predictor variables. On the other hand, a major advantage of resource partitioning has been its biological realism. Body size and phylogeny have been popular biological variables, with both acting as proxies for a set of different variables - home range size, population dynamics, physiology, and phylogeny (Ziv, 1998; Basset, 1995; Hutchinson, 1959; Johnson, 1986). A common assumption in resource partitioning studies is that interspecific competition is stronger between species that are more closely related (and thereby having higher ecological similarity) (Thompson *et al.*, 1991). However there have been instances where this assumption does not hold (Jaksić *et al.*, 1993).

Several studies have explored species coexistence through character displacement in competing species. Classical studies include those on the Galapagos finches (Grant & Grant, 2014), Caribbean *anolis* lizards (Losos *et al.*, 1998, 2003), and East African cichlids (Meyer, 1993).

- **Predation and Positive Interactions:** Predation has experimentally been verified as an important mediator of species coexistence. A classic experiment that elucidates the importance of predation in structuring communities involves Bob Paine’s experimental manipulation of an intertidal invertebrate community that led to the keystone species and trophic cascades concepts, and understanding the importance of indirect effects in ecological communities. The experiment involved experimental field manipulation of the population densities of a predatory sea star (*Pisaster ochraceus*) that preferentially feeds on a mussel (*Mytilus californianus*) (Paine, 1966). Competitive exclusion (or the corollary, species coexistence) can be a consequence of not just resource-based competition, but any interaction that involves a limiting factor, such as disturbance, stress, or predation (Levin, 1970). This led to the rise of food web models which are an extension of Lotka-Volterra models that offer a more mechanistic interpretation than consumer-resource models (Holt *et al.*, 1994; Vance, 1978). Similarly, there are instances where positive associations have been shown to be important determinants of community structure, affecting species richness and diversity. In a salt marsh in New England, a transplant experiment involving plant and arthropod species, indicated that the most abundant plant species was found to facilitate species diversity, under conditions of intermediate disturbance or stress (Hacker & Gaines, 1997).
- **Disturbance and Stress:** Disturbance and stress are considered important environmental factors that influence community structure and species coexis-

tence. There are several theories and models that have been put forth to help explain different scenarios of coexistence between species. The intermediate disturbance hypothesis was an attempt in explaining the impacts of variation in disturbance (including stress and predation) on community species diversity and composition (Connell, 1978; Wilkinson, 1999). Under this theory, the frequency and intensity of disturbance on a community could drastically impact species diversity, and be a driver of coexistence. There is experimental evidence to support the hypothesis that species diversity is highest at intermediate levels of disturbance and stress (Connell, 1978; Sousa, 1979). There have been several extensions of this model to include predation, competitive displacement, dispersal, and positive interactions (Menge & Sutherland, 1987; Pollock *et al.*, 1998; Huston, 1979, 1999; Shurin, 2001; Hacker & Gaines, 1997). The Menge-Sutherland model differentiates the effects of stress and disturbance from the effects of predation (Menge & Sutherland, 1987). The lottery and neutral models place an emphasis on the roles of random chance and equality on the maintenance of species diversity and thereby influence coexistence (Sale, 1977; Hubbell, 2001).

How biotic interactions, current and historical environment, and biogeographic barriers affect species is considered a fundamental question in ecology. In his classic treatise, “Animal Ecology” (published in 1962), Charles Elton describes community ecology using pithy aphorisms and proverbs that represent the biotic factors influencing species. In brief, these are: (i) “*The large fish eat the small fish, the small fish eat the water insects, the water insects eat plants and mud.*”, (ii) “*Large fowl cannot eat small grain.*”, and (iii) “*One hill cannot shelter two tigers.*” These succinctly cover a variety of species interactions and related ecological concepts: predation and trophic levels, quality vs. quantity and body size vs. resource, and competition, food webs, niches, and population dynamics. Noticeably these are applicable primarily at the

local scale. Such interactions among species within a community at the local scale and effects of these interactions on community structure and species distributions form the basis of this chapter.

In this chapter, I investigate how abiotic factors and biotic interactions affect the distribution of carnivores in a particular landscape, namely in Kasanka National Park (KNP), Zambia. Of the 120 species of mammals thought to occur in KNP, about twenty species are large and meso-carnivores including felids, canids, and mustelids. In this understudied landscape with high biodiversity including threatened and elusive taxa, I studied carnivore community structure in order to understand the role of inter- and intra-guild interactions and species co-occurrence patterns. This pilot study will be a stepping stone for future field research in KNP to explore the role of interactions between carnivore species on their distributions under a hierarchical modeling framework.

CHAPTER 1

MULTI-SPECIES OCCUPANCY MODELS: REVIEW, ROADMAP, AND RECOMMENDATIONS

Abstract

Recent technological and methodological advances have revolutionized wildlife monitoring. Although most biodiversity monitoring initiatives are geared towards focal species of conservation concern, researchers are increasingly studying entire communities, specifically the spatiotemporal drivers of community size and structure and interactions among species. This has resulted in the emergence of multi-species occupancy models (MSOMs) as a promising and efficient approach for the study of community ecology. Given the potential of MSOMs for conservation and management action, it is critical to know whether study design and model assumptions are consistent with inference objectives. This is especially true for studies that are designed for a focal species but can give insights about a community. Here, we review the recent literature on MSOMs, identify areas of improvement in the multi-species study workflow, and provide a reference model for best practices for focal species and community monitoring study design. We reviewed 92 studies published between 2009 and early 2018, spanning 27 countries and a variety of taxa. There is a consistent under-reporting of details that are central to determining the adequacy of designs for generating data that can be used to make inferences about community-level patterns of occupancy, including the spatial and temporal extent, types of detectors used, covariates considered, and choice of field methods and statistical tools. This reporting bias could consequently result in skewed estimates, affecting conservation actions and management plans. On the other hand, comprehensive reporting is likely

to help researchers working on MSOMs assess the robustness of inferences, in addition to making strides in terms of reproducibility and reusability of data. We use our literature review to inform a roadmap with best practices for MSOM studies, from simulations to design considerations and reporting, for the collection of new data as well as those involving existing datasets.

Keywords Community models, Multi-species models, Occupancy, Hierarchical models, Biotic interactions, Reporting Bias

1.1 Introduction

Monitoring the distribution and abundance of wildlife populations is an essential part of advancing ecological understanding and effective conservation management. However, the majority of monitoring initiatives have been geared towards a single focal species, typically those of conservation concern or management interest, likely due to the resource-intensive nature of wildlife monitoring and a lag in statistical and computational tools and methods to handle ecological data. With the growing concern over the effects of global change on community composition, information at the community level is increasingly necessary. At the same time, advances in statistics and the increasing availability of data across taxa are enabling analyses at the community scale (Figure 1.1).

The burgeoning interest in making inferences about communities has led to analytical approaches that utilize data on all observed species, including bycatch species that are obtained incidentally during the course of a study that was designed with one or more focal species in mind (Iknayan *et al.*, 2014; Guillera-Arroita, 2017; Ovaskainen *et al.*, 2017; Steenweg *et al.*, 2019). While the design is optimized for the focal species, there is often information about other species readily or potentially available

for extrapolation. Recently, there has been rapid development of statistical methodologies to investigate important aspects of community ecology (Iknayan *et al.*, 2014; Jarzyna & Jetz, 2016; Ovaskainen *et al.*, 2017). For example, some community ecology projects now formally incorporate imperfect detection and spatial variation in detectability and occurrence patterns (Dorazio & Royle, 2005; Zipkin *et al.*, 2010). These approaches have also been applied to deriving biodiversity metrics and studying changes in community size, composition, and function in space and time (Dorazio *et al.*, 2006; Tobler *et al.*, 2015; Jarzyna & Jetz, 2016) as well as interactions among species (Waddle *et al.*, 2010; Pollock *et al.*, 2014; Rota *et al.*, 2016; Tobler *et al.*, 2019).

Currently, the majority of community models, especially hierarchical models that infer state variables of undetected species while accounting for imperfect detection, have great flexibility in incorporating variation in detectability and occurrence. However, they do not formally account for concerns that result from using a single design to study heterogeneous communities. Recent reviews have attempted to evaluate certain assumptions of community models (Linden *et al.*, 2017; Guillera-Arroita *et al.*, 2019); however, the assumption that the designs are adequate for each species in community analyses, an inherent feature of community monitoring initiatives, has not yet been investigated.

We reviewed the literature on one of the most widely applied classes of community models, the hierarchical multi-species occupancy model (MSOM) (e.g., Dorazio & Royle, 2005 and extensions). We contrast existing approaches to MSOMs and critically evaluate the assumptions of MSOMs in order to identify the potential for biases when studying communities that vary in terms of their spatial ecology and species traits. We use this theoretical approach to develop a set of criteria to consider in the design phase of a community monitoring scheme. Next, we develop a set of recom-

mendations to aid in the design of future community monitoring efforts. We outline a workflow of best practices from definition of the study design to inference and (meta)data reporting that can be adopted as a reference model in multi-species studies. Finally, we report additional observations from the review to highlight aspects of community studies that will facilitate better application and reporting practices in the future.

Box 1: Anatomy of a Multi-Species Occupancy Model

Hierarchical occupancy models are used to estimate the number of sites that are occupied by species of interest in a landscape in an attempt to understand species distribution patterns. The detectability of the study species forms an essential component of occupancy studies, especially in trying to incorporate variation in the detection of the species at different sites. These models involve a separation between the state (occupancy) and observation (detection) processes (MacKenzie *et al.*, 2002).

They can be analyzed using either Bayesian or frequentist approaches, with the former gaining popularity in recent years. Integral to either approach is the detection probability (p) and the occupancy probability (ψ). Parameter p is the probability of detecting the species conditional on the presence of the species at that particular site, and ψ is the probability that a site is occupied by a species. Spatial ('sites') and temporal ('visits') replication is also integral to occupancy modeling.

Box 1: Anatomy of a Multi-Species Occupancy Model (contd.)

The study area is a mosaic of observed occupied and unoccupied sites. However it is difficult to determine whether a site where a species was not detected is truly unoccupied. It is possible the species was not detected due to various reasons such as insufficient visits (temporal replicates) and variation in species detectability. This variation in detectability, which is affected by species traits and survey characteristics, is known as imperfect detection.

Imperfect detection of species could be due to a variety of factors that are biotic or abiotic. These are typically related to species traits (life history, behavior, population density, sex, age, trap shyness), habitat characteristics (vegetation type, terrain, elevation, noise, canopy cover), or survey-related factors (sampling effort, observer experience, method used, spatial and temporal scales, time of the year). Due to their effectiveness in accounting for imperfect detection, occupancy models have become a mainstay of species distribution studies since they were first introduced. While they have been used globally on a range of taxa using a variety of field methods, studies in the first decade of their introduction typically focused on a single, focal species.

Like the classical single species occupancy models (SSOMs), MSOMs are built on the encounter histories of species across sites in a region during repeated visits. They are typically used to estimate species richness (N) at both the community and metacommunity level. MSOMs are based on the concept that a community is an ensemble of species occurring at a site and a metacommunity is the collection of such communities.

Box 1: Anatomy of a Multi-Species Occupancy Model (contd.)

MSOMs combine three levels of hierarchy: metacommunity, community, and individual species. The first level describes the presence of each species $i = 1, 2, \dots, N$ in the metacommunity through an indicator variable (w_i):

$$w_i \sim \text{Bernoulli}(\Omega) \quad (1.1)$$

where Ω is the probability that species i is a member of the metacommunity of size N .

The parameter-expanded data augmentation (DA) technique is typically used to implement the model in a Bayesian framework with Markov Chain Monte Carlo (MCMC) methods (Dorazio & Royle, 2005). The DA technique involves the addition of an arbitrary $M \gg N$ number of all-zero trap frequencies, which can be seen as potentially unobserved species, to the detection matrix Y . In this way, the number of unobserved species in each community can be estimated by evaluating which of the $M - N$ species (rows of the augmented matrix) are members of the metacommunity (sampling zeros, $w_i = 1$) or not (structural zeros, $w_i = 0$). Data augmentation converts the problem of estimating N into the equivalent problem of estimating Ω and species richness N is computed as a derived parameter by summing up the latent indicators w_i since the expectation of N is equal to $M \Omega$ (Kéry & Schaub, 2012).

Box 1: Anatomy of a Multi-Species Occupancy Model (contd.)

The second level of hierarchy of an MSOM defines the occurrence of each species at specific sites $j = 1, 2, \dots, J$, i.e., at the community level (ecological or state process):

$$z_{ij} \sim \text{Bernoulli}(\psi_{ij}w_i) \quad (1.2)$$

where z_{ij} are elements of the true occupancy state matrix Z , of dimension M by J , indicating whether species i is present at site j ($z_{ij} = 1$) or not ($z_{ij} = 0$). The parameter ψ_{ij} represents the species-specific occupancy probability at each site. Note that matrix Z can be used to derive (meta)community-level metrics.

The third level describes the encounter process of individual species and the related false-negative measurement error at each site sampled $k = 1, 2, \dots, K$ times:

$$y_{ij} \sim \text{Binomial}(K, p_{ij}z_{ij}) \text{ or } y_{ijk} \sim \text{Bernoulli}(p_{ijk}z_{ij}) \quad (1.3)$$

where y_{ij} indicates the detection frequency of species i at site j over K sampling occasions, and y_{ijk} is the detection/non-detection at the k th sampling occasion, with detection probability $p_{ij(k)}$.

Box 1: Anatomy of a Multi-Species Occupancy Model (contd.)

Occupancy and detection probabilities can be modeled as a function of covariates (‘cov’):

$$\text{logit}(\psi_{ij}) = \alpha_{\psi,i} + \beta_{\psi,cov,i} cov_j \quad (1.4)$$

$$\text{logit}(p_{ijk}) = \alpha_{p,i} + \beta_{p,cov,i} cov_{jk} \quad (1.5)$$

Further model assumptions are defined to characterize heterogeneity in occurrence and detectability among species, and to estimate occurrence of species members of the community not observed in any site. Often, species are assumed to have a similar, but not identical, response to environmental changes (Dorazio *et al.*, 2011; Kéry & Royle, 2015). In the case of interspecific interactions, where occurrence of a species is affected by the presence or absence of another species, patterns of co-occurrence should be considered in lieu of ecological similarity (MacKenzie *et al.*, 2004).

When ecological similarity is assumed, unobserved sources of heterogeneity in occurrence and detection among species can be modeled by adding a further hierarchical level and assuming that species-specific parameters in the related linear predictors (α_i and β_i in equations (1.4) and (1.5)) are independent random effects: $\alpha_{\theta,i} \sim \text{Normal}(\mu_{\alpha_\theta}, \sigma_{\alpha_\theta}^2)$ and $\beta_{\theta,cov,i} \sim \text{Normal}(\mu_{\beta_{\theta,cov}}, \sigma_{\beta_{\theta,cov}}^2)$ with $\theta = (\psi, p)$. In this way, species-specific estimates are ‘shrunk’ toward the mean parameter value of the community. A correlation structure between occupancy and detection probability can also be included if detectability is expected to increase as species abundance increases (Dorazio, 2007).

1.2 Multi-species Occupancy Models: State of the Field

There are different types of MSOMs, based on study objectives. Often, ‘community occupancy’ and ‘multi-species occupancy’ are used interchangeably, although subtle differences exist (Guillera-Arroita, 2017). MSOMs encompass both co-occurrence models that incorporate interactions between a few species (typically coupled dominant-subordinate interactions) as well as community models that usually involve some estimate of species richness without including biotic interactions (Figure 1.1). Co-occurrence models include biotic interactions in addition to habitat and abiotic factors, and modeling the detection and occurrence hinges on species traits and the nature of the interactions. Frequently, assumptions on the nature of the interactions need to be made in order to model them appropriately. These could take the form of competitive interactions or prey-predator systems, and assumptions made include body size-based hierarchy in the event of a dominant-subordinate species coupling (Figure 1.1).

The MSOM can jointly estimate detection and occurrence probabilities of each species in the community, including those not detected. As with the single species occupancy model (SSOM), MSOMs have at their core the fundamental inference objective of estimating species occupancy rates in the presence of imperfect detection (see Box 1). This requires repeated sampling of multiple spatial locations (MacKenzie *et al.*, 2002, 2017).

There are many limitations to MSOMs and several are related to the statistical framework used. Bayesian inference can be challenging in terms of being computationally intensive, with model selection being problematic (Broms *et al.*, 2016; Tenan *et al.*, 2014). These types of models often entail considerable training to code and

interpret. Furthermore, incorporating interactions has consistently been a challenge, requiring careful deliberation about the variables used.

1.2.1 Model Assumptions Under Community Sampling

Data collected on multiple species by a particular array of detectors (e.g., trail cameras, traps, transects, and point counts) are a function of within-community variation in species-specific traits such as mobility, density, habitat requirements, and behavior, as well as inter- and intra-specific interactions. For reliable inferences, the resulting data must meet, to varying levels of strictness, specific model assumptions (MacKenzie *et al.*, 2017): demographic and geographic closure, independence, correctness in identification, and ecological similarity. Whether these assumptions are met is related to the ecological traits of the species of interest and the spatiotemporal characteristics of the monitoring design. It follows, therefore, that inherent variability in ecological traits within a community produces variability in the extent to which assumptions are violated or adhered to. For instance, the home range size of the species is correlated tightly with the assumptions of geographic closure and independence. Therefore, the issue of whether community-level inferences are reliable is more of a design-based than a model-based consideration, yet current developments and publication trends would suggest the reverse.

The basic assumptions of an MSOM are similar to those of the SSOM and include:

- **Geographic and Demographic Closure:** The sites represent closed populations, and there are no births, deaths, colonization, or extinction in the span of the surveys. When this assumption is violated, there tends to be an overestimation of occupancy while detection is low, which leads to inflated species richness estimates (Kéry & Royle, 2015). This assumption can be maintained with the help of *a priori* simulations that inform study design and assist in

identifying the spatial and temporal replicates necessary, as well as being cognizant of detector attributes with regard to species traits such as home ranges, rarity, elusiveness, and mobility (Linden *et al.*, 2017).

- **Independence:** At a site, the probability of detecting a species and that of the site being occupied are independent of the occupancy and detection probability of another site. Violations of this assumption typically happen when there is oversampling or clustered sampling (instead of a random sampling scheme), especially while using camera traps and acoustic recording equipment, during studies involving rare and elusive species. The number of sampling units as well as the sampling methodology have an impact on whether this assumption is violated, while spatial correlations often do not result in a violation. Any autocorrelation and violations of this assumption can be tested statistically (Wright *et al.*, 2016). A violation of this assumption can lead to overestimated precision for species occupancy, detection, and richness (McNew & Handel, 2015). One solution proposed to address this problem and decrease uncertainty around the estimates involves modifying the detection-level component of the model (Wright *et al.*, 2016). This could, for instance, involve determining detector spacing during study design based on the home ranges of the study species, identifying adequate number of replicates and detectors, and the optimal distance between detectors for the community study.
- **Accurate identification:** Errors in species identification, either due to fluctuations in detectability or observer error, can significantly impact and bias occupancy estimates (Dorazio *et al.*, 2011). This assumption could be violated in surveys where the detection and identification of species is through their vocalizations (e.g., amphibians, birds, insects) where misidentifications often occur (McClintock *et al.*, 2010; Simons *et al.*, 2007). This is also problematic

in situations where the skill level of the observers is variable (Genet & Sargent, 2003). A violation of this assumption could result in an overestimation of species through erroneous detection at sites where they were actually absent. One mechanism to address this issue is through the inclusion of parameters for false-positives as well as false-negatives in detection (Royle & Link, 2006), although this may not be effective where the misidentification and detection probabilities are similar.

- **Ecological similarity:** Often community monitoring studies assume that species in the community are similar, resulting in species-specific random effects that are drawn from the same distribution, typically the bivariate normal distribution (Kéry & Royle, 2015). A consequence of violating this distributional assumption is a deterioration in the occupancy, detection, and richness estimates, resulting in prediction errors. This assumption can be maintained by keeping in view the problem statement and the inferences made.

1.2.2 A Review of the Community Occupancy Modeling Literature

We conducted a literature review on MSOMs with the objectives of identifying weaknesses in current implementations and helping inform the ideal composition of these models. The Web of Science portal was used to identify literature pertinent to multi-species models. The topic search term used in May 2018 was: “*multi-species occupancy*” OR “*multispecies occupancy*” OR “*community occupancy*” OR “*two-species occupancy*” OR “*joint occupancy*” OR “*co-occurrence of interacting species*”. This resulted in a total of 106 publications, of which 92 were relevant to this review.

These were then accessed through the multimedia data manager ViXeN (Rachandran & Devarajan, 2018) as a project. Each publication was viewed and the tags annotated. The entered data were then exported as a comma separated

value (csv) file for subsequent analysis. The analysis was done using the statistical package R version 3.4.4 (2018-03-15; The R Foundation for Statistical Computing) (R Core Team, 2012), which was also used for cleaning the review data, analysis, and visualization (RStudio Team, 2018; Wickham & Chang, 2008; Wickham, 2010). The tags were broadly classified into study question, study organisms, study area, study period, study methods, covariates, and publication details (Figure 1.2). The broad ecological and conservation context was inferred based on the study questions.

There were 92 publications involving field-based multi-species occupancy studies published between 2009 and 2018 (Figure 1.3) considered for this systematic review. The number of studies for the year 2018 only cover the first half of the year when data collection for the review was completed. Based on the year of publication, there seems to be a general and consistent increasing trend in studies involving MSOMs (Figure 1.3).

The field studies spanned 6 continents (Antarctica is the exception) and 27 countries (Figure 1.4). However, a majority of the studies were conducted in North America, particularly the USA (Figure 1.4), suggesting a geographic bias in MSOMs. Moreover, marine and aquatic communities were vastly underrepresented suggesting a taxonomic bias towards terrestrial organisms. Vertebrates are much better covered than other taxa. These trends have been highlighted as issues for biodiversity data (Geijzenendorffer *et al.*, 2016).

The focus of the studies was variable. Many of the studies involving MSOMs were interested in questions relating to species richness, species conservation, and habitat conservation. Total species richness or taxonomic diversity, along with phylogenetic and functional diversity, is considered to be extremely influential for conservation,

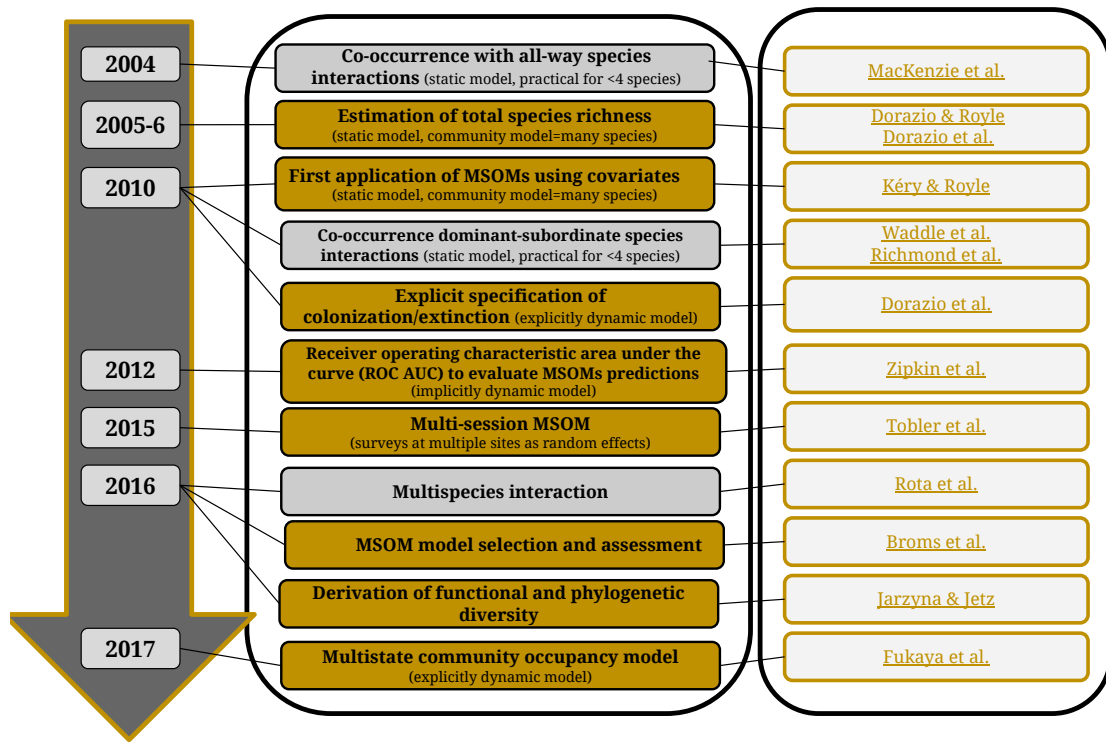


Figure 1.1. Key methodological developments in the history of MSOMs. The associated publications for these are hyperlinked for convenience. The developments related to species interactions are in grey boxes.

management, and policy decisions (Guillera-Arroita *et al.*, 2019). Although species richness was mentioned to be the focus of about 40% of the studies in the review, most of them (84%) do not report the total number of species found in the study.

Given the importance of study design in occupancy studies (Guillera-Arroita *et al.*, 2010), the transfer of design considerations is unlikely to be seamless between the focal and bycatch species. It is necessary to account for these disparate design requirements, or at least acknowledge the biases and errors associated with this in MSOMs involving bycatch data. About a quarter of the studies (27 of 92) considered in the

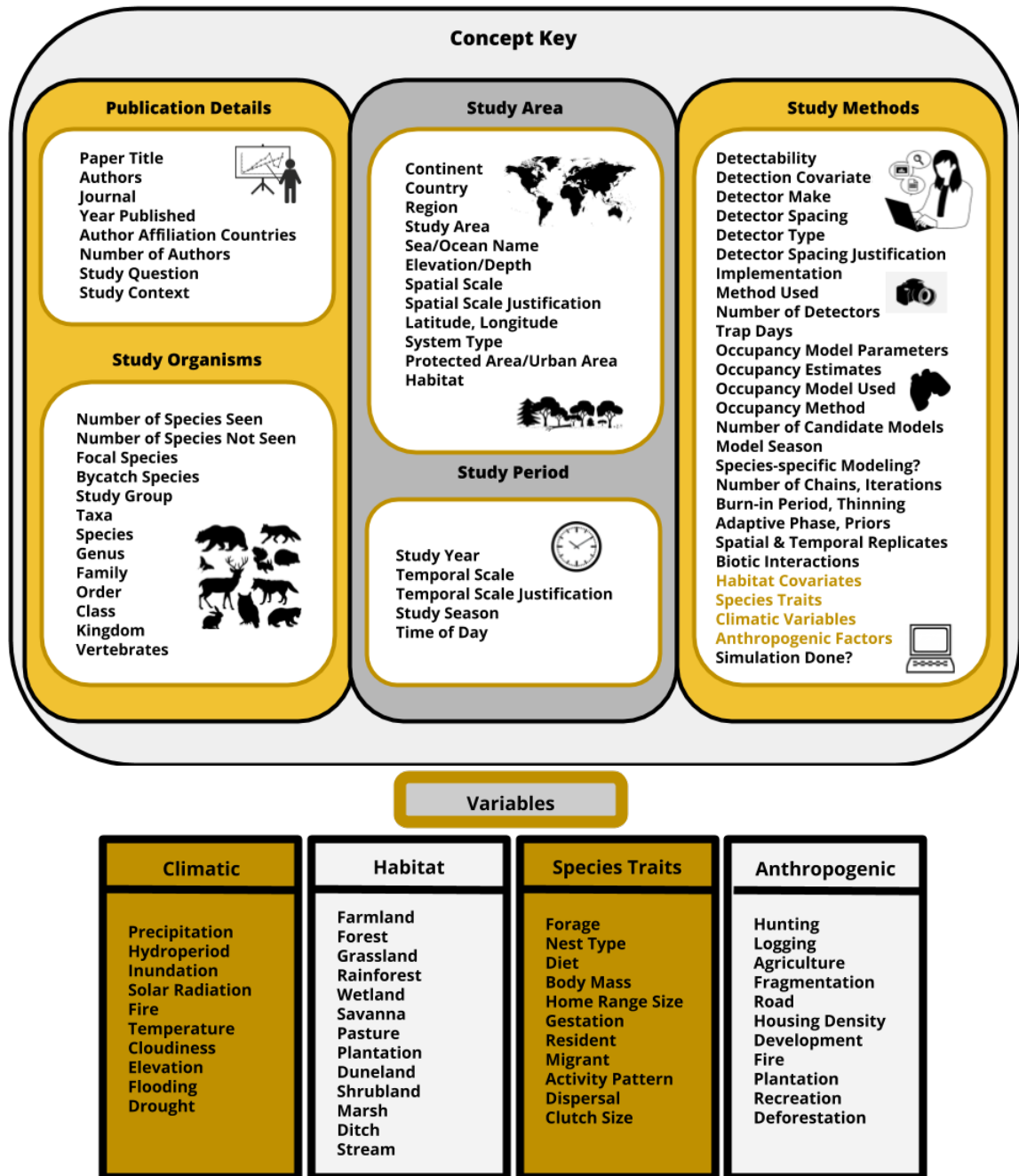


Figure 1.2. Concept key and tags included in the literature review. The variables considered as important predictors by studies used in the review are categorized into climatic, habitat, species traits, and anthropogenic variables in the table below the concept key.

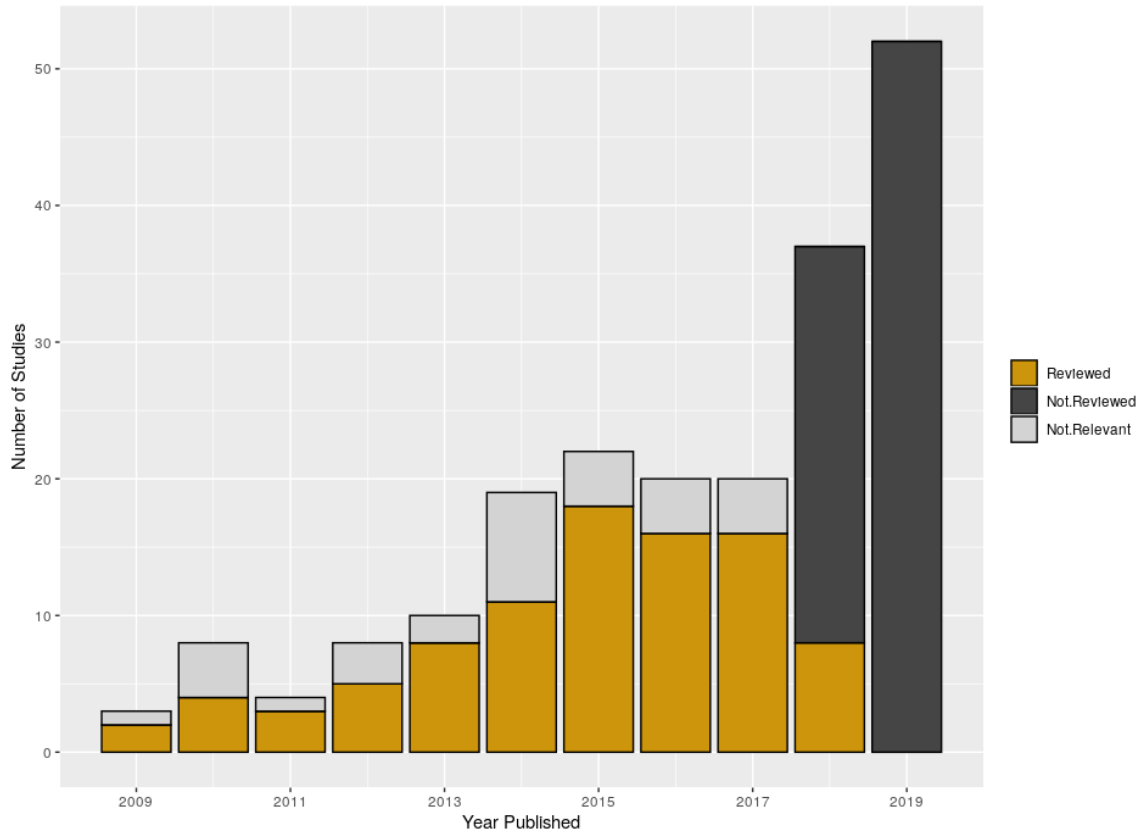
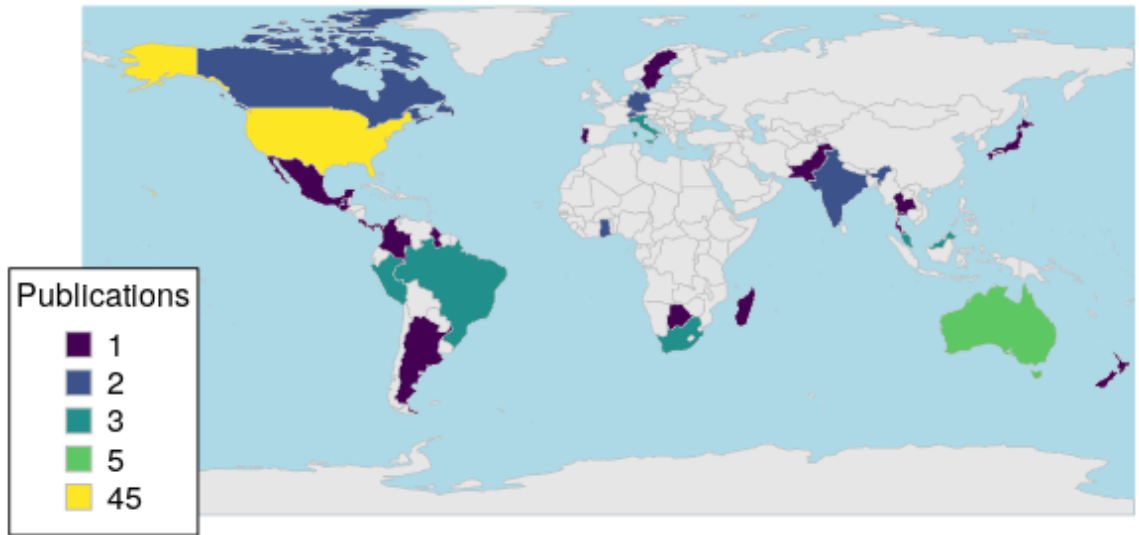
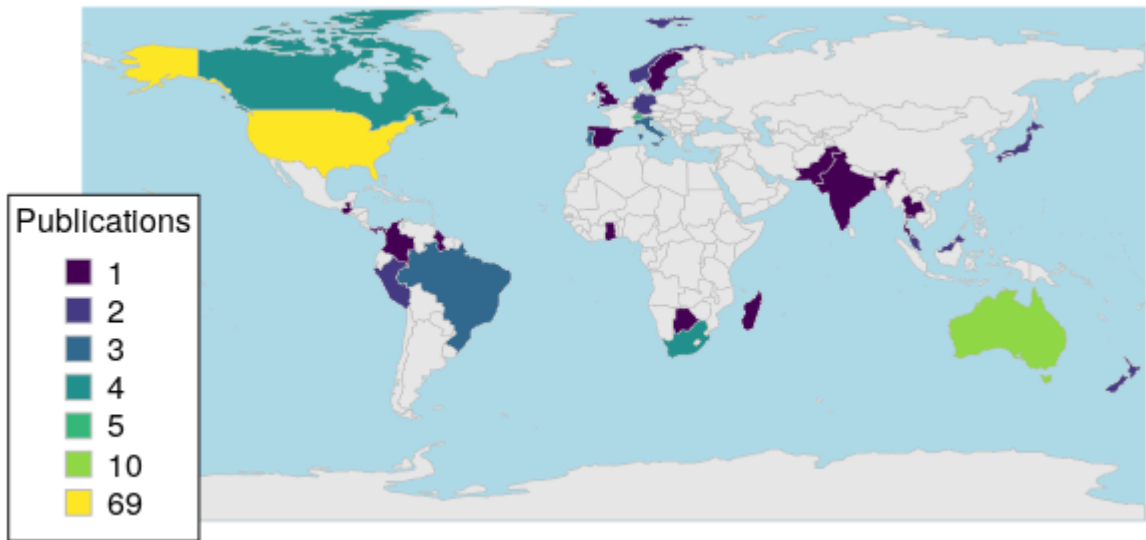


Figure 1.3. The trend in publications covering multi-species occupancy models over the years. The literature review covers studies that were published until April 2018. The light grey bars represent the number of studies that were not considered for the review including those that were outside the scope of the review.

review mention the presence of other species in the area which can be considered bycatch, albeit without providing a list outside of the focal species. Approximately a third of the studies (31%) provide an estimate of the number of bycatch species that were found. However, it is difficult to glean exactly how many of the publications analyzed bycatch species from a study that was originally designed for different focal species, although some of the studies alluded to this (24 out of 92 studies). The actual number of bycatch species ranged from 1 to 472 (Kingdom: *Plantae*), with a majority of studies mentioning less than twenty.



(a) Global distribution of field locations of studies considered in the review.



(b) Global distribution of author affiliations of publications considered in the review.

Figure 1.4. Study field locations and author affiliations of multi-species occupancy studies of the publications considered in the review indicate a match between the two. Field studies tended to have at least one collaborator from the country who is an author on the publication, with a few exceptions, such as a mismatch in parts of Central and South America, and disproportionately more authors from North America and Australia included in publications overall.

There might be an underestimation of species richness when relevant predictors are not included in the model, such as the habitat covariates used, the choice of detec-

tion covariates, and whether biotic interactions need to be considered for occupancy or detection (Guillera-Arroita *et al.*, 2019). Biotic interactions are crucial in community ecology studies and are known to be important predictors of species distribution patterns (Pollock *et al.*, 2014; Rota *et al.*, 2016; Ovaskainen *et al.*, 2017). Species detectability needs to be factored in as well so as to reduce the number of species missed (Dorazio & Royle, 2005; Zipkin *et al.*, 2010; Karenyi *et al.*, 2016). Despite the critical nature of detection covariates, as many as 15 papers (16%) did not explicitly mention which detection covariates were used. Often the rationale behind the choice of predictors was not mentioned either. Only 28% of the publications in this review mentioned considering biotic interactions for either occupancy or detection. A majority of the studies in the review did not explicitly state the detectability of the species, not even qualitatively (e.g., the species was easily detected).

Reporting on spatial and temporal aspects of the studies was also lacking. Of the studies considered in the review, almost a quarter (23%) did not report the number of sampling occasions or temporal replicates, 15% made no mention of a temporal scale for the whole study, and close to 90% did not provide any justification on their choice of temporal scale. The same rationale applies to the spatial scale and number of sampling sites or spatial replicates as well. While a majority of the studies (88%) report the number of spatial replicates, approximately half of them (44 out of 92 studies; 47%) have no mention of the spatial scale and only 15% of the total studies provide any justification for the spatial scale of the study. Most of the studies were conducted in protected areas which could be a potential source of bias since inference is restricted to a single type of area and under specific management conditions (namely, protected). In the same vein, most studies were conducted in the summer (see Appendix for Chapter One), which could also result in inference and reporting biases.

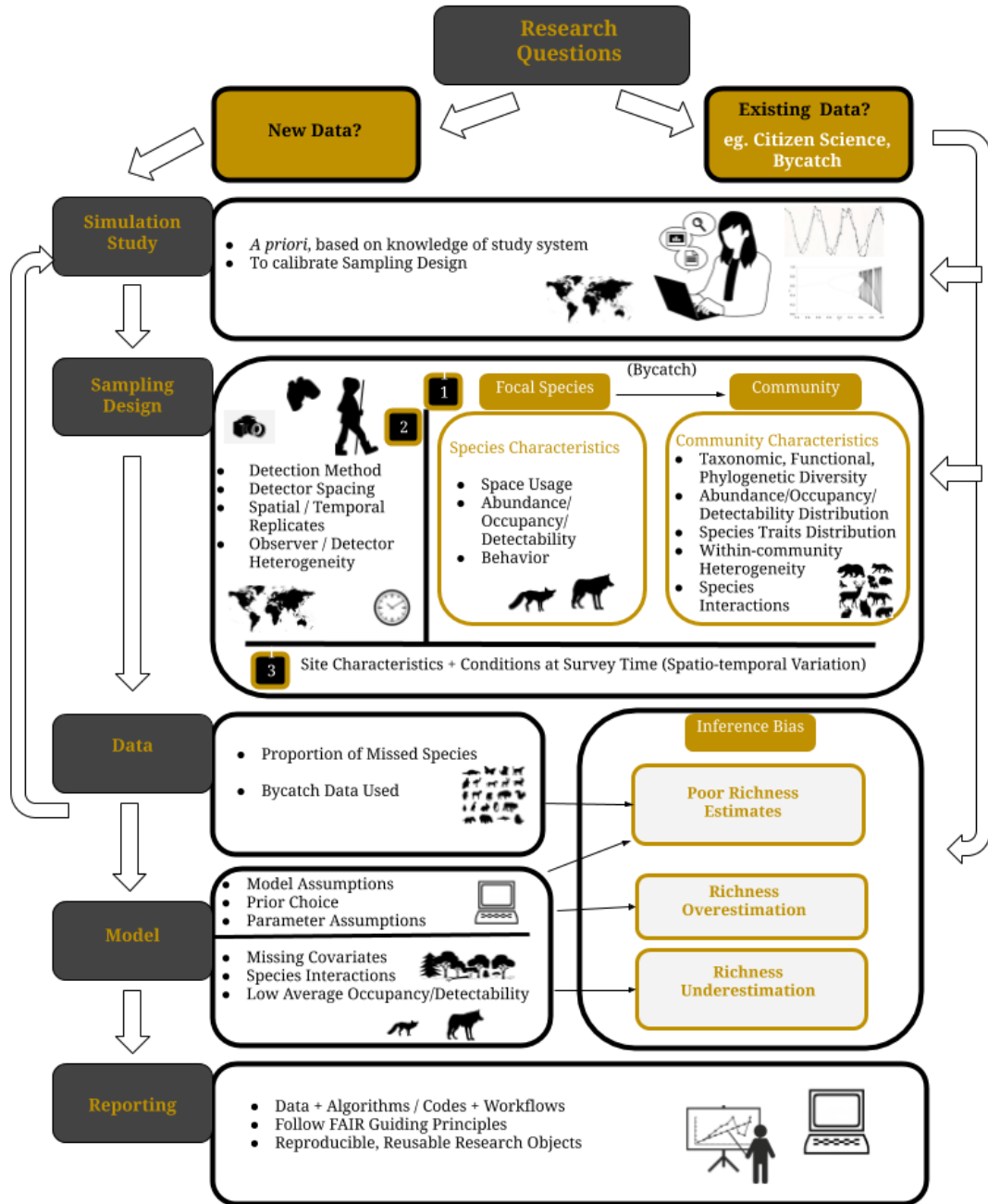


Figure 1.5. A schematic workflow and roadmap for best practices while implementing an MSOM. Conceptual representation of an ideal protocol for multi-species studies, from *a priori* simulations to reporting results. The research questions and objectives for the study would determine the type of data that are likely to be used for obtaining the occupancy estimates; in case of existing data, such as from citizen science projects or involving bycatch from a study designed for focal species, the steps followed would differ from when a study is planned for focal species from the ground up.

Incomplete reporting was a problem in other areas as well. Only a small fraction of the studies (15 out of 92) even mention the number of species that went undetected during the course of the research. While nearly all the studies provide some information on the detectors used, 57% provide no information on the detector make and 66% do not state the spacing between detectors. Nearly a quarter (23%) of the studies provide little or no information on the implementation of the study and sampling methodology employed, such as whether they followed a systematic, random, or stratified random sampling approach. Decisions related to the detectors used including the type of detector, spacing between detectors, and the implementation (sampling methodology) need to be given considerable thought. Detector spacing is typically calibrated in relation to a specific focal species and thereby affecting the detection of bycatch species with different space usage.

Typically, the longer the monitoring, the higher the chance of detecting most or even all of the species present in an area (Guillera-Arroita *et al.*, 2019), as long as the assumptions of demographic and geographic closure are met. In some cases, more visits or temporal replicates do not necessarily correspond with higher detection, and there is a trade-off between effort and detection estimates. By and large, however, the temporal scale is positively correlated with a reduction in the possibility of missing species (Guillera-Arroita *et al.*, 2019). Given this, a justification of the temporal scale chosen and employed in MSOMs is of immense importance.

It was challenging to identify the studies that evaluated assumptions of demographic and geographic closure. These are crucial assumptions of MSOMs, given the inevitable differences in life-history traits among species in a community, on which reporting was extremely sparse. An explicit method to test closure is by fitting an open MSOM using Pollock’s robust design framework (Pollock, 1982) over short time

intervals and evaluating the parameter constraints (Rota *et al.*, 2009). An indirect way to glean this information from the studies is by checking if studies conducted Goodness-of-Fit (GOF) (Broms *et al.*, 2016) tests or temporally thinned their data to see if signs changed. However, this was challenging as well since the use of GOF tests and temporal thinning of data went largely unreported (Zipkin *et al.*, 2009). Alternatively, staggered-entry SSOMs (Kendall *et al.*, 2013) which permit inference about the within-season patterns of species arrival and departure at sampling sites (Chambert *et al.*, 2015) could be used to test closure of the system.

The review shows a slant in the literature towards the use of Bayesian models for obtaining multi-species occupancy estimates, with about 65% of the studies implemented using some instance of BUGS, JAGS, or `stan`. The choice of priors is considered crucial in Bayesian analysis and has been found to bias estimates (Guillera-Arroita *et al.*, 2019). For instance, choosing incorrectly informative priors is likely to result in a frequentist bias. Despite the importance of prior definition in the Bayesian framework, most studies do not elaborate on the decision process involved. Only half of the studies using Bayesian methods reported the kind of prior that was used, with more than 70% of these (24 out of 33 studies) indicating uninformative priors. Lastly, simulation studies are considered important in evaluating the sensitivity of the estimates obtained in the application to empirical data (Peck, 2004; Kleijnen, 1998). Only 14 of the 92 publications considered for this review indicate having used simulations in order to gauge model sensitivity.

1.3 Best Practices for MSOMs

Based on our literature review, we propose a framework outlining best practices for implementing an MSOM (Figure 1.5). The MSOM should start with a simulation study which is done *a priori* based on the researchers' knowledge of the study system,

in order to calibrate the study design. MSOMs will be more or less sensitive to some factors such as detectability, detector spacing, and certain covariates. The study needs to be carefully designed as not to violate assumptions of closure; considering timing of reproduction and dispersal is key.

The study question determines the design. During this phase, it is important to ascertain whether the study question can rely on existing data (e.g., citizen science and bycatch datasets) or whether new data need to be collected. Appropriate detection methods would have to be chosen based on the nature of the study. This would, in turn, lead to deciding on adequate spacing between the detectors, as well as the spatial and temporal replicates necessary. It is also important to be cognizant of heterogeneity in observers and detectors, which can subsequently help account for imperfect detection.

If the ecological system involves focal species, species characteristics such as home ranges and space usage, detectability, and behavior will need to be considered. On the other hand, if the focus is a community of species or in situations where by-catch species from an existing study are considered, community characteristics will need to be taken into account. These include taxonomic, phylogenetic, and functional diversity, as well as species detectability and traits distribution, and interactions among species (Pollock *et al.*, 2017; Guillera-Arroita *et al.*, 2019). In addition to the species and community characteristics, it is crucial to consider site characteristics as well as the survey conditions which account for any spatio-temporal variation in the system (Guillera-Arroita, 2017). Taken together, these would comprise the variables thought to influence occupancy and abundance.

The measurements collected for these covariates would form the data which feed into the model. The community data collected should ideally have some estimate of the proportion of missed species as well as the bycatch data used. This is necessary since not accounting for these could result in poor species richness estimates, leading to inference bias (Guillera-Arroita *et al.*, 2019). Similarly, during the modeling process, adequate thought needs to be given to the choice of priors and parameter assumptions. Failure to do so could result in overestimation of species richness estimates. If there were any missing covariates, or in situations with low detectability or abundance, there could be inference bias in the form of underestimation of species richness. Lastly, not accounting for biotic interactions could result in biased richness, occupancy, and abundance estimates (Tobler *et al.*, 2019).

Finally, once the study has been completed, when publishing the research, the data, algorithms, and workflows used should be reported (Powers & Hampton, 2019). We recommend following the FAIR (Findability, Accessibility, Interoperability, and Reusability) guiding principles for managing scientific data (Wilkinson *et al.*, 2016). Scientific data may be standalone, citable products due to which the research objects such as the methodology, algorithms, and workflows used should be reproducible, and the data and code reusable. This makes the data easier to find and access, and enhances the authenticity of the research. Issues such as the lack of information on the statistical modeling aspects such as the priors used can be minimized by sharing the supplemental code for running the model. Similarly, information on whether model validation was done and checking for any violations of model assumptions ought to be provided as supplemental code.

1.4 Conclusions and Synthesis

MSOMs are increasingly being used to monitor species distribution and abundance (Beaudrot *et al.*, 2016). The assumptions and limitations of the traditional single species models propagate to the multi-species framework, with some additional factors that need to be considered. MSOMs are important since they are resource efficient, capable of accounting for biological interactions such as competition and predation, used for existing data, and can be used to monitor entire landscapes and communities, as opposed to just one species. By allowing the monitoring of spatio-temporal changes in community and metacommunity size, composition and functioning, the framework thus allows inference at local, landscape and macro scales.

Conservation and management plans tend to target either a species or region of conservation importance (Zipkin *et al.*, 2010). Focusing on a single species frequently results in ignoring other interacting organisms, consequently introducing biases which are often not accounted for. When the focus is on a region, it is more efficient to look at community-level distribution and abundance patterns in order to design an appropriate management plan.

A common method for monitoring programs at the habitat level involves estimating species richness and composition, both of which can vary across the landscape due to biotic and abiotic factors. Due to this reason, it is important to consider species-specific detection when community-level studies are implemented. A multi-species occupancy approach is likely to provide better species richness and community composition estimates by simultaneously accounting for imperfect detection as well as species rarity and elusiveness. Furthermore, there are likely to be differences in the responses to habitat changes based on whether the taxa are rare or common. This too has implications on the detection of the species. Statistical tools to un-

derstand community-level dynamics and species-specific distribution estimates are gaining traction. However, so far, despite the increasing popularity of community models, incorporating biotic interactions is not common due to several reasons, including but not limited to logistical and statistical challenges.

With technological and statistical advances, and a growth in citizen science initiatives, distribution studies are resulting in increasingly large datasets that need to be managed (Hampton *et al.*, 2013; Hines *et al.*, 2015; Sun *et al.*, 2019). There has also been an associated increase in software to manage such projects (Ramachandran & Devarajan, 2018; Thomson *et al.*, 2018; Young *et al.*, 2018; Bubnicki *et al.*, 2016; Krishnappa & Turner, 2014; Niedballa *et al.*, 2016).

The importance of including detailed information on (meta)data and following best practices is not only of concern to researchers. Evaluating the robustness of specific studies is also relevant to conservation biologists and wildlife managers who apply these tools, write transparent reports to inform decision-making processes, and ensure that their study follows an acknowledged protocol. In addition, having detailed information on (meta)data and followed best practices enhances the reusability of data (Wilkinson *et al.*, 2016). In light of policy reporting needs and the recently proposed Essential Biodiversity Variables (Pereira *et al.*, 2013; Kissling *et al.*, 2018), MSOMs can simultaneously provide estimates of community composition, species populations (i.e., occupancy), and species traits. These are essential measurement classes required for the study, reporting, and management of biodiversity changes.

The linking of multi-faceted biodiversity metrics (i.e., taxonomic, phylogenetic and functional) with spatial conservation science can help identify more efficient strategies for the conservation of biological diversity (Pollock *et al.*, 2017). Given this, the proper

use of analytical tools like MSOMs, that provide estimates of biodiversity metrics while accounting for imperfect detection, will be fundamental to robust inference.

Data Accessibility

The dataset associated with the literature review has been deposited in the online data repository Figshare: <https://doi.org/10.6084/m9.figshare.11608449.v1>.

CHAPTER 2

MULTIPLE DIMENSIONS OF CARNIVORE COMMUNITY DIVERSITY ACROSS THE GLOBAL TROPICS

Abstract Carnivores are threatened by anthropogenic change at the global scale with richness decreasing as a function of disturbance. Given the charismatic nature of carnivores, they are often considered flagship species for conservation purposes. Broadly, decreases in biodiversity often diminish ecosystem function and stability, in addition to diluting the evolutionary history of communities. However, the relationship between the taxonomic, phylogenetic, and functional diversity of communities is not well understood. Here, we use a dataset of 515 carnivore communities in protected areas (PAs) across the global tropics and sub-tropics including species traits such as body size and diet, International Union for Conservation of Nature (IUCN) Red List status, and environmental variables associated with the PAs to study how different biodiversity metrics track one another. We use these measures of biodiversity to help identify global hotspots for carnivore conservation.

2.1 Introduction

“Nothing in biology makes sense except in light of evolution” – Theodosius

Dobzhansky.

“And many, if not most, of the compelling kaleidoscope of patterns in biological diversity make little sense unless placed in an explicit geographic context.” – Mark

Lomolino (Biogeography - A Very Short Introduction)

Mammalian carnivores belong to the species-rich order Carnivora and are distributed widely, spanning several biogeographical realms and all continents, and are found in marine, aquatic, and terrestrial environments (Gittleman, 2019). Carnivore diversity patterns are considered critical measures of overall ecosystem health due to their sensitivity to anthropogenic disturbance while carnivore community richness corresponds with overall mammalian diversity in different landscapes (Gittleman, 2019; Loiseau *et al.*, 2020). However, carnivores are under enormous threat from habitat loss, poaching, prey depletion, global change, and disease (Gittleman *et al.*, 2001; Gámez & Harris, 2020). While several species are considered endangered, some are on the verge of extinction, with many terrestrial carnivores experiencing range contractions (Wolf & Ripple, 2017).

Carnivores form an integral part of ecosystem function, directly and indirectly influencing the environment through biotic interactions (Ripple *et al.*, 2014). For instance, they exert top-down control on a variety of prey species and influence the distribution and habitat use of other predators through competitive interactions as well as intra-guild predation (Palomares & Caro, 1999; Gompper *et al.*, 2016). Tropical systems harbor a disproportionately high amount of biodiversity and biomass. However, habitats in the global tropics are facing threats ranging from deforestation and fragmentation to invasives and climate change (Hansen *et al.*, 2013; Wolf & Ripple, 2017; Cartagena-Matos *et al.*, 2017). Carnivores in the tropics are especially vulnerable to the impacts of global change. Given the importance of carnivores, it is of high conservation priority to understand the processes and patterns driving carnivore community assemblages in tropical systems (Linnell *et al.*, 2001; Loyola *et al.*, 2008).

It is, therefore, critical to initiate and bolster conservation action for such species. However, there are ecological, socio-economic, political, and epidemiological challenges to carnivore conservation (Sillero-Zubiri *et al.*, 2001, 2004; Wolf & Ripple, 2017; Cartagena-Matos *et al.*, 2017; Loyola *et al.*, 2008; Morcatty *et al.*, 2020; Mendiratta *et al.*, 2021). Possibly as a consequence of these challenges, prioritizing the conservation needs of and implementing management plans for carnivores have historically focused on a single species of interest (Devarajan *et al.*, 2020). Nevertheless, given the resource-intensive nature of wildlife monitoring, there seems to be increasing interest in community-level studies involving different species in a variety of landscapes (Devarajan *et al.*, 2020). Patterns of carnivore community composition, richness, and distribution have been studied at various scales (Linnell & Strand, 2000; Linnell *et al.*, 2001; Loyola *et al.*, 2008; Schuette *et al.*, 2013; Davis *et al.*, 2018; Gompper *et al.*, 2016). However, research on other dimensions of diversity impacting carnivore communities at the global scale, such as phylogenetic and functional diversity, is lacking (Herrera, 2017). Similarly, little is known about the degree to which these dimensions of diversity are reflected in carnivore community composition and richness across the globe (Pollock *et al.*, 2017).

Table 2.1. Summary of the regions covered and the corresponding number of PAs considered as well as total mammal and carnivore richness for each region.

Region	Number of Protected Areas Considered	Mammal Richness	Carnivore Richness
Africa	170	277	71
Madagascar	105	107	9
Indomalayan	120	242	77
Central & South America	120	232	45

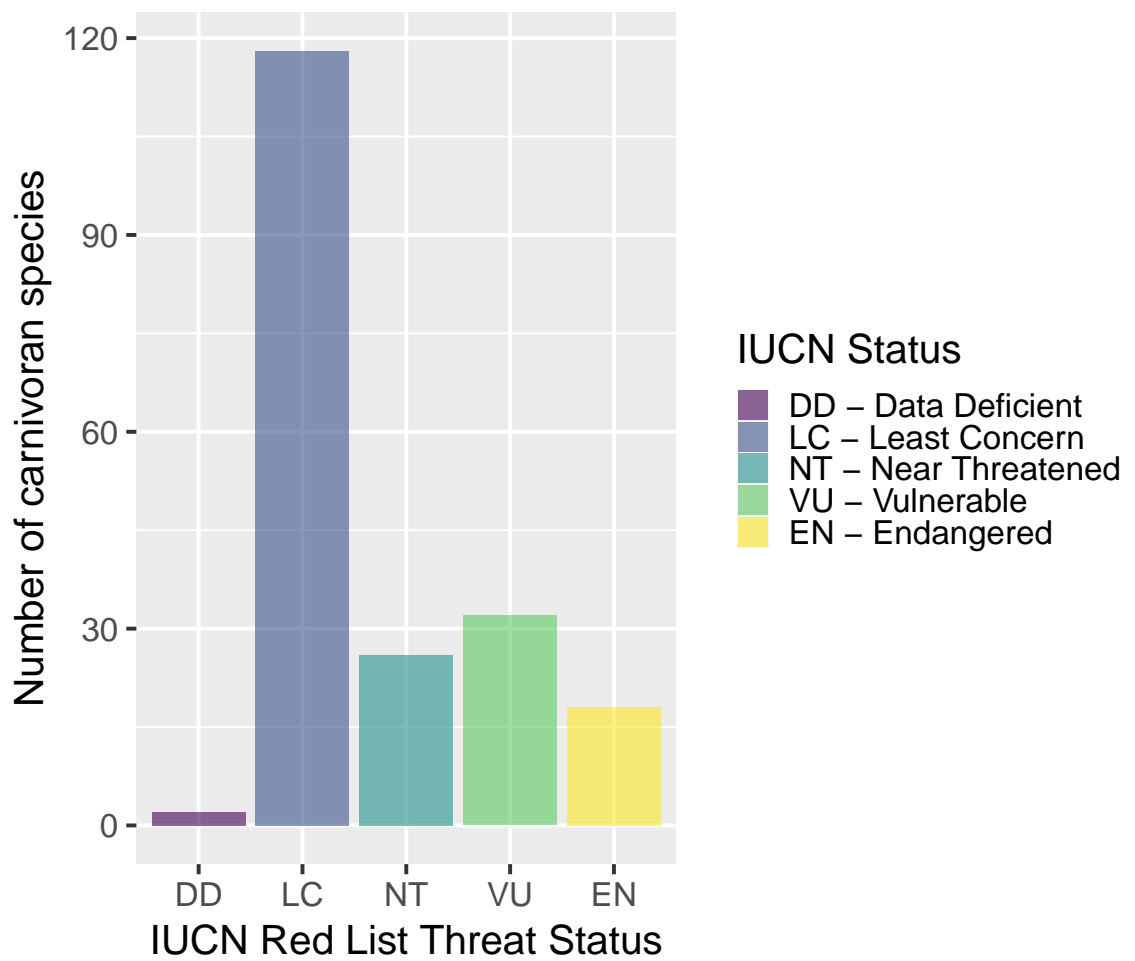


Figure 2.1. Bar plot of number of carnivorous species in each IUCN Red List category.

Table 2.2. Summary of number of carnivores that fall under different IUCN Red List threat categories and the regions in which the species are found.

IUCN Red List Category	Number of Species	Region
Data Deficient (0)	2	Africa
Least Concern (1)	118	Africa, Madagascar, Indomalayan, Central & South America
Near Threatened (2)	26	Africa, Indomalayan, Central & South America
Vulnerable (3)	32	Africa, Madagascar, Indomalayan, Central & South America
Endangered (4)	18	Africa, Madagascar, Indomalayan, Central & South America

Conservation plans generally have two broad objectives: (i) prioritizing certain rare or at risk species, and (ii) conserving habitats or communities (Herrera, 2017; Pimm, 2021). To address both these objectives, we characterize the carnivore communities based on the dimensions of threat levels of carnivorans as well as overall diversity of carnivore communities in 515 protected areas in the global tropics and sub-tropics. We ask (i) how do carnivore community size and composition vary across the global tropics and subtropics?; (ii) do more diverse carnivore communities correspond with more rare or distinctive taxa?; and (iii) how is carnivore community size related to phylogenetic and functional diversity? Specifically, we identify biodiversity metrics to understand: (Q1) how do species traits such as diet and body mass correlate with carnivore community richness? and (Q2) how does phylogenetic diversity relate to carnivore community diversity? We then build on these biodiversity metrics to identify conservation metrics to answer: (Q3) does carnivore body size correspond with conservation status? and (Q4) does protected area size influence carnivore community richness?

We combine carnivore community richness data, carnivore trait data, bioclimatic variables, and protected area features such as location and size to understand how multiple measures of biodiversity relate to one another (Q1 and Q2). We use multiple biodiversity metrics to identify global hotspots for carnivore conservation (Q3 and Q4). We predict that body size and diets of the carnivores would be important determinants of carnivore community structure (Ripple *et al.*, 2014; Gittleman, 2019) (Q1). In all regions, we expect carnivore community richness to correspond with increasing phylogenetic diversity (Jensen *et al.*, 2016) (Q2). In terms of conservation, we predict that carnivore body size is likely to be related to threat status where larger carnivores are more threatened (Gittleman, 2019) (32). We do not expect protected area size to influence carnivore community richness since generally environmental heterogeneity is considered more influential than area (Udy *et al.*, 2021) (Q4).

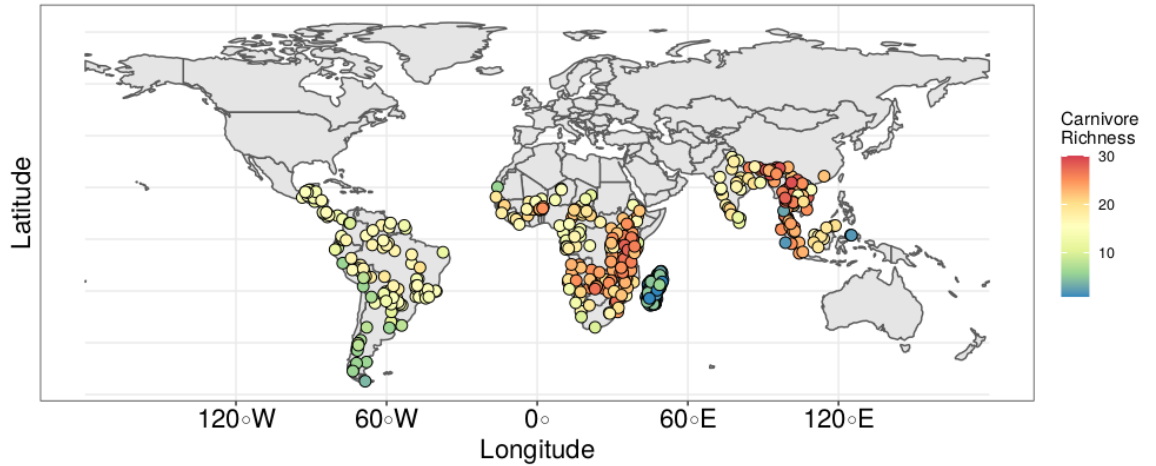
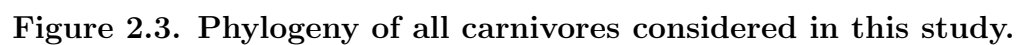


Figure 2.2. Map of carnivore communities in 515 protected areas across the global tropics and sub-tropics color-coded by carnivore species richness in each community. This map covers three biogeographical regions spread across four continents, namely: Afrotropics (including Madagascar), Central and South America, and Indomalaya.



This study provides insights on the variation in carnivore community metrics such as diversity and distribution in tropical protected areas. We found regional differences in the influence of phylogenetic and functional traits on carnivore community richness, which are likely due to the divergent evolutionary and biogeographical histories of the regions (Fleagle & Gilbert, 2006; Svenning *et al.*, 2015). Our results indicate that the different biodiversity metrics (taxonomic richness, endemism, evolutionary distinctiveness, and phylogenetic diversity) do not align perfectly in the different regions. We highlight the importance of considering evolutionary histories along with other biodiversity metrics for carnivore conservation at the community level.

2.2 Methods

We utilized a subset focusing only on carnivores from a checklist-based dataset on 515 mammal communities in protected areas of the global tropics and subtropics (Rowan *et al.*, 2020). This resulting dataset consisted of 515 carnivore communities covering the Afrotropical ($n=170$), Malagasy ($n=105$), and Indomalayan ($n=120$) biogeographical realms, as well as the Central and South American region ($n=120$) (Tables 2.1 and 2.2). Across the global region considered, the carnivore dataset was composed of 196 species from a single order (Carnivora), 13 families, and 96 genera. We also created a dataset of protected area size (in km^2) from Protected Planet: The World Database on Protected Areas (WDPA) (UNEP-WCMC & IUCN, 2020; Hanson, 2020). This includes data on 515 protected areas from 62 countries across four continents (Africa, North America, South America, and Asia) and three biogeographical realms (Afrotropics including Malagasy, Central and South America, and Indomalayan).

We extracted functional trait data for each of the carnivore species (Rowan *et al.*, 2020). For functional trait analyses, we utilized body mass (species average mass in

grams) and species threat status based on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2021) (Data Deficient, Endangered, Least Concern, Near Threatened, and Vulnerable) obtained through Phylacine (Faurby *et al.*, 2018). We also used diet data (consumes vertebrates, mammalian / avian / reptile-amphibian / fish / invertebrate prey, and/or plant matter such as seed / fruit / nectar / root / woody / herbaceous / other) from the MammalDIET dataset (Kissling *et al.*, 2014).

We used correlation matrices to determine the relationship between different variables for each protected area in the checklist. We removed communities with less than three species (only three sites in Asia) for this analysis. The traits [Table 2.3] used for the correlation matrices were body mass and dietary principal coordinates analysis (PCoA; first two axes, PCoA1 and PCoA2) obtained from (Rowan *et al.*, 2020). PCoA is a multidimensional scaling technique used to explore similarities and differences in data. More simply, it is a method to reduce the dimensionality of the dataset, which allows for a more easily interpretable comparison of the samples.

The dietary PCoA was based on the MammalDIET dataset (Kissling *et al.*, 2014). A subset of this dataset (Rowan *et al.*, 2020) focused on 13 food groups consumed by mammal species (including the carnivores considered in this study) to characterize dietary diversity. This subset mammal community data involved MammalDIET rank scores for each species such that a rank of 0 corresponds with ‘food category not consumed’, 1 with ‘food category rarely consumed’, 2 with ‘food category frequently consumed’, and 3 being ‘primary food category’. PCoA1 and PCoA2 accounted for nearly 83% of variation in the mammal diets.

We used the the species-level mammal phylogeny of Faurby and Svenning (Faurby & Svenning, 2015) for the phylogenetic analyses since it is a comprehensive and robust species-level estimate and includes all the carnivores considered in this study. Furthermore, this phylogeny is consistent with current IUCN Red List classification (IUCN, 2021). The biodiversity metrics (Kraft & Ackerly, 2010) used were range (trait range in a community where higher values indicates greater range), SDNdr (the standard deviation of neighbor distances of trait values for species within a community divided by the overall trait range of that community where higher values indicate greater spacing in niche space for community members), NRI (the net relatedness index or average phylogenetic distance among all species within a community where lower values indicate higher overall phylogenetic diversity), and NTI (the nearest taxon index or phylogenetic distance between the two most closely related species in a community where lower values indicate greater phylogenetic distance). For functional trait analysis, a constant (100) was added to all values when logging. The rationale for choosing these measures was to understand how the trait values ‘scale up’ from the species level to that of the carnivore communities.

In the correlation matrices [Figure 2.5 ; see Table 2.3 for variable key], BM.Range, PCoA1, and PCoA2 are trait ranges in a community where higher values correspond with greater range. SDNdr (for BM, PCoA1, and PCoA2) is the standard deviation of neighbor distances of trait values for species within a community divided by the overall trait range of that community where higher values correspond with greater spacing in niche space for community members. NRI is the average phylogenetic distance among all species within a community where lower values correspond with higher overall phylogenetic diversity, and NTI is phylogenetic distance between the two most closely related species in a community where lower values indicate greater phylogenetic distance.

For each protected area (PA), we characterized 19 modern bioclimatic variables representing various measures of rainfall and temperature. These variables were compiled from WorldClim (Hijmans *et al.*, 2005) and are presented in Appendix C. The central latitude and longitude for each protected area were used to obtain present-day bioclimatic data at 2.5' resolution.

2.3 Results

Total carnivore richness considered in this study is 196 species across 62 countries in the Afrotropics, Indomalayan, and Central and South American regions, spanning 13 families (Figure 2.2). The most species-rich families are: Felidae and Herpestidae ($n=34$) followed by Mustelidae ($n=33$), Viverridae ($n=30$), and Canidae ($n=27$) (Figures 2.3 and 2.4). The carnivores that occur in more than one biogeographical realm are: golden jackal (*Canis aureus*), caracal (*Caracal caracal*), wildcat (*Felis silvestris*), striped hyena (*Hyaena hyaena*), honey badger or ratel (*Mellivora capensis*), and leopard (*Panthera pardus*). All of them are found in both Africa and the Indomalayan region. Carnivore community richness (25 to 30 species per protected area) is highest in south-central and east Africa, parts of west Africa, and south and south-east Asia (including the Himalyan belt) (Figures 2.2 and 2.4). The most depauperate regions of the global tropics and subtropics in terms of carnivore richness are Madagascar and southern South America (Figure 2.2). While a majority of the carnivores fall under the IUCN Red List category of Least Concern (Figure 2.1), when body size was considered in combination with threat status (Figure 2.6), we found that larger carnivores were more threatened and considered Vulnerable or Endangered.

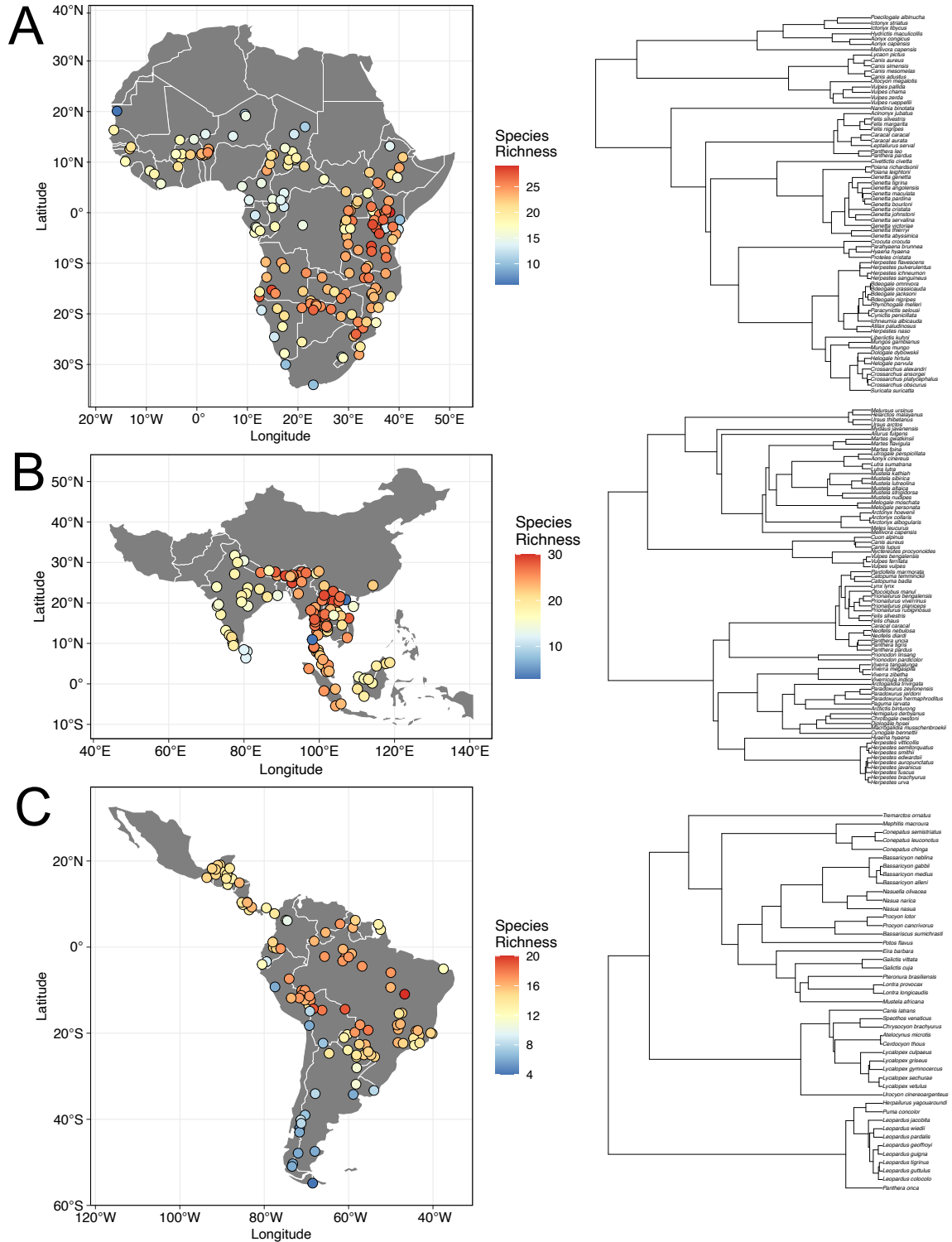


Figure 2.4. The distribution of protected areas color-coded by carnivore community size in each location and the phylogenetic structure of the carnivore species considered in this study in each of the major biogeographical regions. A: Africa; B: Indomalayan region; C: Central and South America

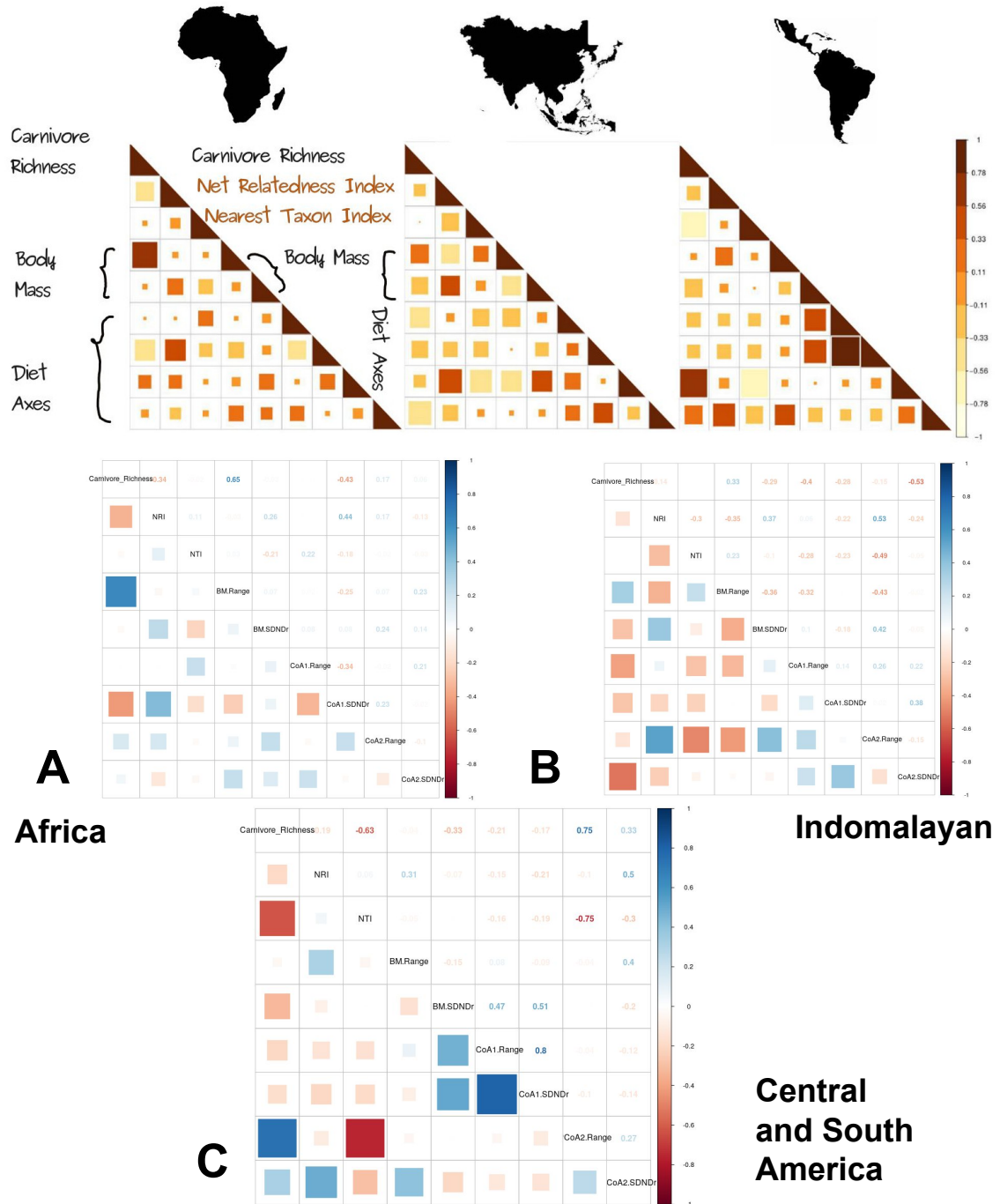


Figure 2.5. Correlation matrices of multiple biodiversity metrics in relation to carnivore richness for each of the major biogeographical regions considered in this study. *Carnivore_Richness*: Carnivore community size ; *NRI*: Net Relatedness Index ; *NTI*: Nearest Taxon Index ; *BM.Range*: Body mass range ; *BM.SDNDR*: Body mass SDNDR (standard deviation of neighbor distance divided by the overall range) ; *PCoA1.Range* and *PCoA2.Range*: Principal Coordinate Axes (PCoA) 1 and 2 of diet range ; *PCoA1.SDNDR* and *PCoA2.SDNDR*: PCoA 1 and 2 of diet SDNDR. The color gradient scale indicates the strength and direction of correlation. (See Appendix B for higher resolution images for each continent.)

2.3.1 Biodiversity Metrics

(Q1) Relationship between carnivore community richness and species traits

As expected, carnivore richness in Africa, the Indomalayan region, and Central and South America was correlated with body mass range and dietary axes range with regional differences in degree and extent of correlation (Table 2.3 and Figure 2.5). Carnivore richness in Africa was positively correlated with body mass range of the species. For the Indomalayan region, carnivore richness was moderately positively correlated with body mass range and strongly negatively correlated with the second dietary axis (PCoA2.SDNDr). In Central and South America, carnivore richness was strongly positively correlated with the dietary range (PCoA2).

(Q2) Relationship between carnivore community richness and phylogenetic diversity

The NRI values for carnivore communities in all three regions were low, indicating high overall phylogenetic diversity. The overall phylogenetic diversity was highest in Central and South America and lowest in the Indomalayan region, with African communities being intermediate. For Africa, richness was negatively correlated with NRI (lower values are indicative of higher overall phylogenetic diversity). In other words, carnivore richness in African communities corresponded with greater phylogenetic diversity. In the Indomalayan region, PCoA2 range was positively correlated with NRI (higher values indicating lower overall phylogenetic diversity) and negatively correlated with body mass range as well as NTI (indicating higher phylogenetic distance). In Central and South America, the NTI was strongest for dietary axes as well for this region (strong negative correlation and low values indicate greater phylogenetic distance). The carnivore richness for this region seemed to correspond with greater phylogenetic distance in general.

2.3.2 Conservation Metrics

(Q3) Relationship between carnivore body size and conservation status

Most small carnivores (< 10 kg) are endangered, near threatened, or vulnerable, while most medium-sized carnivores (> 10 kg) are vulnerable. Ten of the 16 endangered and 13 out of 32 vulnerable carnivores were found in the Indomalayan region, amounting to 23 out of 48 threatened carnivores, about half the threatened carnivore species in the tropics. The Indomalayan region has about 40% of total carnivore richness (77 carnivorans out of 196 carnivore species considered here) which corresponds with a disproportionate number of threatened species (62% endangered and 40% vulnerable carnivores). The smallest carnivore is the mountain weasel (*Mustela altaica*), which is found in the Indomalayan region, weighs 171 grams, and is near threatened. The two carnivores with the highest body mass are also found in Indomalaya - the tiger (*Panthera tigris*) which has a mean weight of about 160 kg and is endangered, and the brown bear (*Ursus arctos*) which has a mean weight of 180 kg and is categorized as least concern.

The majority of the species are considered to be of Least Concern (LC) according to the IUCN Red List threat classification (Figure 2.6). The two carnivores that are Data Deficient (DD; Pousargues's mongoose - *Dologale dybowskii* and Abyssinian genet - *Genetta abyssinica*) are both with low body mass and found in Africa. Several large carnivores (> 25 kg) seem to be of LC. However, the majority of large carnivores are considered Endangered (EN), Vulnerable (VU), or Near Threatened (NT).

(Q4) Relationship between carnivore community richness and protected area size

Protected area sizes varied from 0.25 km² (La Selva Biological Station in Costa Rica) to 251569.05 km² (Pantanal Wetlands in Brazil) (Figures 2.8 and 2.9). For the

410 protected areas across countries in continental Africa, Central and South America, and the Indomalayan realm, there does not seem to be a correlation between protected area size (in km²) and carnivore community richness. This absence of any significant species-area relationship (Figures 2.8 and 2.9) is likely to be a consequence of environmental heterogeneity and bioclimatic gradients such as elevation and precipitation ranges being better predictors of species richness patterns than PA size (Udy *et al.*, 2021; Mazel *et al.*, 2014). This is particularly stark in the Indomalayan region where protected areas tend to be small but having substantial heterogeneity with large elevation and precipitation gradients and disproportionately high carnivore community richness (in fact the highest of all the biogeographic regions considered here).

Bioclimatic variables considered in this study for each of the major biogeographic regions in the global tropics and subtropics are available in Appendix B. This includes maps of protected areas in each region color-coded with mean annual temperature and mean annual precipitation. Appendix B also includes plots for the Indomalayan region as well as Central and South America that correspond to the variation in species richness with latitude of protected areas as well as regional variation of all 19 bioclimatic variables considered here.

2.3.2.1 Carnivore Diversity and Conservation in Madagascar

Madagascar was considered separately from the other major biogeographical regions in terms of carnivore diversity, richness, and conservation (Cartagena-Matos *et al.*, 2017; Herrera, 2017) (Figure 2.7). Given the unique geological history of the region, there is a high degree of endemism in the island (Battistini & Richard-Vindard, 2013). The country is also susceptible to a range of anthropogenic impacts particularly deforestation, habitat loss, and land use change (Gerber *et al.*, 2012b; Morelli *et al.*, 2020).

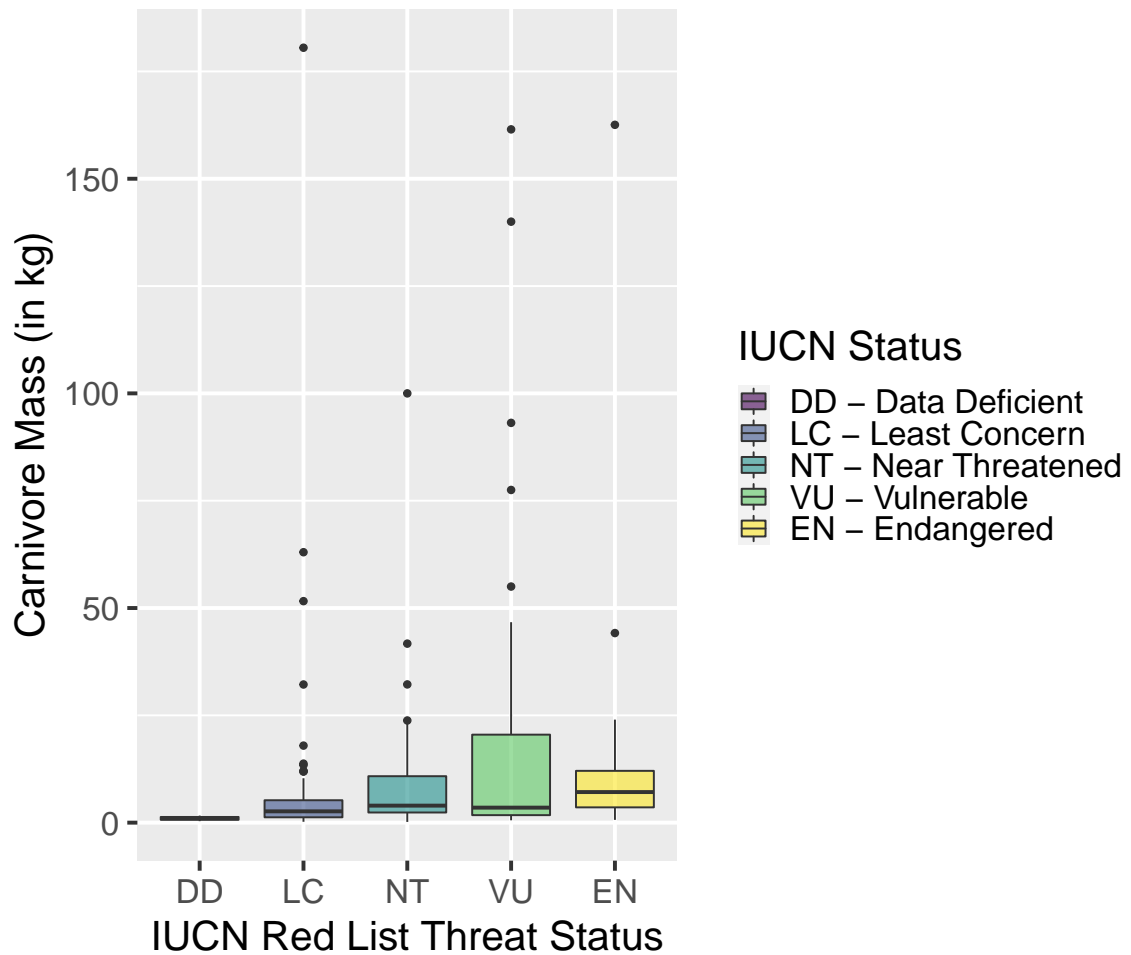


Figure 2.6. Boxplot showing the relationship between number of species in each of the IUCN Red List categories and the body mass of the species in kilograms. *DD*: Data Deficient ; *LC*: Least Concern ; *NT*: Near Threatened ; *VU*: Vulnerable ; *EN*: Endangered.

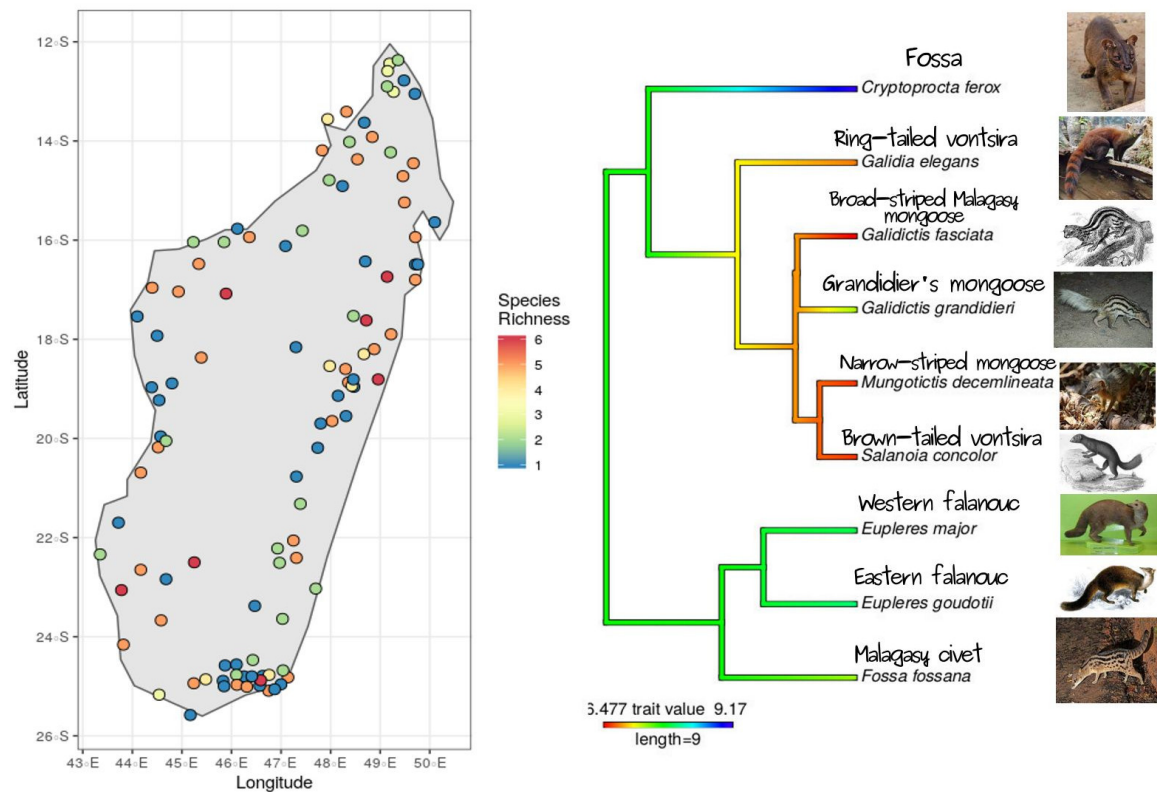


Figure 2.7. Community richness and phylogenetic diversity of carnivore communities in Madagascar. Malagasy carnivore images: Wikimedia Commons.

The Malagasy carnivore community is distinct due to the small size of and high relatedness among the species. Of the nine carnivoran species found in Madagascar, all are of small body mass (<10 kg), endemic, and rank high on distinctiveness despite low relative richness compared to other regions.

The Malagasy carnivores belong to a single family (Eupleridae) and seven genera, all of which are endemic to Madagascar, found nowhere else on the planet, and threatened by habitat destruction as well as predation and competition with non-native species. Out of these species, three are endangered (western falanouc - *Eupleres major*, Grandidier's mongoose or vontsira - *Galidictis grandidieri*, and narrow-striped mongoose - *Mungotictis decemlineata*) and five are vulnerable (fossa - *Cryptoprocta ferox*, Eastern falanouc - *Eupleres goudotii*, Malagasy civet or fanaloka - *Fossa fossana*, broad-striped Malagasy mongoose - *Galidictis fasciata*, and Malagasy brown-tailed mongoose or salano - *Salanoia concolor*), while only one carnivore native to Madagascar is of least concern (ring-tailed vontsira - *Galidia elegans*). While Malagasy carnivores tend to be of small body size, a disproportionate number of these carnivores are threatened, with 8 out of 9 carnivores categorized as endangered or vulnerable. This is anomalous with threatened carnivores in the other regions considered where a larger body size corresponds with a greater threat status, emphasizing the importance of holistically considering evolutionary history and endemism along with other biodiversity metrics for carnivore conservation.

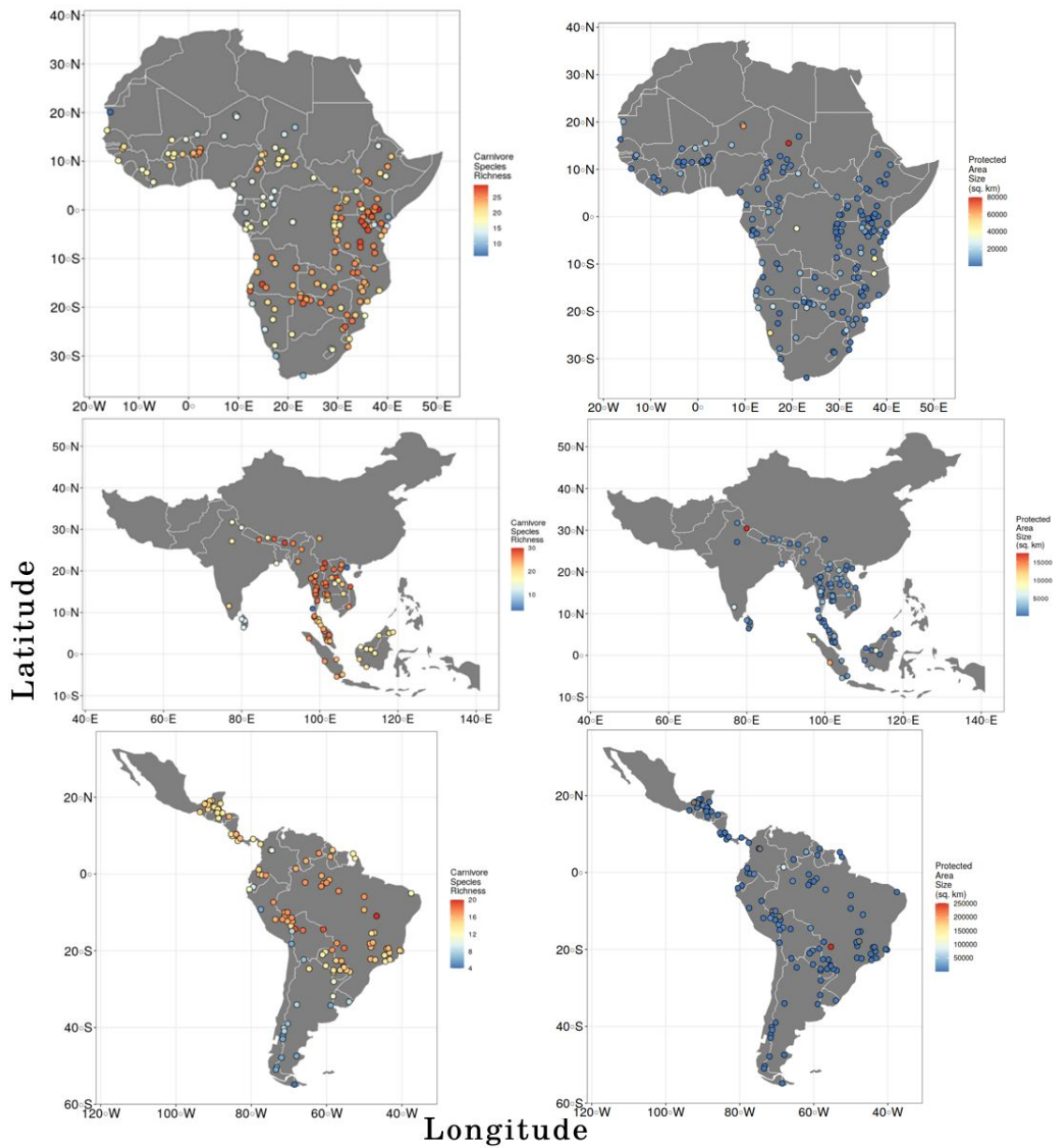


Figure 2.8. The distribution of carnivore species richness and protected areas across the major biogeographical realms in the tropics and subtropics: Africa, Indomalayan region, and Central and South America.

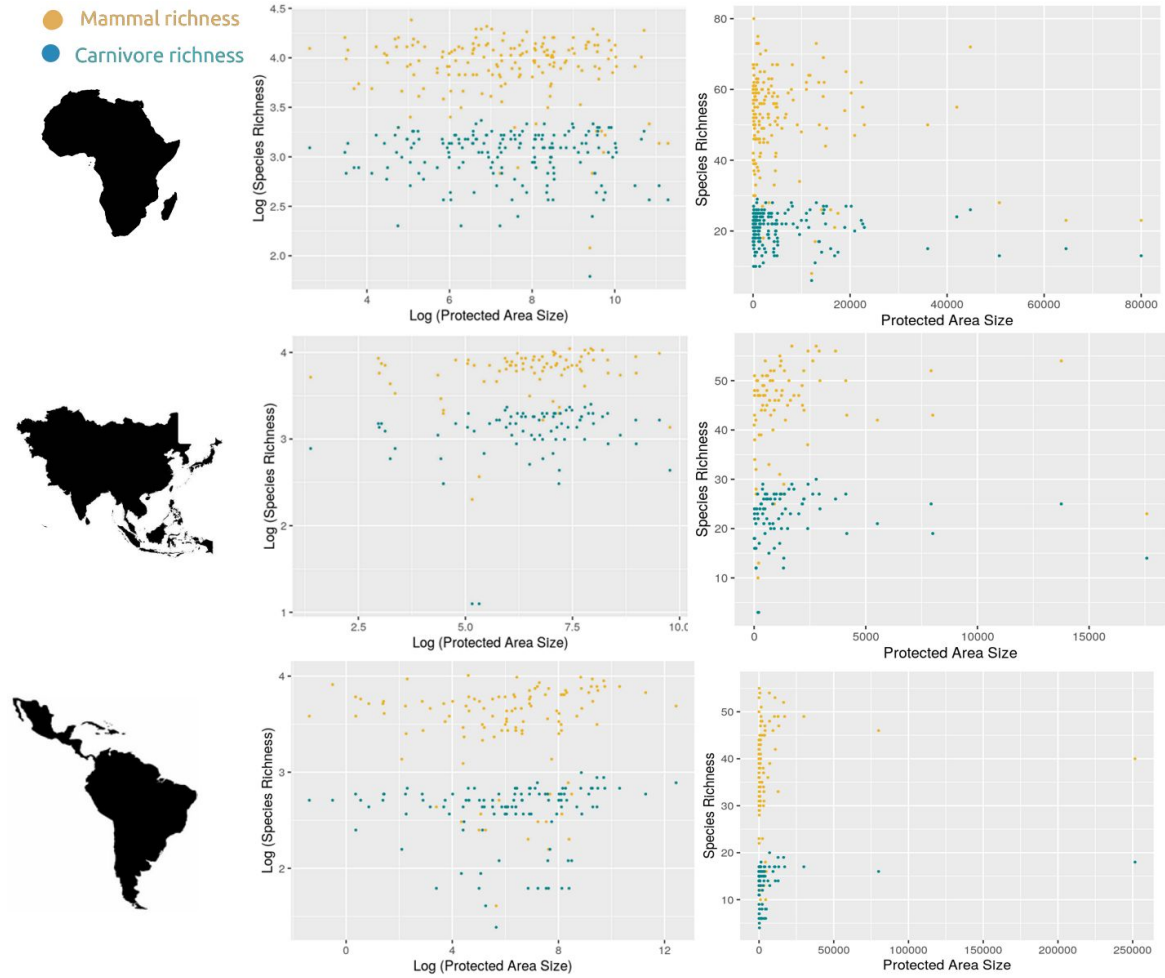


Figure 2.9. Scatterplots of the relationship between species richness and protected area size for each major biogeographical region in the tropics and subtropics: Africa, Indomalayan region, and Central and South America. *Yellow*: Total mammal richness in each protected area; *Blue*: Total carnivore richness in each protected area. The x-axis is the logarithm of protected area size in km^2 and protected area size respectively, while the y-axis is the logarithm of species richness and species richness (total mammal and carnivore) respectively.

2.4 Discussion

In this chapter we investigated: (i) how carnivore community size, structure, and composition vary across countries in the global tropics and subtropics; (ii) whether more diverse carnivore communities correspond with more rare or distinctive taxa; and (iii) if carnivore community size is related to phylogenetic and functional diversity. We find that there is enormous variation in carnivore community size, structure and composition at all the major biogeographical realms we considered, spanning the global tropics and subtropics.

The distinct patterns of carnivore community composition and richness between the regions is likely to be influenced by the unique evolutionary and biogeographic history of each region (Hubbell, 2001; Fleagle & Gilbert, 2006; Svenning *et al.*, 2015; Farris *et al.*, 2016). No single pattern fits all regions given the varied geological histories of Africa, Indomalaya, and Central and South America, along with the dispersal of species through evolutionary time, resulting in distinctive community compositions at different scales in each region. For instance, the carnivore community richness and evolutionary distinctiveness of species is likely to vary between islands and the mainland, as can be seen for Madagascar.

2.4.1 Biodiversity and Conservation Metrics for Carnivores

As expected, carnivore community size correlated with phylogenetic and functional diversity (Figures 2.4 and 2.5) (Q1 and Q2). Broad trends included more species-rich communities along eastern edges of the biogeographical regions at the continental scale (Figures 2.1 and 2.2). The Indomalayan region was the most speciose while lower latitudes of South America and Africa such as Madagascar had the communities with fewest carnivores. However, while the latter communities had lower richness, they did have a high proportion of evolutionarily distinct and threatened taxa. Thus

the most and least diverse carnivore communities both corresponded with more rare and distinctive taxa (Figures 2.4 and 2.7).

There is substantial variation in the diets of carnivores. Many taxa are not obligate carnivores and have a significant portion of their diet composed of plant matter. We can expect body mass to be correlated with dietary range (Figure 2.5) as a general trend such that species with higher body mass are likely to be obligate carnivores while mesocarnivores are more likely to be omnivorous and have larger dietary ranges with some plant matter in their diets.

Body size is an important consideration for mammal conservation especially for species threatened by climate change (McCain & King, 2014) (Q3). Large carnivores influence the distribution and densities of other species through a variety of interactions - predation, commensalism, competition, and mutualism (Linnell & Strand, 2000; Linnell *et al.*, 2001; Schuette *et al.*, 2013; Gompper *et al.*, 2016; Jiménez *et al.*, 2017). By exerting top-down control, variation in the distribution and abundances of apex predators is thought to cause trophic cascades and mesopredator release, directly and indirectly affecting species across trophic levels. Carnivores also help in the structure and function of tropical forests through seed dispersal, pollination, and carbon sequestration (Gompper *et al.*, 2016; Jiménez *et al.*, 2017). However, there is also bottom-up control, through primary productivity and nutrient cycling, exerted at the ecosystem level in tropical forests. Harnessing the charismatic nature of tropical carnivores like the jaguar and tiger, carnivore community conservation efforts could be a tool for tropical forest conservation and vice versa. Furthermore, both common as well as rare carnivores are important in different ecosystems, and even at low abundances predators are influential in ecosystem functioning (Mateo-Tomás *et al.*, 2017).

When considering the influence of protected area size (Figures 2.8 and 2.9), we found that PA size did not correspond with carnivore richness (Q4), potentially because environmental heterogeneity is considered more important for community diversity (Udy *et al.*, 2021). This means that communities in protected areas with greater environmental heterogeneity have more speciose carnivore communities. While PAs in the Indomalayan region might be small, the substantial habitat gradient results in highly diverse carnivore communities. Our results highlight the importance of focusing conservation efforts on both these extremes, the species-rich as well as depauperate communities, to maximize conserving the most endangered, rare, and distinct fauna.

Evolutionary distinctiveness, phylogenetic diversity, endemism, and taxonomic richness do not align perfectly as can be seen from our results (Figures 2.4 and 2.5). Consequently there is a need for different priority areas and hotspots for carnivore conservation (Isaac *et al.*, 2007; Jensen *et al.*, 2016; Webb *et al.*, 2002; Mazel *et al.*, 2014). From a conservation perspective, it is important to understand if community size is reflective of higher proportions of threatened taxa (for instance using IUCN status as a metric for rarity or vulnerability to extinction) (Loiseau *et al.*, 2020). Our results indicate that community size at either extreme correlates with endangered and threatened species. On the other hand, if carnivores are distributed randomly, there is a trade-off between prioritizing communities and specific species that might be threatened. This has direct consequences for wildlife conservation and the development of conservation plans. For instance, given limited resources, conservationists are often confronted with tricky issues like conserving multiple species in a community and specific habitats which may hypothetically harbor few rare or threatened species and protecting individual species in depauperate communities with high endemism, rarity, distinctiveness, and potentially at the brink of extinction.

Based on our analyses and results, considering the evolutionary histories of the different communities in combination with species traits, abiotic factors, and contemporary carnivore community composition and diversity is important for carnivore conservation. Given the number of threatened carnivores found in the Indomalayan region and since the region is highly vulnerable to anthropogenic threats such as fragmentation, habitat loss, and land use change, it is emerging as a critical biodiversity hotspot in dire need of attention for carnivore conservation.

2.4.2 Additional Considerations for Carnivore Conservation

It is also critical to identify biodiversity hotspots at large spatial scales for conserving carnivores at the community level keeping connectivity in perspective. Increasingly, there is evidence that habitat gradients and diversity are better predictors of species richness in communities than protected area size (Udy *et al.*, 2021; Mazel *et al.*, 2014). This adds nuance to the single large or several small (SLOSS) debate in relation to protected area size (Lindenmayer *et al.*, 2015; Udy *et al.*, 2021; Mazel *et al.*, 2014). Furthermore, given that evolutionary distinctiveness, phylogenetic diversity, endemism, and taxonomic richness do not align perfectly as seen from our results, it is therefore important for priority areas to be identified for carnivore communities.

The 3Cs approach (Cores, Corridors, and Carnivores), a conservation planning framework, emphasizes the role of carnivores as umbrella species as well as climate change buffers when taken as a community (Carroll & Noss, 2021). Recent research also shows how armed conflicts exacerbate population declines in threatened mammal species along with associated conservation issues such as hunting and habitat degradation (Mendiratta *et al.*, 2021). These are important to take into consideration for carnivore conservation, especially for wide-ranging, threatened, and evolutionarily distinct carnivore taxa.

The Serengeti Rules (Carroll, 2016) on regulation in natural systems state that: (i) some animals are more equal than others and keystone species impact community assembly and diversity, (ii) some species have strong indirect effects on other species through trophic cascades, (iii) the regulation of some species depends on density, and (iv) nature is resilient and given sufficient time and protection, systems and communities can rebound. This has been shown to hold true in multiple landscapes and taxa including carnivores such as through the reintroduction of wolves in Yellowstone (Smith & Peterson, 2021) and wild dogs in Gorongosa (Bouley *et al.*, 2021). However there is a relationship between community richness and stability where more species-rich communities tend to be more stable (Ives & Carpenter, 2007). This implies that the impacts of carnivore introductions in communities with greater species diversity would vary substantially from introducing a large predator into a depauperate carnivore community. Similarly losing a species in a relatively speciose community (e.g., those with 20 carnivores) is unlikely to destabilize the habitats and community the way losing species in a depauperate community would impact landscape and community composition, structure, and function.

With technological and methodological advances including remote sensing, camera trapping, and audio recordings, there is rising interest in modeling communities (Ik-nayan *et al.*, 2014; Warton *et al.*, 2015; Ramachandran & Devarajan, 2018; Devarajan *et al.*, 2020). There are multiple approaches emerging to deriving biodiversity metrics as well as studying changes in community composition, function, and size across space and time (Warton *et al.*, 2015; Ovaskainen *et al.*, 2017; Tikhonov *et al.*, 2020; Devarajan *et al.*, 2020; Anderson *et al.*, 2021). For instance, Hierarchical Modelling of Species Communities (HMSC) is a promising framework for analyzing community data while considering traits, phylogeny, and occurrence alongside environmental covariates (Ovaskainen *et al.*, 2017).

Multispecies occupancy models (MSOMs) (Devarajan *et al.*, 2020) are considered robust approaches to explore the distribution of several species within a community. They help address the problem of imperfect detection in such studies at various scales. However they have several assumptions that should not be violated and specific conditions in order to be implemented. For instance, occupancy models are built on encounter histories for each species at multiple sites (spatial replicates) during multiple visits (temporal replicates). Thus, in order to use occupancy modeling approaches, it is important to keep these considerations during the study design phase. This means that MSOMs cannot be applied for existing datasets that do not have both spatial and temporal replicates, among other considerations including not having species presence-absence data. In this study, at the continental scale or biogeographical realms considered, while each protected area (site) can be treated as a spatial replicate, the presence-absence of species in each PA is based on a single snapshot of whether the species is known to be present in the PA or not. Thus given the lack of temporal occurrence data for the species in each protected area, MSOMs cannot be applied for this community data.

The linking of multiple measures of biodiversity such as taxonomic, phylogenetic, and functional metrics at different spatial and temporal scales with conservation biology helps formulate more effective strategies for biodiversity conservation (Pollock *et al.*, 2017; Pimm, 2021; Pease *et al.*, 2021). Given this, the use of analytical tools that provide estimates of biodiversity metrics is essential for robust inference and the development of effective conservation plans.

Table 2.3. Variables considered for evaluating biodiversity metrics.

Variable	Expansion	Explanation
NRI	Net Relatedness Index	Average phylogenetic distance among all species within a community (lower values = higher overall phylogenetic diversity)
NTI	Nearest Taxon Index	Phylogenetic distance between the two most closely related species in a community (lower values = greater phylogenetic distance)
BM.Range	Body Mass Range	Trait (body mass) range in a community (higher values = greater range)
BM.SDNDr	Standard Deviation of Neighbor Distances of Species Body Mass / Overall Body Mass Range in Community	Standard deviation of neighbor distances of trait (body mass) values for species within a community divided by the overall trait (body mass) range of that community (higher values = greater spacing in niche space for community members)
PCoA1.Range	First Dietary Principle Coordinates Axis (PCoA) Range	Trait (first dietary PCoA axis) range in a community (higher values = greater range)
PCoA1.SDNDr	Standard Deviation of Neighbor Distances of Species Diet / Overall Dietary Range in Community	Standard deviation of neighbor distances of trait (first dietary PCoA axis) values for species within a community divided by the overall trait (PCoA1) range of that community (higher values = greater spacing in niche space for community members)
PCoA2.Range	Second Dietary PCoA Range	Trait (second dietary PCoA axis) range in a community (higher values = greater range)
PCoA2.SDNDr	Standard Deviation of Neighbor Distances of Species Diet / Overall Dietary Range in Community	Standard deviation of neighbor distances of trait (second dietary PCoA axis) values for species within a community divided by the overall trait (PCoA2) range of that community (higher values = greater spacing in niche space for community members)

CHAPTER 3

THE COMPANY CANIDS CONFRONT: SPATIOTEMPORAL PARTITIONING AT LOCAL SCALES FACILITATES CARNIVORE COEXISTENCE AT THE LANDSCAPE LEVEL

Abstract

Canids are the most widely distributed carnivores in the world. The increasing impacts of commensal carnivores such as free-ranging dogs on wildlife communities has resulted in an urgent need to understand putative interactions within carnivore guilds. It is therefore imperative to understand the processes driving canid assemblages in different landscapes and at multiple spatial and temporal scales, in order to conserve and manage wildlife communities. I investigate spatial, temporal, and habitat partitioning within a guild of four co-occurring canids, namely desert fox (*Vulpes vulpes pusilla*), Indian fox (*Vulpes bengalensis*), golden jackal (*Canis aureus*), and domestic dog (*Canis lupus familiaris*), the arid northwest of India. My study provides essential baseline information on the occurrence and distribution patterns of multiple canids in a human-dominated and understudied landscape threatened by global change. The results of this study indicate that co-occurrence at the local spatial scale between species corresponds with temporal partitioning in intra-guild carnivores that are of similar body size. My results show that, for canids, avoidance at the local scale through facultative and behavioral character displacement such as temporal partitioning enables coexistence at the landscape scale.

Now, here, you see, it takes all the running you can do, to keep in the same place.

–The Red Queen, in Lewis Carroll’s Through the Looking-Glass

A class of alternative ideas, here termed Court Jester hypotheses, share the basic tenet that changes in the physical environment rather than biotic interactions themselves are the initiators of major changes in organisms and ecosystems.

“Maybe it is time for the Court Jester to marry the Red Queen.” That is, perhaps the dichotomy between the two hypotheses is really a dichotomy of scale, and that as we look for ways to travel across biological levels, we will find ways to resolve the dichotomies.

– Anthony Barnosky (Barnosky, 2001)

3.1 Introduction

Carnivores are distributed widely, found in almost all landscapes and land cover types on earth, and exhibit enormous variation in terms of traits and adaptations (Gittleman, 2019). They influence community assembly and ecosystem function through their direct and indirect interactions with other species at different trophic levels, including top-down control on prey and competition for habitat and food (Linnell & Strand, 2000; Sillero-Zubiri *et al.*, 2001; Linnell *et al.*, 2001; Schuette *et al.*, 2013; Gompper *et al.*, 2016; Jiménez *et al.*, 2017). Carnivores in resource-limited areas, such as arid and semi-arid ecosystems, are especially vulnerable to threats (Cardillo *et al.*, 2005; Ripple *et al.*, 2014), since these unique regions are often under-studied, under-protected, face rapid conversion, and are threatened by encroachment, monocultures, invasive species, fragmentation, and climate change, potentially resulting in species extinctions (Sodhi *et al.*, 2004; Dunn *et al.*, 2009; Gerber *et al.*, 2012b). Despite these issues, species-rich carnivore communities continue to persist in heavily human-dominated and human-modified habitats (Linnell *et al.*, 2001; Sillero-Zubiri *et al.*, 2001; Schuette *et al.*, 2013).

Multi-species carnivore assemblages are seen almost globally and given resource limitations, interference competition is now accepted as a crucial factor in the distribution and composition of mammalian communities (Estes *et al.*, 2011). A number of studies have established that a “landscape of fear” exists not just in prey-predator interactions but even in intra-guild interactions. In the latter case, as is true for carnivores, dominance is typically based on size (Palomares & Caro, 1999). This has given rise to the notion of “species-scapes”, which has been defined as a “spatial plane of species interactions that combines with resources and habitat structure to drive species distributions” (Fisher *et al.*, 2013).

Wild canids are the most widely distributed of carnivores and are found in all continents with the exception of Antarctica (Sillero-Zubiri *et al.*, 2004; Gittleman, 2019). A common trend is that two or three species of canids tend to occur in sympatry (Kamler *et al.*, 2004, 2012; Gittleman, 2019). Typically, in systems with multiple sympatric canids, there is resource partitioning of some kind - habitat, spatial, temporal, and/or dietary (Kamler *et al.*, 2012; Gámez & Harris, 2020). Conditions that allow several species to coexist usually include either a minimum weight difference between species or massive character displacement, such as in the case of some parts of sub-Saharan Africa with the cape fox, bat-eared fox, and the black-backed jackal (Kamler *et al.*, 2012).

Despite the wide distribution of free-ranging dogs, it is rare to find systems with multiple canids so that guild-level interactions can be understood. One of the few places in the world where multiple canids co-occur is in the Banni grasslands of Kutch in northwest India which harbor five co-occurring canids: desert or white-footed fox (*Vulpes vulpes pusilla*), Indian or Bengal fox (*Vulpes bengalensis*), golden jackal (*Canis aureus*), and Indian wolf (*Canis lupus pallipes*) along with high densi-

ties of free-ranging domestic dog (*Canis lupus familiaris*). The Indian wolf however is rarely seen here and could possibly be using the landscape only while dispersing. Current understanding of the species ecology indicates that dogs are human commensals, jackals are likely to be habitat generalists, while the fox species are considered habitat specialists with the Indian fox tightly coupled with grasslands and the desert fox associated with arid areas (Figure 3.1) (Sillero-Zubiri *et al.*, 2004). Here, I aim to understand how these multiple competing canid species interact over space and time, and the spatiotemporal associations facilitating their co-existence. I compare patterns of habitat use, as well as spatial and temporal segregation of four species of canids found in the study area (Figures 3.1 and 3.2).

I predict that (i) the canids will vary in their distribution, with dogs and jackals more likely to be found close to human habitation such as villages (since both species have a generalist diet and are commensals in the region) and the two fox species less likely to be close to villages (Figures 3.4 and 3.5a), (ii) the presence of wild canids will likely vary based on habitat type with jackals widely distributed and found in areas with the invasive *Prosopis juliflora* (also called mesquite) and other mixed vegetation types, whereas the Indian fox is more likely to be associated with grassy areas, and the desert fox is more likely to be found in saline desert habitat (Figure 3.5a), and (iii) spatial overlap between two species will likely result in temporal partitioning or other behavioral character displacement between the species. Resources are limited for carnivores so spatial overlap at local scales is likely to result in temporal partitioning or other behavioral character displacement to enable coexistence at larger scales (Farris *et al.*, 2015, 2016). I used data from a camera trap survey under a multi-species occupancy modeling (MSOM) (Waddle *et al.*, 2010; Rota *et al.*, 2016; Devarajan *et al.*, 2020) framework to account for imperfect detection and estimate

the influence of the habitat and environmental variables, as well as the presence of the other species, on the co-occurrence of a given species (Figures 3.3-3.7).

3.2 Methods

3.2.1 Study Area

I conducted field data collection for this study in the Banni grasslands located in the Kutch district of Gujarat in north-west India (Figure 3.2) between September 2014 and March 2015. Spread over an area of 2500 km², the Banni grasslands are considered the largest tropical grassland in Asia and the largest natural grassland in the Indian subcontinent. These grasslands are a mosaic of seasonal grassland patches and arid desert patches with salt pans.

The region harbors a high mammal diversity. Apart from the five canid species, some of the other mammalian carnivores that can be found here include the desert cat (*Felis lybica ornata*), caracal (*Caracal caracal*), jungle cat (*Felis chaus*), and striped hyena (*Hyaena hyaena*). While the Indian wolf has been an integral part of the carnivore assemblage historically, the species is very rarely seen in the region in recent years and hence was excluded from this study. Other species include Indian grey mongoose (*Herpestes edwardsi*), chinkara (*Gazella bennettii*), nilgai (*Boselaphus tragocamelus*), Indian crested porcupine (*Hystrix indica*), Indian long-eared hedgehog (*Hemiechinus collaris*), black-naped hare (*Lepus nigricollis*), and Indian desert jird or gerbil (*Meriones hurrianae*). Birds, reptiles, invertebrates, livestock, and humans also emerged as bycatch from the camera trap study.



Figure 3.1. Brief natural history description of the four species of canids included in this study.

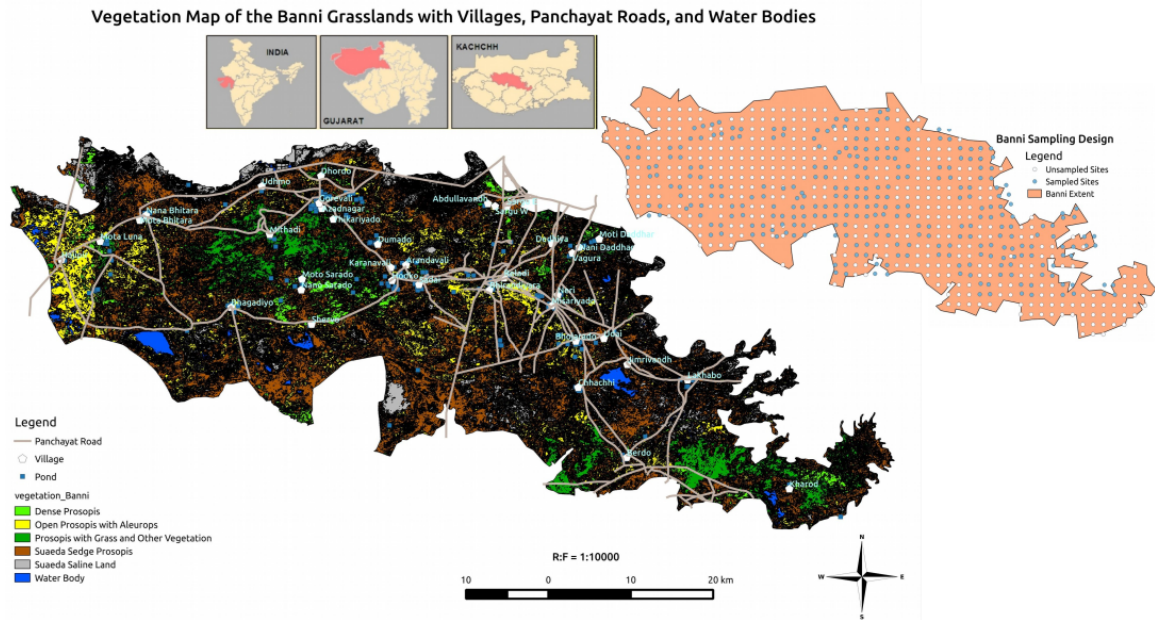


Figure 3.2. Vegetation map of Banni. A map of the study area in the Banni grasslands depicting vegetation cover, roads, villages and water bodies along with some villages and adjoining regions, with the inset maps showing location of Banni in the Kutch district of Gujarat state in India as well as the sampling design employed. The gaps in sampling can be attributed to the presence of water bodies at some of the sites and due to an inability to obtain permission to set up camera traps in restricted areas. *Figure based on GIS layers courtesy of K-Link Foundation, India.*

The spatial scale for this study reflects coverage of the whole Banni grassland landscape encompassing the unique canid community present. The temporal scale was chosen to minimize violating the demographic closure assumption on the basis of running a single season MSOM during the dry season, since it is logistically infeasible to set camera traps in the study area during the wet season when many parts of the area are inundated.

3.2.2 Survey Design

Camera traps were used to determine the occurrence of each of the species in order to understand habitat, spatial, and temporal partitioning between them. A grid-based sampling approach with a systematic sampling design was used by superimposing a 2×2 km grid over the entire study area of 2500 km². I assumed that this cell size represented the home range of the largest species of wild canid (golden jackal) (Aiyadurai & Jhala, 2006). The home range of the Indian fox is between 1.6 and 3 km². Since little is known about the ecology of the desert fox, I assumed a home range of about 4 km² considering that it is intermediate in size relative to the jackal and Indian fox.

The cell size thus helps account for the assumptions of geographic closure and independence in MSOMs (Devarajan *et al.*, 2020). The assumption of demographic closure is also not violated since this is a single season study. All four canids belong to the same guild which minimizes chances of violating the crucial assumption of ecological similarity due to their relatedness within carnivores. Despite their taxonomic relatedness, they are easy to tell apart in the camera trap videos, which reduces violation of the assumption of accurate identification, an important consideration in MSOMs (Devarajan *et al.*, 2020). This grid-based systematic sampling design resulted in 296 sample grids while a further 380 sites were taken as unsampled sites,

giving a total of 670 sites for which the probability of occurrence estimates for each species were obtained (Figures 3.2, 3.4, and 3.5c). I deployed a single Moultrie M990i No-Glow Game camera trap per grid for four consecutive nights as temporal replicates for modeling the detection probability, resulting in 1184 camera trap days in total.

Table 3.1. Species occurrences. Site-specific species occurrences obtained from metadata extracted from camera trap videos annotated through ViXen for the 296 sampled sites (camera locations) and 6221 videos based on the sampling design shown in Figure 3.2. The occupancy estimate (ψ) values shown for each species are from the MSOM using body size-based interactions and habitat covariates covering 670 (290 sampled and 380 unsampled) sites across the landscape as shown in Figure 3.2. Refer Figure 3.7 and the model output shared as supplementary information through Figshare (Devarajan, 2020b) for the species association estimates as well as the species-specific effects of the habitat covariates.















Species	Number of videos with ≥ 1 individual of each canid species	Number of videos with ≥ 1 individual of same species	Number of grids with occurrence of a canid species	Number of grids with recurrences of a canid species	Number of grids with videos of two or more canid species	Number of grids with videos of ≥ 1 wild mammals	Number of grids with videos of ≥ 1 co-occurring domesticated mammal	Estimated occupancy probability for each species
 Free-ranging Dog	19	2	14	2	9	1	6	0.799
 Golden Jackal	180	18	65	43	24	17	18	0.875
 Desert Fox	53	0	28	4	12	8	3	0.666
 Indian Fox	62	0	25	19	13	6	7	0.422

Table 3.2. Site-specific species co-occurrences based on the camera trap videos obtained as described in Table 3.1.

Canid species	Co-occurrence grids
	0
	0
	1
	1
	7
	0
	1
	8
	7
	3

Thirty two of these cameras were deployed in the field at any given time during the study. Since all cameras were from the same manufacturer, and belonged to the same model, any bias introduced from mixing camera trap types was avoided. In the absence of any sturdy trees on which camera traps can be securely mounted in the study area, custom camera trap mounts or stands were used.

In order to maximize species detections, a drop of lure (Cross Breed Food Lure from Kishel’s Scents, USA) was used for every camera trap. While this is considered an ‘active system’ method, lures are not as strong incentives as bait and hence unlikely to introduce any associated bias into the study (Garrote *et al.*, 2012; Gerber *et al.*, 2012a). For each camera trap site, the remotely-sensed covariates, such as the Banni extent, village locations, waterbody locations, roads, and vegetation (Figure 3.2), were obtained from land cover maps provided by the organizations K-Link Foundation and Sahjeevan.

A body size-based hierarchy was assumed for the canids (Figures 3.1 and 3.5) and the interaction was built into the model for each corresponding species. In the model, this hierarchy was incorporated to account for occupancy estimates of a species for a site with and without one or more of the other species. Dogs are the largest among the canids in this study, followed by jackals. The Indian fox is the smallest of the canids, while the desert fox is intermediate between the jackal and Indian fox in terms of body size. This assumption implies that the smaller canids are affected by interactions with the larger canids, while the larger canids are unaffected by the remaining canids. The Indian fox is thus influenced by the desert fox, golden jackal, and dog while the dog is not influenced by the other three canids.

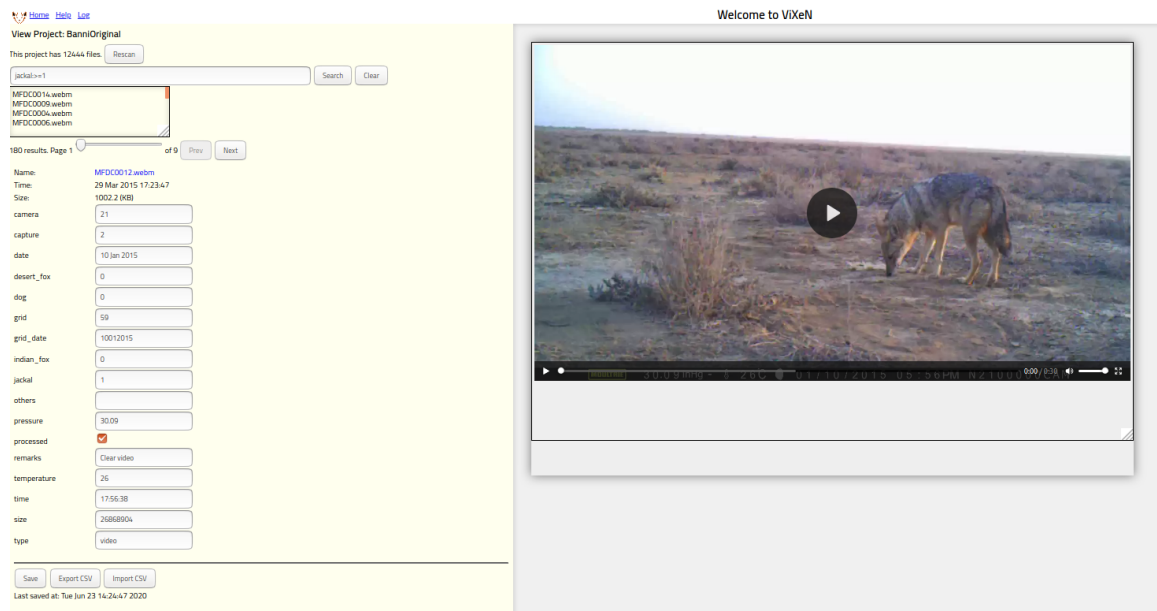


Figure 3.3. Project management through ViXeN. The ViXeN project interface for managing the camera trap videos with the corresponding tags that were created to extract variables of interest such as the species present in each video. The metadata seen to the left of the media viewer (used to view the camera trap videos converted to **webm** format) was extracted as a **CSV** file for subsequent analysis.

3.2.3 Analysis

The videos obtained from the camera trap were accessed using ViXeN (Ramachandran & Devarajan, 2018; Devarajan & Ramachandran, 2020), an open source multimedia file manager for viewing the media, adding custom tags, and annotating metadata associated with media files such as videos, images, audio, and text (Figure 3.3). Custom tags representing the variables of interest were created. The associated variables for each video included information on whether any of the study species were present in the video and if so, the corresponding number of individuals (see Figure 3.3). These metadata of species occurrences were saved as a comma separated value (CSV) file. These metadata were combined with geospatial data based on the grid and camera trap numbers.

The resulting CSV data file was cleaned and exported for further statistical analysis and visualization (Team, 2020; Wickham, 2016; Wickham *et al.*, 2016; Devarajan, 2020a) in R ver. 3.4.4 (Team *et al.*, 2013) and Python version 2.7.6 (Van Rossum & Drake Jr, 1995). The Python libraries **pandas** (McKinney, 2015) and **numpy** (Oliphant, 2007; Virtanen *et al.*, 2020) were also used for the data cleaning and processing done in the analysis.

I extracted information on the ambient temperature at the time of detection and timestamp of canid captured in the camera, and used this metadata to infer a rough time-activity budget (Figure 3.6a) for each species. I used remote-sensing data to understand anthropogenic impacts on species-specific occurrences, as well as local site-level variation in habitat features.

The covariates used for the MSOM were the proportion of the dominant vegetation types (dense *Prosopis* [DP]; *Prosopis*, grass, and other vegetation [PGOV];

Suaeda saline land [SSL]; and water body [WB]) in each grid, along with distance between the camera location and the nearest village and nearest road segment for each grid. These covariate values were obtained from remotely sensed data obtained as geographic information system (GIS) layers acquired from local organizations operating in the region (Sahjeevan and K-Link Foundation). I expect that *Prosopis* has a positive effect on the distribution of dogs (due to the increased presence of the invasive plant near villages) and jackals (which are habitat generalists with an affinity for woody vegetation). The smaller canids are both habitat specialists due to which I expect that the Indian fox is more likely in areas with grass while the desert fox is likely to be positively associated with saline desert areas.

Multi-species Occupancy Modeling

The final occupancy estimate is represented by the species-specific probability ψ_{ij} and indicates the probability of site use across the landscape for each species ($i = 1, 2, \dots, N$) at specific sites ($j = 1, 2, \dots, J$) and sampling occasions ($k = 1, 2, \dots, K$). The occupancy and detection probabilities (ψ_{ij} and p_{ijk} respectively) are modeled as a function of covariates ('cov') such as the proportion of dense *Prosopis* [DP] and proximity of each camera trap location (site) to the nearest village, simultaneously factoring in the occurrence of the larger canids based on the body size hierarchy assumed.

$$w_i \sim \text{Bernoulli}(\Omega) \quad (3.1)$$

where w_i is the indicator variable and Ω represents the probability that species i is part of the canid guild of size $N = 4$ in this case.

$$z_{ij} \sim \text{Bernoulli}(\psi_{ij}w_i) \quad (3.2)$$

where z_{ij} is the true occupancy state matrix (if species i is present at site j then $z_{ij} = 1$ else $z_{ij} = 0$).

$$y_{ijk} \sim \text{Bernoulli}(p_{ijk}z_{ij}) \quad (3.3)$$

$$\text{logit}(\psi_{ij}) = \alpha_{\psi,j} + \beta_{\psi,cov,i}\text{COV}_j \quad (3.4)$$

$$\text{logit}(p_{ijk}) = \alpha_{p,i} + \beta_{p,cov,i}\text{COV}_{jk} \quad (3.5)$$

α and β are linear predictors, and y_{ijk} is the detection/non-detection of species i at site j over the k th sampling occasion having p_{ijk} detection probability.

The MSOM (see (Waddle *et al.*, 2010; Rota *et al.*, 2016; Devarajan *et al.*, 2020) for more information on MSOM implementation) was implemented under a Bayesian framework with **JAGS** using **jagsUI** in R. It was parallelized for a faster run using eight cores. The **JAGS** code provided as supplementary information through Figshare (Devarajan, 2020b) has the parametrization for each species.

The model was parameterized with habitat covariates at the grid level (proportion in each grid of DP, PGOV, SSL, and WB) as well as proximity to nearest village and segment of road for each camera location along with the body size-based interaction described earlier. These were considered important in identifying the spatiotemporal patterns of distribution for all four canids. Evaluating multiple models under a Bayesian modeling framework is challenging. For this reason, the analysis under a Bayesian framework described here used the habitat covariates that made the most ecological sense given the constraints and practicalities of Bayesian model selection. Thus all dominant habitat covariates were used for all species in the study while the body size hierarchy was used to model the interactions.

The MSOM is based on comparing the estimated conditional probability of occurrence for each canid species when one or more of the other species, on the basis of the body size hierarchy, was present or not present, and plotting the highest occupancy estimates of each canid on a map of the study area in order to glean patterns of spatial overlap in occurrence. The estimates are based on three chains of 220000 iterations with burn-in of 6000 and adaptation of 12000 iterations, and a thin rate of 10, yielding 64200 samples from the joint posterior. I examined the convergence of the models through visual inspection of the trace plots and by using the Gelman-Rubin convergence diagnostic (Gelman *et al.*, 1992).

3.3 Results

The camera trap survey yielded a total of 6221 videos of 30 seconds each from 296 camera locations for a total video footage duration of 3110 minutes. There were 315 videos with at least one canid identified and 797 videos with other taxa including livestock such as buffaloes, camels, horses, and goats ($n=596$), wild mammals such as other carnivores, herbivores, and rodents ($n=142$), birds ($n=52$), and invertebrates ($n=5$). The raw occurrences and co-occurrences based on the camera trap videos are provided in Tables 3.1 and 3.2. The spatiotemporal partitioning results are shown in Figures 3.5 and 3.6, while Figure 3.7 is a visual summary of the MSOM results.

The model output for all species with the occupancy estimates and site-specific ψ estimates used to develop the map of the spatial interactions between the canids (Figure 3.5c) and the visual summary (Figure 3.7) is provided as supplementary information on Figshare (Devarajan, 2020b) and includes the species-specific occupancy estimates, effects of interactions based on whether other species are present or not present, effects of habitat covariates on the occupancy of each canid species, and partial output of the site-specific occupancy.

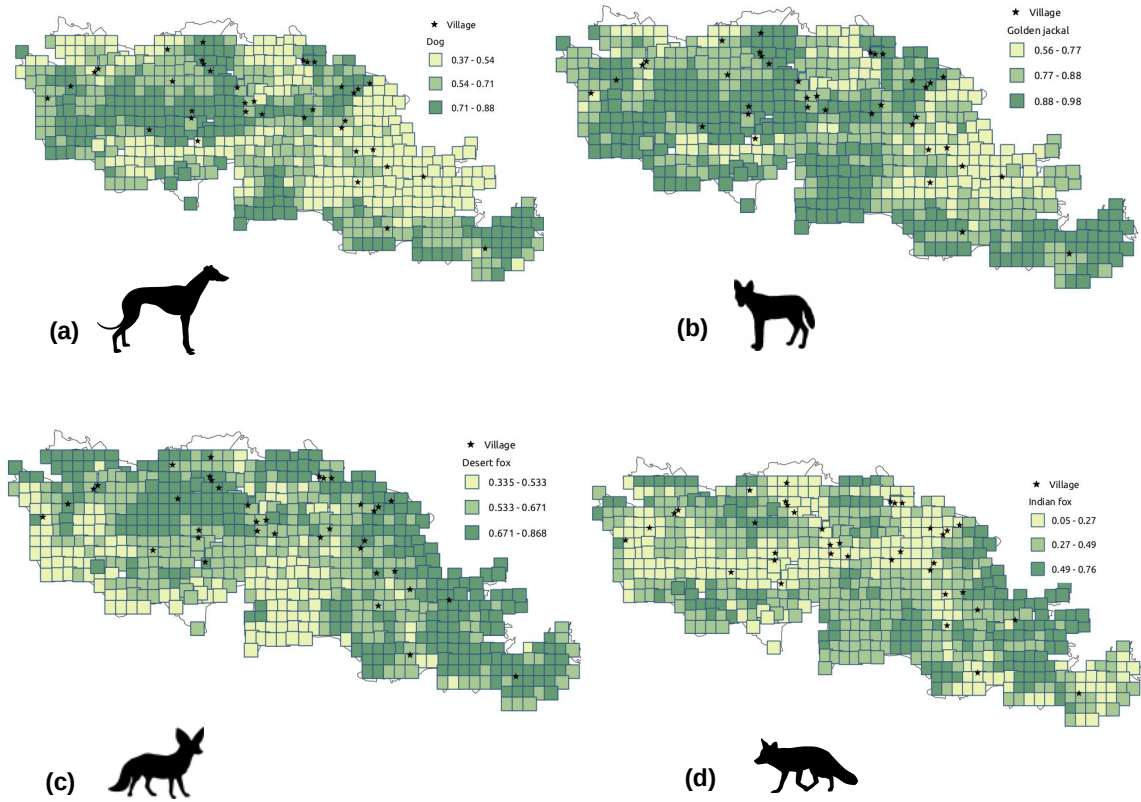


Figure 3.4. Species-specific distribution maps of occupancy probabilities for each grid in the study area for each canid species: (a) dog, (b) golden jackal, (c) desert fox, and (d) Indian fox.

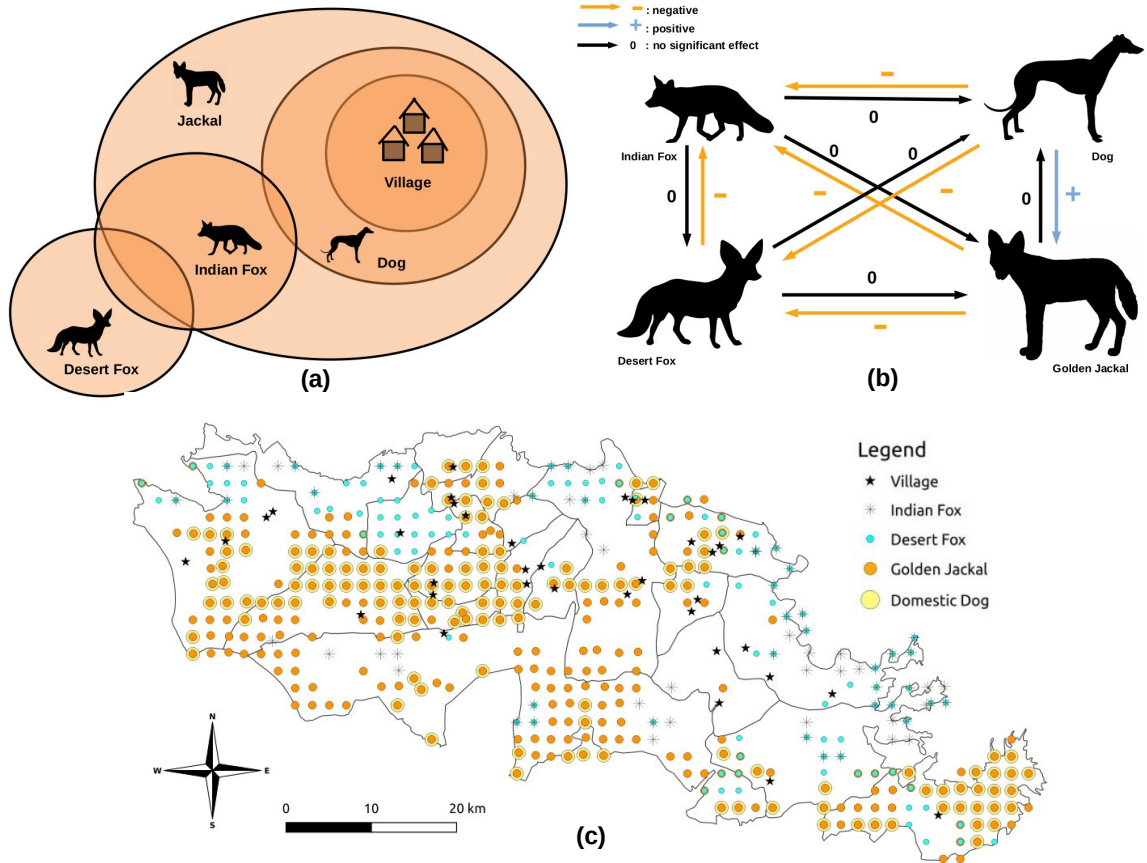
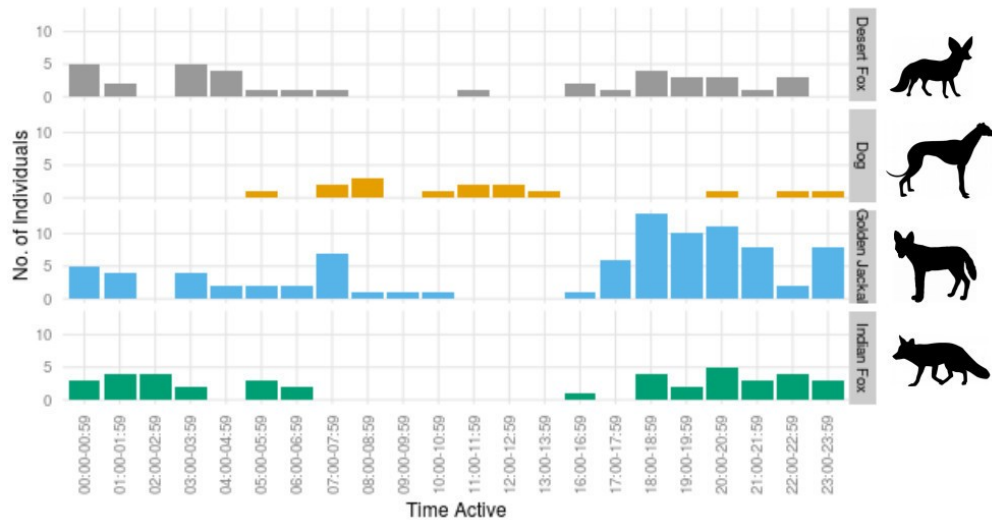


Figure 3.5. Hypotheses, expected interactions, and estimated species occupancy. (a) This depicts the hypotheses the authors were testing which matches the distribution patterns for each species estimated using occupancy analysis as seen in (c). (b) This is a diagrammatic representation of the expected interactions between each species and the presence of the other three species in the area. The black arrows denoted by 0 indicate the body size-based assumption that the presence of this species has no effect on the species near the arrowhead. (c) A map of the study area in the Banni grasslands with the estimated occupancy (ψ) of the different canid species based on the highest probability of occurrence from the MSOM.

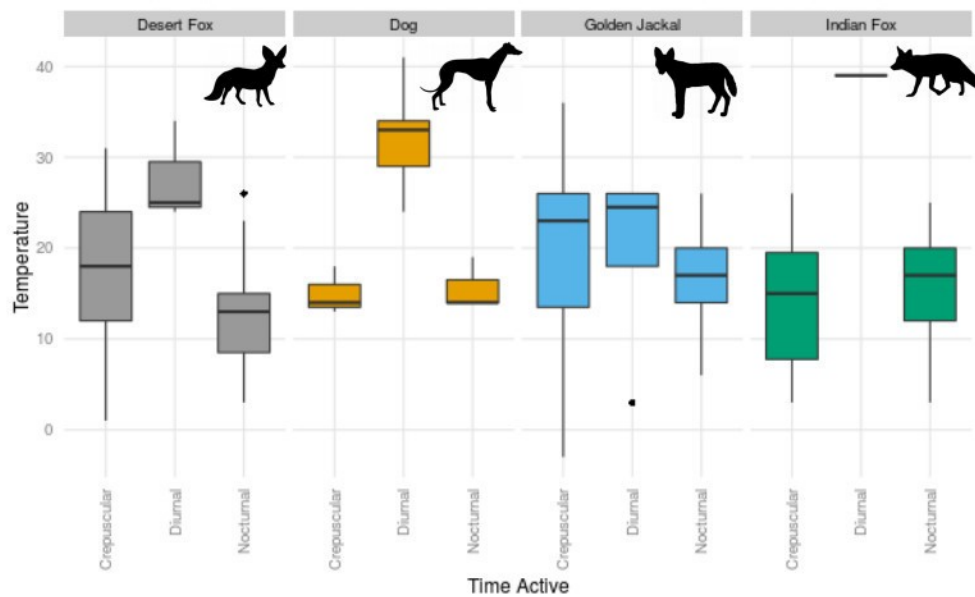
The estimated occupancy is highest for the jackal and lowest for the Indian fox (Table 3.1). I found a positive association between the golden jackal and dog, while the Indian fox shows avoidance of both the larger canids (Figures 3.5 and 3.7). However, the desert fox was negatively associated with only dog presence.

I found that both the fox species were negatively associated with dog presence (Figure 3.7 and supplementary information on Figshare (Devarajan, 2020b)). There is some spatial partitioning between the Indian fox and the other canids, either directly or indirectly (Figures 3.5 and 3.7). Indian fox occurrence is also negatively associated with sites that had a higher proportion of *Prosopis*-dominated habitats (denoted by the covariate Dense *Prosopis*). They are also negatively influenced by proximity to the nearest road. However, while desert fox presence corresponded favorably with Indian fox occurrence, the former occurs in more open *Suaeda fruticosa*-dominated saline habitats and is negatively influenced by proximity to human habitation such as villages.

The activity patterns for the canids based on the camera trap videos showed that free-ranging dogs were mostly diurnal while the wild canids were predominantly nocturnal or crepuscular (Figure 3.6). Both fox species were active at the same time, while none of the wild canids were active when dogs were active. Jackals were crepuscular as well as nocturnal, while both foxes were mostly nocturnal. The activity period for each species corresponded with the temperature ranges tolerated by the species (Figure 3.6(b)). Dogs which were primarily diurnal were active at times corresponding with high temperatures, whereas Indian and desert foxes which were mostly crepuscular and nocturnal were primarily active at lower temperatures.



(a) Activity period for different canid species



(b) Relationship between activity period and temperature for each species

Figure 3.6. Time-activity and temperatures corresponding with activity for the canids. (a) Hourly activity count for each of the study species. The spatial overlap seen between the golden jackal and dog in the map in Figure 4 can potentially be explained by the temporal partitioning between the species seen here - dogs seem predominantly diurnal while the wild canids including the golden jackal seem to be crepuscular and nocturnal. (b) Boxplot comparing the relationship between activity periods and temperature for each of the study species. Temperature is in Celsius and these measurements were obtained from the values recorded in the trail cameras.

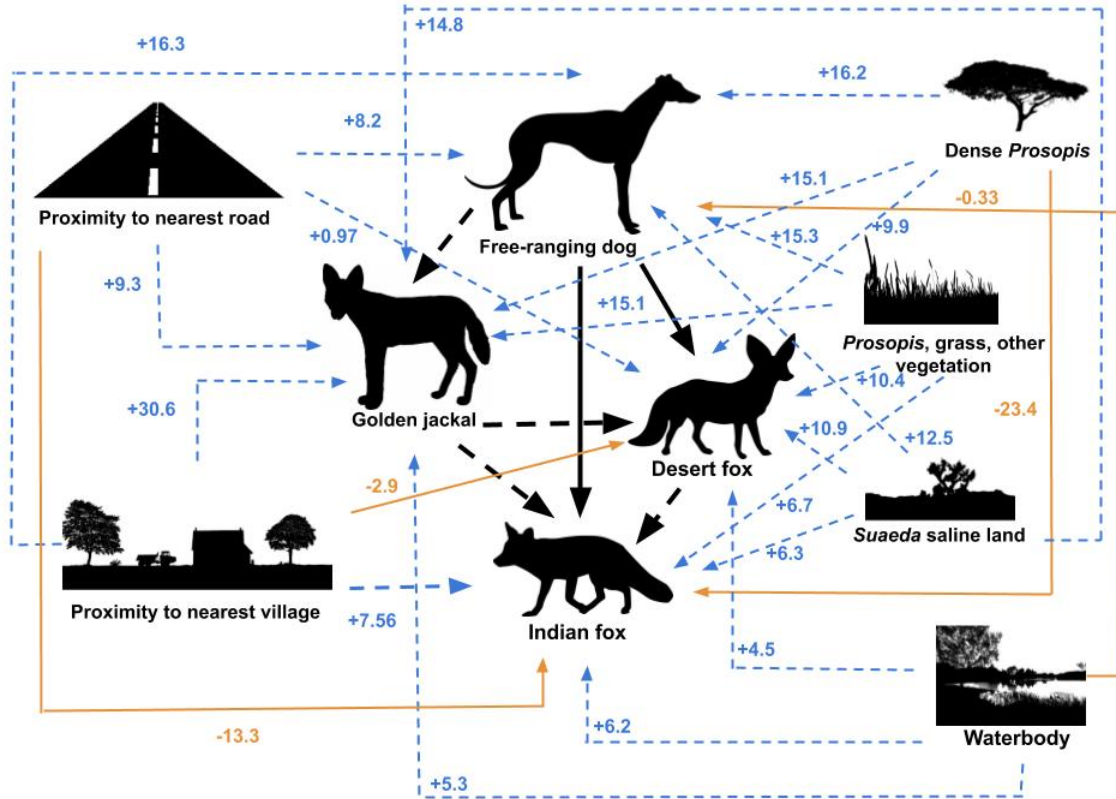


Figure 3.7. Visual summary of the interactions based on the MSOM using a body size-based hierarchy between the canids. For all colors, dashed lines represent a positive relationship while solid lines represent a negative relationship. The species-specific habitat covariate estimates obtained from the MSOM denote the degree and direction of influence of each covariate on the canids. The interactions between the individual canid species is obtained by comparing the conditional probabilities of co-occurrence using the interactions-specific ψ estimates for each species based on whether other species are present or not present. Since dogs are the largest in the size-based hierarchy assumed, they influence all the other canids, although their occupancy is estimated using only the habitat covariates. Refer supplementary file shared through Figshare (Devarajan, 2020b) for model parameterization and model output used for this figure.

When I combined the spatial patterns with the hourly activity data for the canids (Figures 3.5 and 3.6), I observed that although golden jackals and dogs overlap spatially, they seem to be active at different times of the day, which indicates temporal partitioning between the species. On the other hand, while the two fox species seem to partition space, there appear to be pockets where they co-occur. However, there is a demarcation in habitat preferences between the two fox species - the desert fox is more likely to be found in saline and barren areas (*Suaeda* saline land) whereas the Indian fox is a known grassland specialist, with a preference for habitats with *Prosopis*, grass, and other vegetation (PGOV). Furthermore, the Indian fox is negatively associated with proximity to nearest road and areas with dense *Prosopis*, while the desert fox is negatively correlated with distance to nearest village (Figures 3.5 and 3.7). On the other hand, the golden jackal does not seem to be negatively associated with any of the covariates considered and has the largest occupancy estimate of all the canids.

3.4 Discussion

In this study, based on a landscape-scale camera trapping effort, I used hierarchical models to estimate the occupancy of four co-occurring canids while incorporating body size differences between the species and coupled this with temporal data extracted from the camera trap study to understand the time-activity patterns of the canid species. The results of our MSOM show complex patterns of spatiotemporal partitioning between the species. The larger canids, dogs and golden jackals, are positively correlated with most of the covariates I considered and had the highest occupancy in the landscape. The distribution of the smaller canids, the desert fox and Indian fox, were negatively associated with several covariates, specifically the proportion of *Prosopis* in each camera trap grid and the proximity to the nearest village and road respectively. Furthermore, both fox species were negatively associated with

dog presence. There emerged a strongly positive spatial association between dogs and golden jackals, albeit with significant temporal partitioning between them. This suggests that spatial overlap between potentially competing carnivores at the local scale may be complemented with temporal segregation in order to facilitate coexistence at larger scales.

As visible in Figures 3.4-3.7, these results broadly match my hypotheses: (i) dogs and jackals were more likely to be found close to villages while the fox species were more likely to be negatively correlated with anthropogenic influences with the desert fox having a negative association with proximity to village and the Indian fox negatively correlated with proximity to road (Figures 3.4, 3.5, and 3.7), (ii) canid occurrence varied based on the habitat and time (Figures 3.5 and 3.6), and whereas jackals were positively impacted by the proportion of invasive *Prosopis juliflora* in the landscape, the Indian fox was negatively affected by this invasive (Figure 3.7), and (iii) the strong positive relationship between dogs and jackals and resulting spatial overlap corresponded with temporal segregation between the species where dogs were almost entirely diurnal while jackals were nocturnal or crepuscular (Figures 3.5 and 3.6).

Recent research establishes that mere co-occurrence cannot be construed as evidence of ecological interactions (Blanchet *et al.*, 2020; Karanth *et al.*, 2017). While the signal of interaction from observational studies is hard to establish, this study provides insights on how possible interactions as seen through the lens of spatiotemporal association and partitioning, along with habitat type and quality and human presence, affect the distribution and landscape use of a guild of sympatric carnivores. Furthermore, there is evidence of potential interactions through repeated instances of different study species (and other small carnivores) captured on the same camera

trap, often at different times of the day (see Figures 3.5, 3.6, and 3.7, and Tables 3.1 and 3.2).

The Banni grasslands, a seasonally resource-limited system, are rapidly being modified by the invasive *Prosopis juliflora* (commonly known as mesquite). This clearly has impacts on flora and fauna of the region. From the habitat preferences of the canids, there emerges evidence that human-subsidized or commensal carnivores such as dogs and jackals are adapting better to this invasive species whereas the two fox species are negatively impacted. Furthermore, dogs are considered invasives in many parts of the world including India and are reservoirs of disease, and the rise in dog populations has been shown to have severe negative effects on wildlife including other carnivores as well as prey species (Home *et al.*, 2018). The results of this study add to the body of evidence that indicates that the fox species, the smallest canids considered, are potentially negatively impacted by dog presence. In a landscape with increasing amounts of mesquite and proximity to roads (anecdotal evidence for both), land-use changes such as a reduction in grassland habitats (Figure 3.7) are likely to adversely affect Indian fox populations, which already have the lowest occupancy of the canids in this study. It is important to control dog populations in order to ameliorate the negative impacts of dogs on wild carnivores.

In summary, through this study, I provide baseline information on the distribution of three species of wild carnivores. In addition, I explore intra-guild dynamics under an environmental gradient (using habitat covariates) in a human-dominated landscape (using proximity to villages and roads as proxies for anthropogenic influence). Furthermore, this research adds to the literature on a threatened and understudied landscape with multiple canid species. It offers additional insights on how human-subsidized canids affect other canids in a community with multiple carnivores. The

results of this study will hopefully prove beneficial in informing habitat and wildlife management at the community level, particularly in human-dominated landscapes that are vulnerable to precipitating changes from different angles.

Ethics Statement

The study was conducted inside and outside protected areas in Gujarat and research permits to carry out ecological research required for the study were obtained from the Office of the Chief Wildlife Warden - Gujarat (Permit No. WLP/28/C/150-52/2014-148) and the Gujarat Biodiversity Board. Since the methods used were non-invasive and protected species were not sampled, animal ethics committee approval was not required.

Data Accessibility

Data used in this study can be accessed through Figshare: <https://doi.org/10.6084/m9.figshare.13075097.v1> (Devarajan, 2020a). The JAGS code to run the single season MSOM for all four species (assuming body size-based effects of interactions between the species) with six covariates as described in the Methods section along with the output obtained is also available through Figshare: <https://doi.org/10.6084/m9.figshare.13089140.v1> (Devarajan, 2020b).

CHAPTER 4

MODELING CARNIVORE COMMUNITIES AT THE LOCAL SCALE

Abstract Carnivores are widely distributed and have a high degree of variability in community diversity. While there are numerous studies on individual carnivore species, community-level studies are few. Given the important roles carnivore play in different landscapes, it is essential to understand how carnivore communities are structured and how species within these communities are distributed in order to better conserve them and the landscapes they occur in. Here I focus on an understudied protected area (Kasanka National Park in Zambia) and use camera trap surveys to determine the mammal diversity in the region. I further use this preliminary trail camera survey to determine the structure of the carnivore community as well as the distribution patterns of the carnivore species using occupancy models to account for imperfect detection. This pilot study helps understand the role of abiotic factors on carnivore communities at the local scale.

4.1 Introduction

The mechanisms that drive the coexistence of species have been the focus of several theoretical and experimental community ecology studies (Sale, 1977; Hubbell, 2001; Grant & Grant, 2014; Losos *et al.*, 2003; Basset, 1995; Farris *et al.*, 2016). This expansive research on species coexistence in ecological communities has resulted in the development of modeling tools, theoretical frameworks, and datasets that have further advanced the field of community ecology. Despite numerous studies on this

theme, the term ‘coexistence’ is often misunderstood and often mere co-occurrence is conflated with competition and causal relations involving species interactions ascribed without providing evidence or on the basis of correlations (Blanchet *et al.*, 2020). In addition, the pervasive problem of scale in ecology permeates into species coexistence research as well (Levin, 1992; Schneider, 2001). The first step to studying coexistence and species interactions is to understand community composition and species distributions within communities.

Here I investigate how abiotic factors affect the distribution of carnivores in a particular landscape, namely in Kasanka National Park (KNP), Zambia (Figures 4.1 and 4.2). In an understudied landscape with high biodiversity including threatened and elusive taxa, I implement a camera trap survey of KNP to understand the structure of the carnivore community and the distribution patterns of the different carnivore species within the community. Of the 120 species of mammals thought to occur in KNP, some twenty species are large and meso-carnivores including felids, canids, mustelids, and viverrids.

Research Objectives

- *Understand the effects of abiotic factors on carnivore community composition and dynamics:* The focus of the study is to understand carnivore distributions and habitat use at KNP, a small protected area in northern Zambia. I investigated how abiotic factors such as habitat type affect the distribution of carnivores in KNP. In an understudied landscape with high biodiversity including threatened and elusive taxa, I studied the variation in distribution patterns for closely related species (eg. water, slender, banded, and dwarf mongooses) and distantly related species (eg. dwarf mongoose, African civet, side-striped

jackal, and large spotted genet). I hypothesized that competition among closely related species and predation between distantly related species inform carnivore distribution patterns and that closely related taxa are likely to be separated in either space or time, while distantly related species will likely have different diets, especially if there is spatial overlap between them (Kamler *et al.*, 2012). These hypotheses will be tested in a follow up study involving a more comprehensive coverage of KNP to test for the role of biotic interactions between the species in structuring the carnivore community.

- *Formulate baseline information on the carnivore community in KNP*: This study provides baseline information on the distribution of several species at once, and insights on community-level dynamics under an environmental gradient with stressors such as habitat loss and poaching. This survey adds to the literature on an understudied landscape and multiple carnivorous taxa, and has resulted in a unique collection of camera trap videos and images that are beneficial in obtaining a snapshot of the mammal community within the national park. This research covers a large guild of carnivores while accounting for interactions between the species and is the first such study in KNP where past research has focused primarily on bats and baboons.

I aim to understand how the species in the entire carnivore guild at KNP interact over space and time along with the spatiotemporal associations facilitating their cooccurrence. I compare patterns of habitat use, as well as spatial and temporal segregation between all the species detected using camera trap surveys of the study area. In this preliminary study I focus on determining the distribution of the different carnivore species in Kasanka using single season, single species occupancy models (SSOMs) to account for imperfect detection.

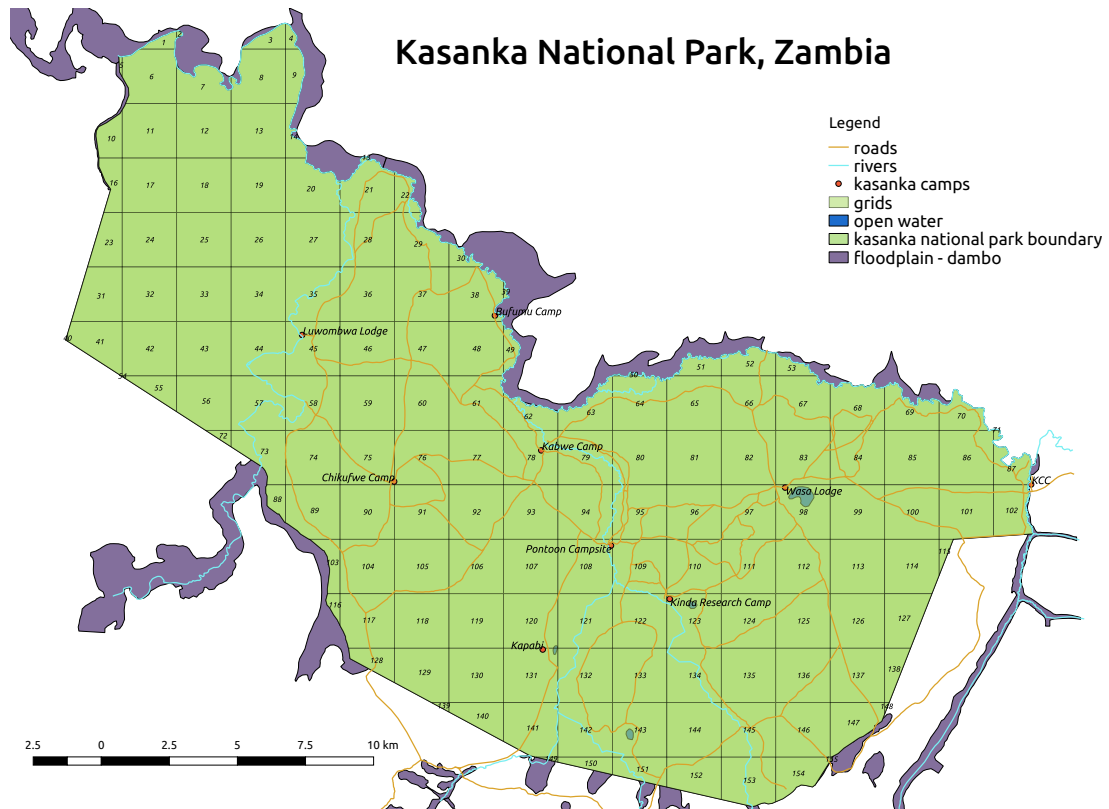


Figure 4.1. Study design for setting up camera traps in Kasanka National Park involving systematic sampling of grids.
Map generated based on GIS layers obtained from the Kasanka Trust Limited.

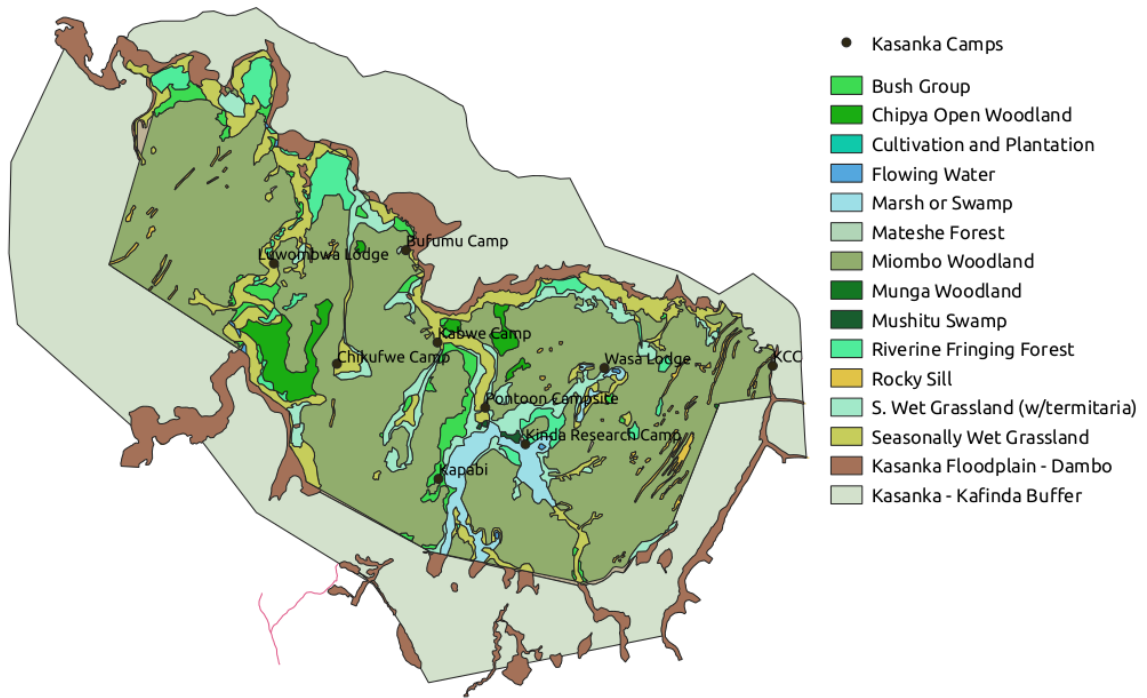


Figure 4.2. Map of Kasanka habitats. The most dominant habitat type is miombo woodland. These woodlands are also interspersed with chipya woodlands and seasonally wet grasslands. The waterbodies in the NP have associated vegetation types falling under riverine fringing forest and mushitu swamp categories. *Map generated based on GIS layers obtained from the Kasanka Trust Limited.*

4.2 Methods

4.2.1 Study Area

This study was conducted in Kasanka National Park (KNP) located in the Serenje District of the Central Province in Zambia (Figure 4.1) between June and July 2018. Spread over an area of 390 km², KNP is one of the smallest national parks in Zambia. It is a mosaic of grassland patches and woodlands interspersed with floodplains and swamps. It has several permanent waterbodies, the largest of which is Lake Wasa, and five perennial rivers, the largest of which is the Luwombwa River, which is also the sole river that drains into KNP.

The national park has several habitat types as can be seen in Figure 4.2 resulting in a substantial faunal diversity within a relatively small area. The predominant habitat type in KNP is miombo woodland, a tropical and subtropical grassland, shrubland, and savanna biome that is dominated by *Brachystegia*, *Isoberlinia*, and *Julbernardia* tree species. This Central Zambezian miombo woodland covers about 70% of the park. The miombo woodland is often interspersed with dambos, grassy basins and drainage channels. The other major habitat type is the chipya or lake basin woodlands, which have a more open canopy than miombo woodlands. There are three types of evergreen forests that are found in Kasanka. These include the mushitu or swamp forests, mateshe or dry evergreen forests, and riverine forests. The last important habitat type in KNP is the papyrus swamp which includes large swathes of papyrus vegetation.

KNP has a high faunal diversity with over a hundred species of mammals. The landscape is most well-known for the annual migration of ten million straw-colored fruit bats (*Eidolon helvum*), widely considered the largest mammal migration in the world. Other species found in the park include sitatunga (*Tragelaphus spekii*),

sable antelope (*Hippotragus niger*), African bush elephant (*Loxodonta africana*), hippopotamus (*Hippopotamus amphibius*), puku (*Kobus vardonii*), common duiker (*Sylvicapra grimmia*), bushbuck (*Tragelaphus scriptus*), hartebeest (*Alcelaphus buselaphus*), plains zebra (*Equus quagga*), roan antelope (*Hippotragus equinus*), defassa waterbuck (*Kobus ellipsiprymnus*), northern grysbok (*Raphicerus sharpei*), common reedbuck (*Redunca arundinum*), African buffalo (*Syncerus caffer*), yellow-backed duiker (*Cephalophus silvicultor*), common warthog (*Phacochoerus africanus*), blue or diademed monkey (*Cercopithecus mitis*), vervet monkey (*Chlorocebus pygerythrus*), Kinda baboon (*Papio kindae*), Cape porcupine (*Hystrix africaeaustralis*), and several species of carnivores which are described below. Birds, reptiles, and invertebrates also emerged as bycatch from the trail camera study.

Kasanka National Park in Zambia has a carnivore community composed of twenty carnivores (Figure 4.4): leopard (*Panthera pardus*), spotted hyena (*Crocuta crocuta*), side-striped jackal (*Canis adustus*), caracal (*Caracal caracal*), serval (*Leptailurus serval*), honey badger (*Mellivora capensis*), African civet (*Civettictis civetta*), water or marsh mongoose (*Atilax pauludinosus*), slender mongoose (*Galerella sanguinea*), banded mongoose (*Mungos mungo*), dwarf mongoose (*Helogale parvula*), white-tailed mongoose (*Ichneumia albicauda*), Meller's mongoose (*Rhynchogale melleri*), bushy-tailed mongoose (*Bdeogale crassicauda*), Egyptian mongoose (*Herpestes ichneumon*), large spotted genet (*Genetta tigrina*), miombo genet (*Genetta angolensis*), rusty-spotted genet (*Genetta maculata*), African clawless otter (*Aonyx capensis*), and spotted-necked otter (*Hydrictis maculicollis*). The carnivore species detected using the camera trap survey are listed in Table 4.1. While the carnivore community at KNP is diverse, the population densities of each carnivore species is likely to vary substantially, with some of the mesocarnivores being more abundant while leopards and hyenas are known to be rare and in very low densities.

The spatial scale for this study reflects coverage of the entire national park, encompassing the unique carnivore community present. The temporal scale was selected in order to minimize any violation of the demographic closure assumption, due to which it was treated as a single season MSOM during the dry season, since it is logistically infeasible to set camera traps in the study area during the wet season due to accessibility issues.

4.2.2 Study Design

To understand community composition and infer interactions, I used a multi-pronged approach involving camera traps for spatio-temporal interactions. A camera trap approach to occupancy is useful in maximizing coverage for carnivore communities. In addition to providing insights into the spatial distribution patterns of mammals, time-activity data can be obtained based on camera timestamps.

I employed a systematic study design for setting up camera traps across the 390 km² park such that all major habitat types were covered (Figures 4.1 and 4.2). Each motion-triggered camera ran for a sampling period of five consecutive days at each site. The distance between camera sites was 2 kms so that the home ranges of all the study species are incorporated while ensuring that the MSOM assumption of independence is not violated (Devarajan *et al.*, 2020). Since the pilot study was conducted over a single season, the MSOM assumptions of geographic and demographic closure are not violated. All species were distinct thereby maximizing accuracy in identification. Since all the species were carnivores, the MSOM assumption of ecological similarity was not violated.

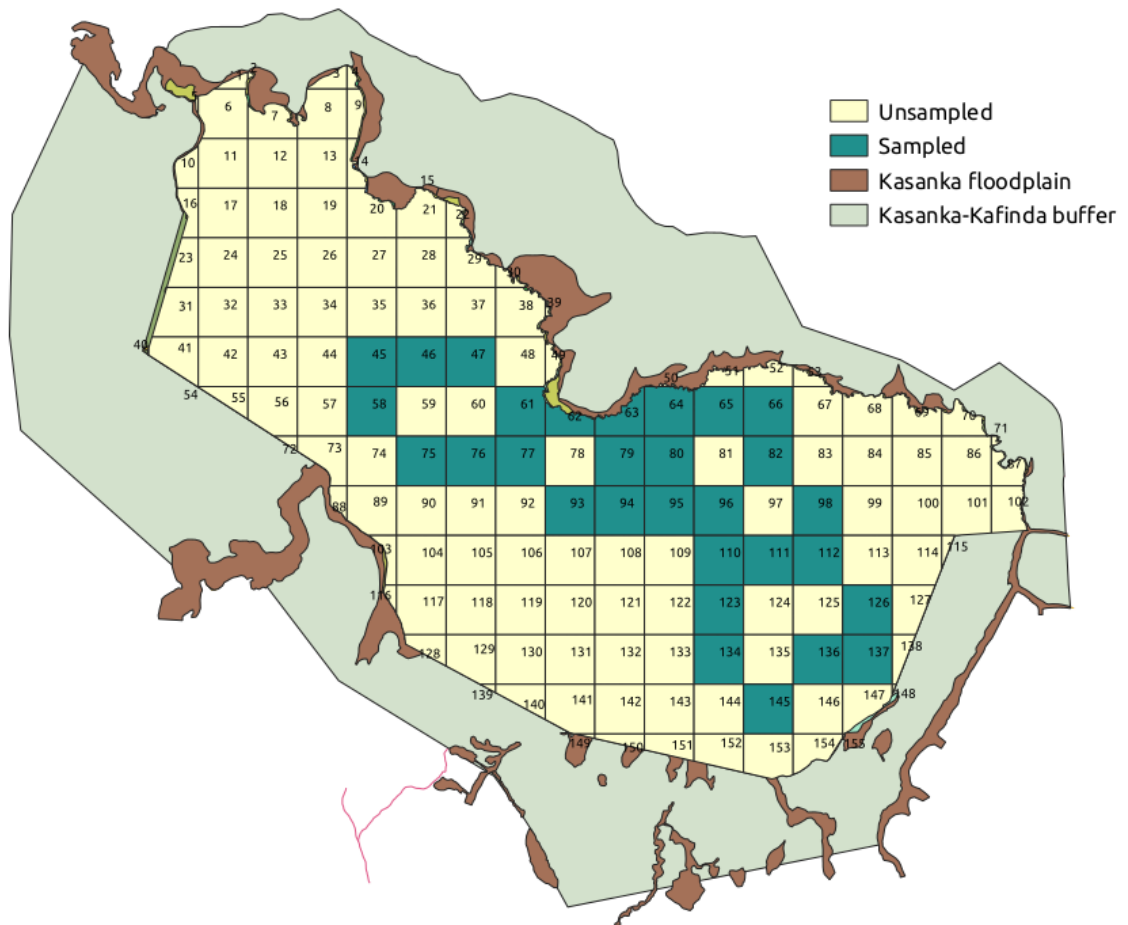


Figure 4.3. Map of the grids sampled in the pilot study.
Map generated based on GIS layers obtained from the Kasanka Trust Limited.

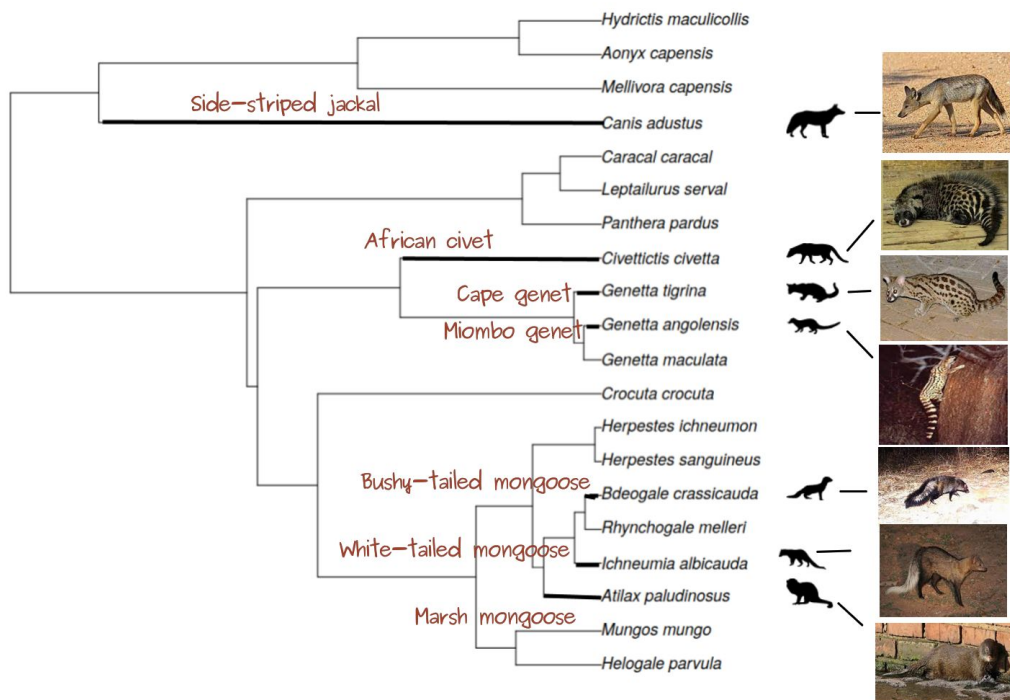


Figure 4.4. Phylogeny of carnivores in known to occur in KNP with those detected during the camera survey highlighted.
Carnivore images: Wikimedia Commons.

This research involved setting up camera traps over four weeks in June 2019 at Kasanka National Park, Zambia. I followed a stratified random study design for setting up camera traps across the 390 km^2 park, stratified by habitat type (such forest and grassland). Each motion-triggered camera ran for a sampling period of five consecutive days at that site. I measured visibility at the site and local site-level variation in habitat features on species-specific carnivore occurrences.

The size of the grids and spacing between cameras helps ensure that the assumptions of geographic closure and independence in MSOMs are not violated (Devarajan *et al.*, 2020). The assumption of demographic closure is also accounted for since this is a single season study. All focal species belong to the same order of placental mammals (Carnivora) thereby reducing chances of violating the crucial assumption of ecological similarity. Despite their relatedness, they are easy to tell apart in the trail camera videos, thereby not violating an important assumption of MSOMs, that of accurate identification (Devarajan *et al.*, 2020).

Using an occupancy framework helps account for imperfect detection, an important consideration in species monitoring studies (Devarajan *et al.*, 2020). The images and videos from the trail cameras were accessed using ViXen (Ramachandran & Devarajan, 2018), an open-source multimedia data manager. The camera trap metadata was converted into a comma separated value (`csv`) file for subsequent analysis. I also collected data such as visibility at the site and local site-level variation in habitat features on species-specific carnivore occurrences. This was combined with remotely sensed data on habitat and climate, and analyzed under an occupancy framework using `unmarked` in R. Distribution maps were generated using QGIS and R.

The camera trapping exercise resulted in a total of 2569 videos, each of 30 seconds duration. During the pilot study, a total of 30 grids covering different parts of the park were sampled. These are the spatial replicates or ‘sites’ considered for occupancy analysis. Each camera was set for five days which were the temporal replicates or ‘visits’ used in hierarchical modeling approaches. Along with the 30 sampled grids, 125 sites were considered as unsampled sites for the occupancy analysis, giving a total of 155 sites.

I employed fifteen trail cameras of different makes (CamPark, Bushnell, and Moultrie) but with video-recording capabilities that work at night as well. Since the capabilities of all the cameras was similar, any bias due to using different camera makes was minimized. These trail cameras were securely mounted on sturdy trees at each site at a height of about 1 m from the ground. A single camera was deployed per sampled grid for five consecutive nights resulting in a total of 150 camera trap days. At any given time ten cameras were deployed in the field during the pilot study.

A drop of lure (Cross Breed Food Lure from Kishel’s Scents, USA) was used in front of each trail camera to maximize detections. Although the use of lure is considered an ‘active system’, since lures are not strong incentives unlike bait, they are not thought to introduce any bias (Garrote *et al.*, 2012; Gerber *et al.*, 2012a). For each camera location, remotely-sensed covariates, such as the KNP extent, camp locations, waterbody locations, roads, and vegetation (Figures 4.1 and 4.2), were obtained from land cover maps provided by the Kasanka Trust.

These data were combined with remotely sensed data on habitat and climate for statistical analysis using an occupancy framework. Distribution maps were generated using Geographical Information Systems (GIS) and programming languages such as

R (using RStudio) and Python (R Core Team, 2012; Team, 2020; Van Rossum & Drake Jr, 1995; Van Rossum & Drake, 2009). The images and videos from the trail cameras were accessed using ViXen (Ramachandran & Devarajan, 2018), an open-source multimedia data manager. The camera trap metadata was converted into a comma separated value (csv) file for subsequent analysis.

Table 4.1. Carnivore species and silhouettes used in the figures








Silhouette	Common Name	Scientific Name	Genus	Family
	Side-striped Jackal	<i>Lupulella adusta</i>	<i>Lupulella</i>	Canidae
	African Civet	<i>Civettictis civetta</i>	<i>Civettictis</i>	Viverridae
	Large-spotted or Cape Genet	<i>Genetta tigrina</i>	<i>Genetta</i>	Viverridae
	Miombo or Angolan Genet	<i>Genetta angolensis</i>	<i>Genetta</i>	Viverridae
	Bushy-tailed Mongoose	<i>Bdeogale crassicauda</i>	<i>Bdeogale</i>	Herpestidae
	Marsh or Water Mongoose	<i>Atilax paludinosus</i>	<i>Atilax</i>	Herpestidae
	White-tailed Mongoose	<i>Ichneumia albicauda</i>	<i>Ichneumia</i>	Herpestidae

Table 4.2. Carnivore species occurrences. Site-specific species occurrences obtained from metadata extracted from camera trap videos annotated through ViXen (Figure 4.5) for the 30 sampled sites (camera locations) and 2569 videos based on the sampling design shown in Figure 4.2, covering 155 (30 sampled and 125 unsampled) sites across the landscape as shown in Figure 4.3.








Species	Total number of videos with ≥ 1 individual of each carnivore species	Number of videos with >1 individual of same species	Number of grids with occurrence of the carnivore species	Number of grids with recurrences of the carnivore species	Number of grids with videos of two or more carnivore species
 Side-striped Jackal	3	0	2	2	1
 African Civet	17	0	6	3	2
 Large-spotted Genet	1	0	1	0	1
 Miombo Genet	1	0	1	0	0
 Bushy-tailed Mongoose	3	2	2	1	2
 Marsh Mongoose	3	0	2	1	2
 White-tailed Mongoose	2	0	1	1	1

Table 4.3. Site-specific species co-occurrences based on the camera trap videos obtained as described in Table 4.2.




Carnivore species	Co-occurrence grids
	0
	1
	1



Figure 4.5. Viewing and annotating camera trap videos using ViXen. This is a trail camera video from Kasanka of an African civet.

4.2.3 Analysis

The videos were extracted from the trail cameras and accessed using ViXen (Ramachandran & Devarajan, 2018; Devarajan & Ramachandran, 2020) which is a gen-

eral purpose, free and open source multimedia project manager for viewing multimedia and annotating metadata associated with media files that allows for setting up custom tags (Figure 4.5). Custom tags associated with the variables were created for all the videos using the viewer once the camera trap videos were converted to **webm** format for portability. These tags included information on the presence of a carnivore species in the video as well as the number of individuals where present (see Figure 4.5). These species occurrence metadata were saved as a comma separated value (**CSV**) file and combined with geospatial data based on the grid and camera trap numbers for subsequent analysis. This CSV data file was cleaned using R and the **pandas** and **numpy** libraries in Python version 2.7.6 (Van Rossum & Drake, 2009; McKinney, 2015; Oliphant, 2007; Virtanen *et al.*, 2020). The cleaned data was exported for further statistical analysis and visualization in R ver. 3.4.4 (Team *et al.*, 2013; Wickham, 2016; Wickham *et al.*, 2016; Team, 2020) and QGIS (QGIS Development Team, 2021).

4.2.4 Occupancy Modeling

Since only 30 grids were sampled during this pilot study, modeling interactions under an occupancy framework is challenging given this insufficient data. Instead of an MSOM, operating within the constraints of this pilot data, single species occupancy models (SSOMs) were implemented for each of the carnivores detected in the camera trap survey. This single season SSOM was implemented with only habitat covariates and no interactions factored in for the carnivore community. An MSOM for the carnivore community at Kasanka will be implemented once a subsequent camera trap survey with more comprehensive coverage is completed.

The parameterization is similar to that implemented for the canid community in Chapter 3 with the difference being the modeling of SSOMs for each of the species

without incorporating interactions in this case as opposed to an MSOM (Devarajan *et al.*, 2020). The habitat covariates used for the SSOM were proportion of chipya woodland, miombo woodland, mushitu forest, and grassland in each grid across the KNP landscape.

The SSOMs were implemented under a Bayesian framework with JAGS using jag-sUI in R, parallelized for a faster run using eight cores. The model was parameterized with habitat covariates at the grid level (proportion in each grid of: miombo woodland, dambo, chipya, and mushitu). These covariates were considered important in identifying the spatial distribution patterns for all carnivores included in this study. The estimates are based on three chains of 300000 iterations with burn-in of 2000 and adaptation of 5000 iterations, and a thin rate of 10, yielding 89400 samples from the joint posterior. The convergence of the models was checked through visual inspection of the trace plots and using the Gelman-Rubin convergence diagnosis (Gelman *et al.*, 1992).

4.3 Preliminary Results

The camera trap survey yielded a total of 2569 videos of 30 seconds each from 30 camera locations for a total video footage duration of 1284.5 minutes. There were 33 videos with at least one carnivore identified and 341 videos with other taxa including herbivores such as African savanna elephant, sable antelope, puku, and common duiker ($n=124$), primates such as Kinda baboon and blue monkey ($n=79$), and other mammals, birds, reptiles, and invertebrates ($n=138$ across all four faunal categories). The raw occurrences and co-occurrences based on the camera trap videos are provided in Tables 4.2 and 4.3.

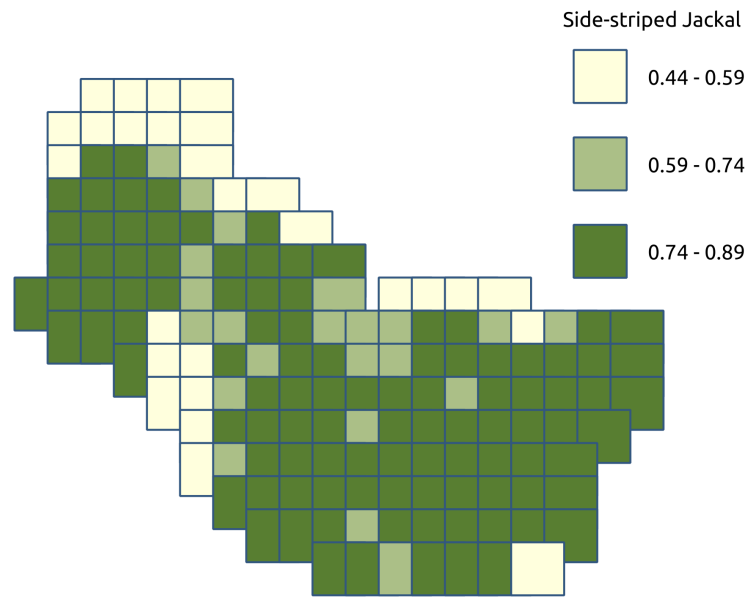


Figure 4.6. Occupancy of side-striped jackal in KNP.

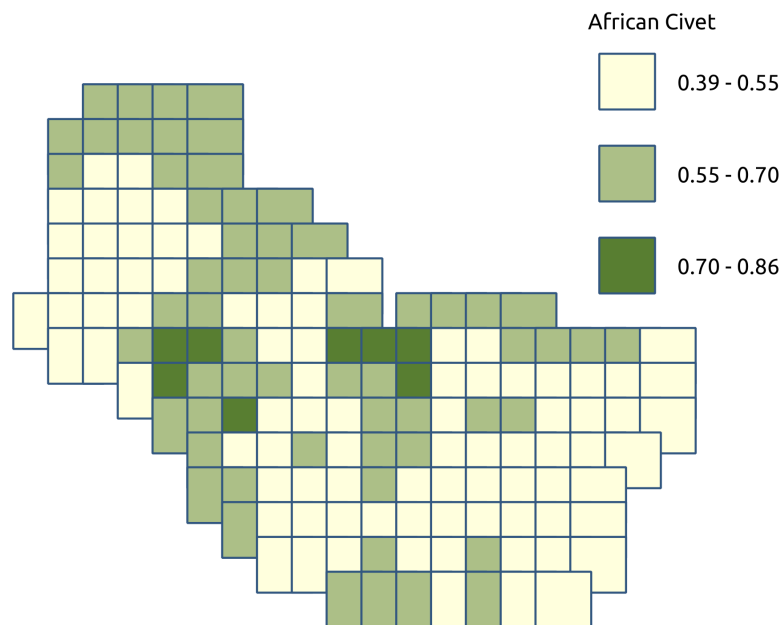


Figure 4.7. Occupancy of African civet in KNP.

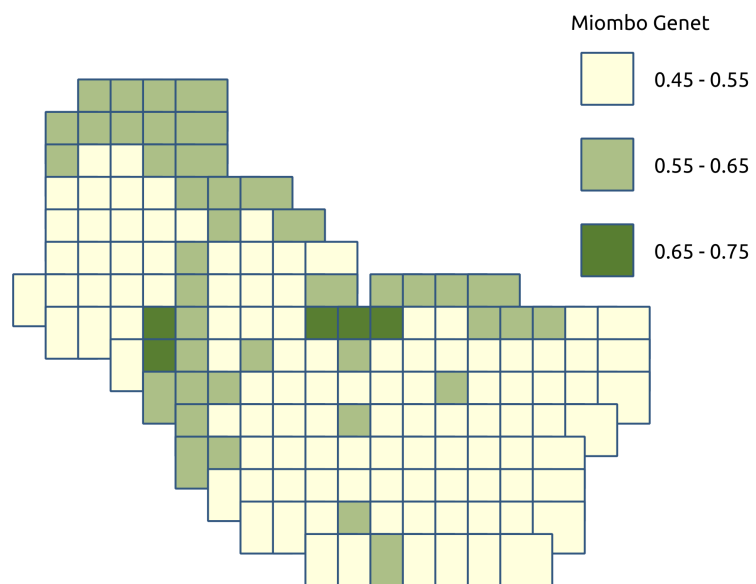


Figure 4.8. Occupancy of miombo genet in KNP.

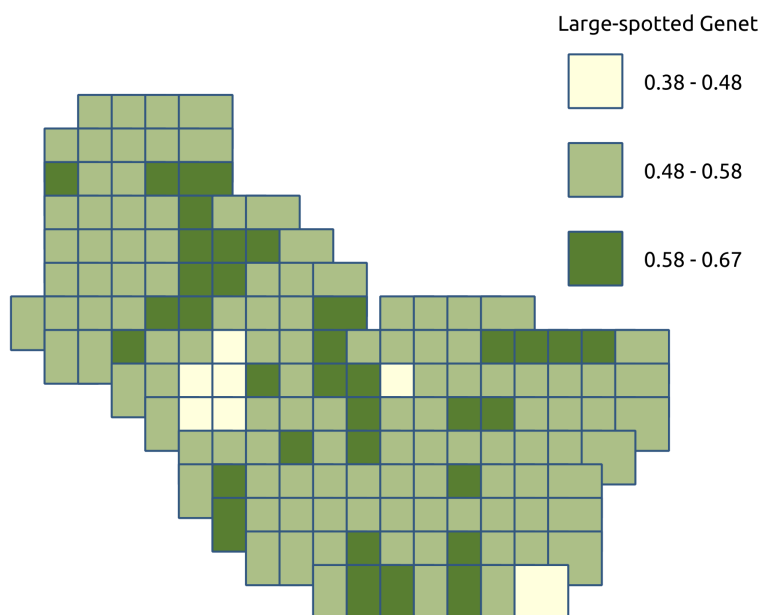


Figure 4.9. Occupancy of large-spotted genet in KNP.

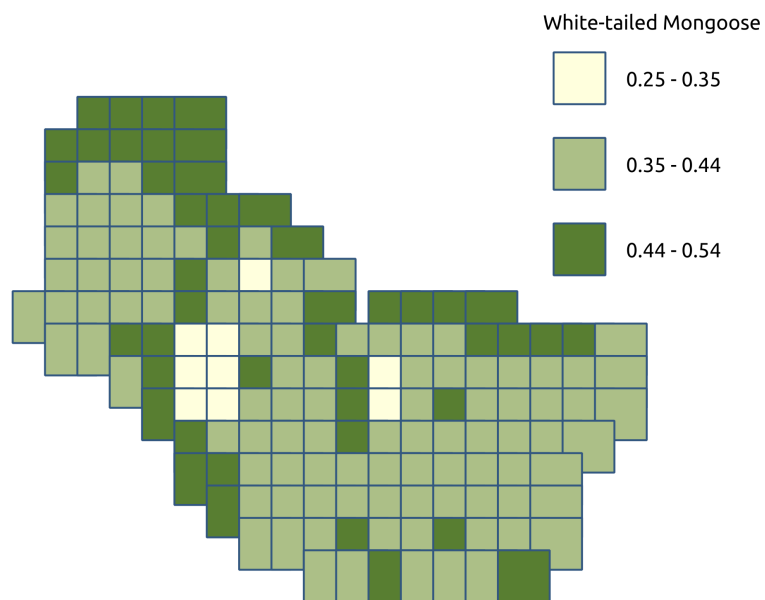


Figure 4.10. Occupancy of white-tailed mongoose in KNP.

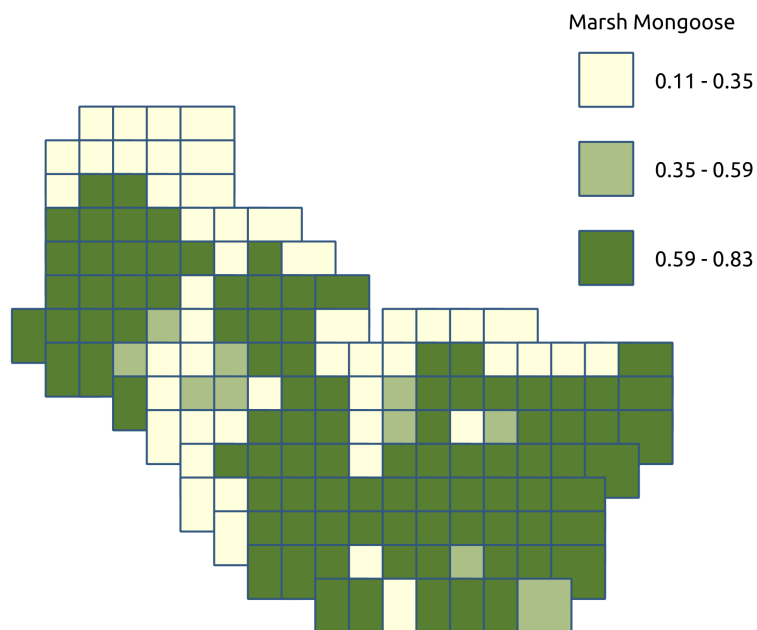


Figure 4.11. Occupancy of marsh mongoose in KNP.

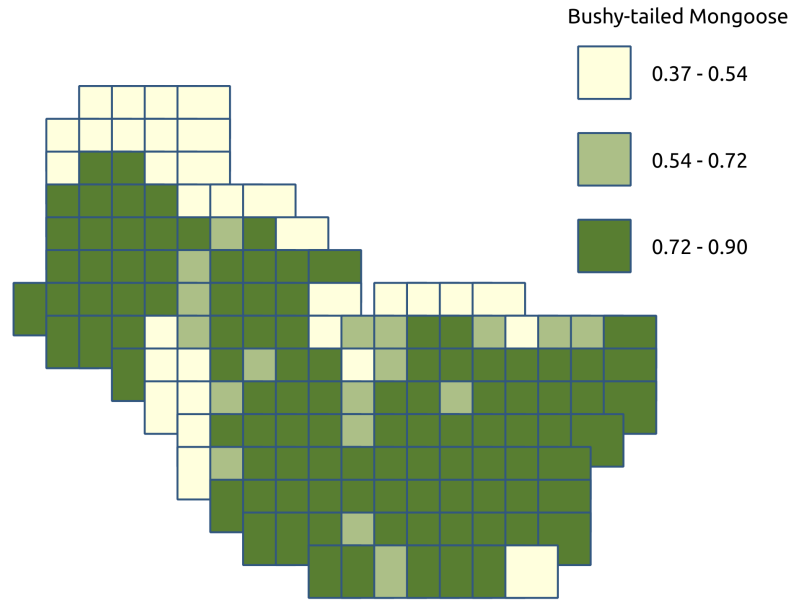


Figure 4.12. Occupancy of bushy-tailed mongoose in KNP.

The carnivore community in KNP comprised the focal species for this pilot study. The preliminary camera trap survey indicated the presence of seven carnivores belonging to six genera and three families (Canidae, Viverridae, and Herpestidae): side-striped jackal, African civet, Angolan or miombo genet, rusty- or large-spotted genet, bushy-tailed mongoose, marsh or water mongoose, and white-tailed mongoose. The probability of occurrence was calculated for each of the seven carnivores and maps were generated based on the occurrence probability (ψ) estimated through the stacked SSOMs (Figures 4.6 – 4.12).

All seven carnivores from this pilot camera trapping effort are considered to be of Least Concern (LC) under the IUCN Red List (IUCN, 2021). Bycatch species from the trail camera survey were mostly categorized as LC (IUCN, 2021) but included species such as the *Zambian sable antelope* (*Hippotragus niger kirkii*) (considered Vulnerable under the IUCN Red List (IUCN, 2021) categorization) and the blue



Figure 4.13. Occupancy of the different carnivore species in KNP.

monkey which is rare. A longer camera trap survey with more a comprehensive spatial coverage of KNP is necessary to make any meaningful inferences about the carnivore community in KNP and design appropriate conservation plans.

APPENDIX A
CHAPTER ONE

A.1 Supplementary figures



Figure A.1. Word cloud of the broad context in publications about studies focusing on community occupancy.

Table A.1. List of variables included in the studies.

Variables			
Climatic	Habitat	Species Traits	Anthropogenic
Precipitation	Farmland	Forage	Hunting
Hydroperiod	Forest	Nest Type	Logging
Inundation	Rainforest	Diet	Agriculture
Solar Radiation	Grassland	Body Mass	Fragmentation
Fire	Wetland	Home Range Size	Road
Temperature	Savanna	Gestation	Housing Density
Cloudiness	Pasture	Resident	Development
Elevation	Plantation	Migrant	Fire
Flooding	Duneland	Activity Pattern	Plantation
Drought	Shrubland	Dispersal	Recreation
	Marsh	Clutch Size	Deforestation
	Ditch		
	Stream		

Table A.2. Concept key and definition of variables used in the review

Variables of interest
<p>Publication details:</p> <ul style="list-style-type: none"> - Paper Title (String): Publication title - Authors (String): Publication author listing - Journal (String): The journal in which the study was published - Year Published (Integer): The year in which the study was published in the journal - Author Affiliation Countries (Integer): The countries in which author affiliations as listed are in - Number of Authors (Integer): The number of authors in the manuscript - Study question and context: What was the study trying to understand?
<p>Study organisms:</p> <ul style="list-style-type: none"> - No. of Species Seen (Integer): The total number of species observed during the study - No. of Species Not Seen (Integer): The species that occur in the area but were not observed during the study - Focal Species (String): The species the study was designed for - Bycatch Species (String): The species on which data were obtained despite not being explicitly designed for it/them - Bycatch Species Seen but Not Listed (Boolean): Whether there is a mention of organisms other than focal species seen during the study even if all the bycatch species are not listed - Study Group (String): Classification of study species based on their known diet

Continued on next page

Table A.2 – *Continued from previous page*

Variables of interest
<ul style="list-style-type: none"> - Taxa (String): Broad taxonomic unit of the study organisms in this publication - Species (String): Basic unit (lowest taxonomic rank) of biological classification in this study - Genus (String): Genera corresponding to each of the study species - Family (String): Taxonomic family corresponding to each species in the study - Order (String): The taxonomic order to which the species studied belong - Class (String): The taxonomic class to which the study species belong - Kingdom (String): The taxonomic kingdom to which the study species belong - Vertebrates (Boolean): Whether the focal species are vertebrates or not
<p>Study area-related:</p> <ul style="list-style-type: none"> - Continent (String): The continent to which the country where the study was conducted belongs - Country (String): The country in which the study location occurs - Region (String): The region in which the study location occurs - Study Area (String): The actual study location - Sea or Ocean Name (String): The name of the sea or ocean in case the study location is a marine area - Elevation (String): Elevation range of study location - Depth (String): Depth range of study location - Spatial Scale (String): The total area covered in the study - Spatial Scale Justification (Boolean): Whether any justification of spatial scale chosen was provided

Continued on next page

Table A.2 – *Continued from previous page*

Variables of interest
<ul style="list-style-type: none"> - Spatial Scale Justification Reason (String): What was the justification for choosing this spatial scale? - Latitude (String): What was the latitude of the study location? - Longitude (String): What was the longitude of the study location? - System Type (String): Whether the study was on a terrestrial, marine, aquatic system - Protected Area (Boolean): Whether the study system is a protected area - Urban Area (Boolean): Whether the study system is considered an urban area - Habitat (String): Broad habitat type of the study system
<p>Study Period:</p> <ul style="list-style-type: none"> - Study Year (Integer): The year in which the study was conducted - Temporal Scale (String): The duration of the study - Temporal Scale Justification (Boolean): Whether any justification for the temporal scale chosen was provided? - Temporal Scale Justification Reason (String): What was the justification provided for choosing this temporal scale? - Study Season (String): The season/s during which the study was conducted - Time of Day (String): Whether the sampling was during the day, at night, or both
<p>Study methods:</p> <ul style="list-style-type: none"> - Detectability (String): Whether the detectability of the species of concern is high or not

Continued on next page

Table A.2 – *Continued from previous page*

Variables of interest
<ul style="list-style-type: none"> - Detection Covariates (String): Detection covariates in the global model - Detector Make (String): The make and model of the detectors used in the study - Detector Spacing (String): The distance between detectors used in the study - Detector Type (String): The type of detector used in the study - Detector Spacing Justification (String): Whether any justification for the spacing between detectors that was chosen for the study was provided - Detector Spacing Justification Reason (String): What justification for detector spacing chosen was provided? - Implementation (String): Sampling methodology and field method - Method Used (String): The type of modeling for which the study is designed - No. of Detectors (Integer): The total number of detectors used for the study - Trap Days (Integer): No. of trap days for the study - Occupancy (Boolean): Whether occupancy modeling was done - Occupancy Model Parameters (String): The occupancy attributes considered in the global model - Occupancy Estimates (String): Values of the occupancy estimates - Occupancy Method (String): What method was used? - Occupancy Model Used (String): Which occupancy model was used? - Number of Candidate Models (String): The total number of candidate models run under a model selection paradigm - Model Season (String): What seasonality is used for the models

Continued on next page

Table A.2 – *Continued from previous page*

Variables of interest
<ul style="list-style-type: none"> - Species Specific Modeling? (Boolean): Were the same detection/occupancy models assumed for all species? If only some are influenced by say temperature, structure is forced on all them - Number of Chains (Integer): Number of chains used in MCMC (if used) - Number of Iterations (Integer): Number of iterations used in MCMC (if used) - Burn-in Period (Integer): Burn-in period in MCMC (if used) - Thinning (Integer): Amount of thinning in MCMC (if used) - Adaptive Phase (Integer): Adaptive phase in MCMC (if used) - Priors (String): Information on priors - Spatial Replicates (String): Number of spatial replicates used - Temporal Replicates (String): Number of temporal replicates used - Biotic Interactions (Boolean): Whether biotic interactions were considered as a covariate for occupancy or detection - Habitat Covariates (String): The habitat covariates that were considered for occupancy or detection - Habitat Included (Boolean): Whether habitat features were considered in the analysis; - Species Traits Included (Boolean): Whether species traits were considered in the analysis - Species Traits (String): Which species traits were considered for the analysis - Climate Included (Boolean): Whether climate variables were considered in the analysis - Climate Covariates (String): Which climate covariates were considered for the analysis

Continued on next page

Table A.2 – <i>Continued from previous page</i>
Variables of interest
- Anthropogenic Factors Included (Boolean): Whether anthropogenic influences were considered in the analysis
- Anthropogenic Covariates (String): Which anthropogenic factors were considered in the analysis
- Simulation Done (Boolean): Whether a simulation was done

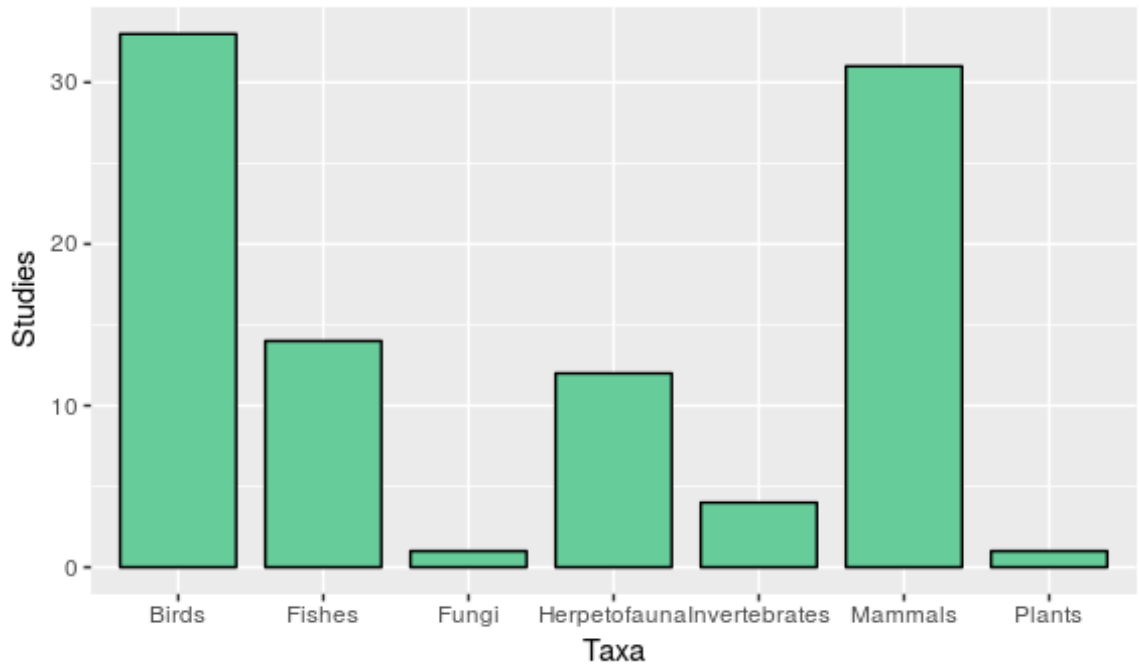


Figure A.2. Bar chart representing the number of studies that focused on each kind of organism.

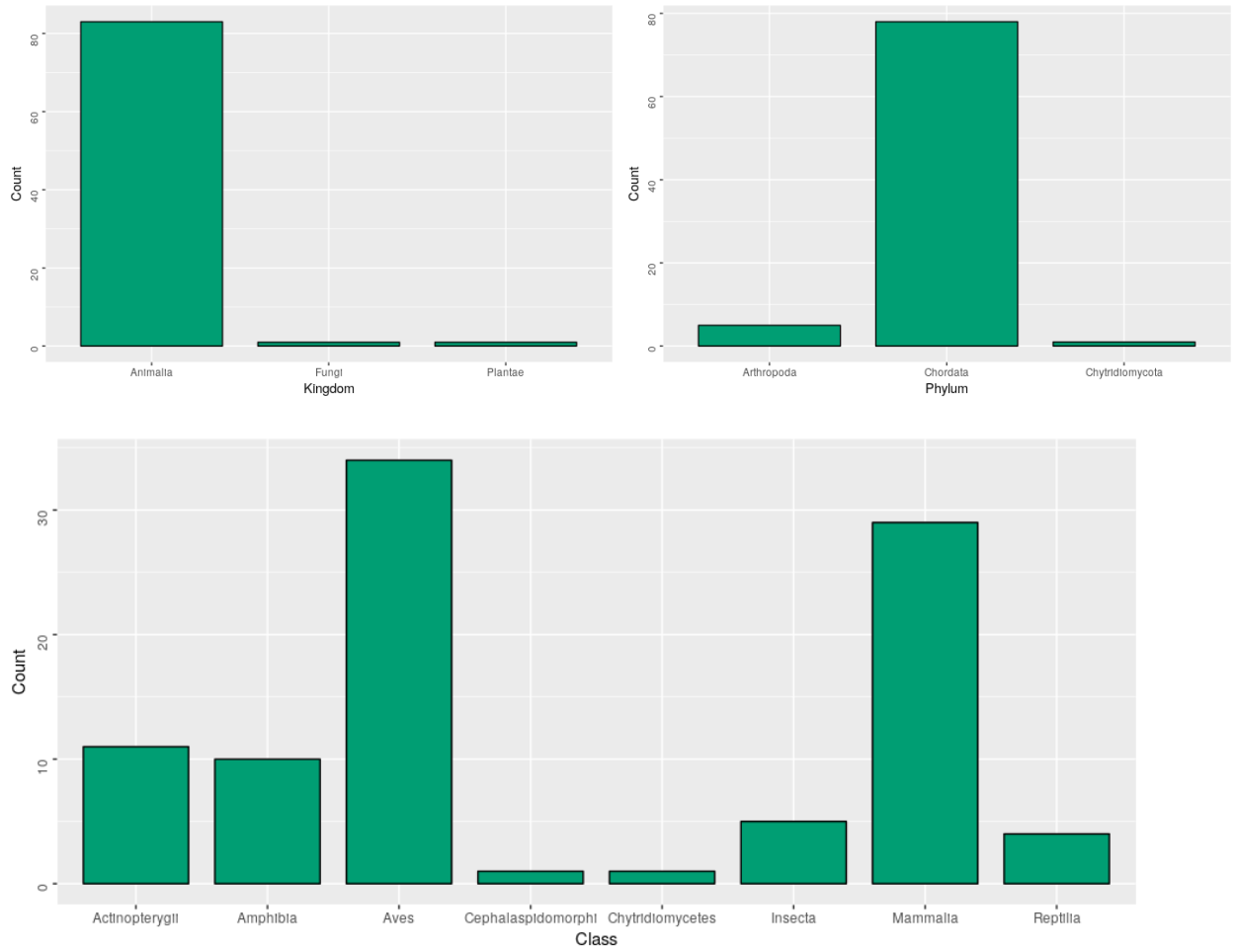


Figure A.3. Bar charts of the taxonomic kingdom, phylum, and class to which organisms that formed a part of multi-species occupancy studies belonged.

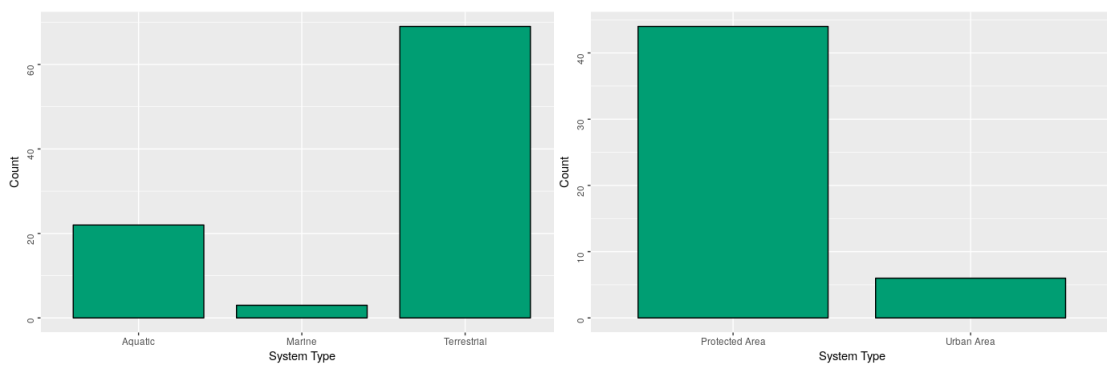


Figure A.4. Study system types. A majority of community occupancy studies were terrestrial and in a protected area.

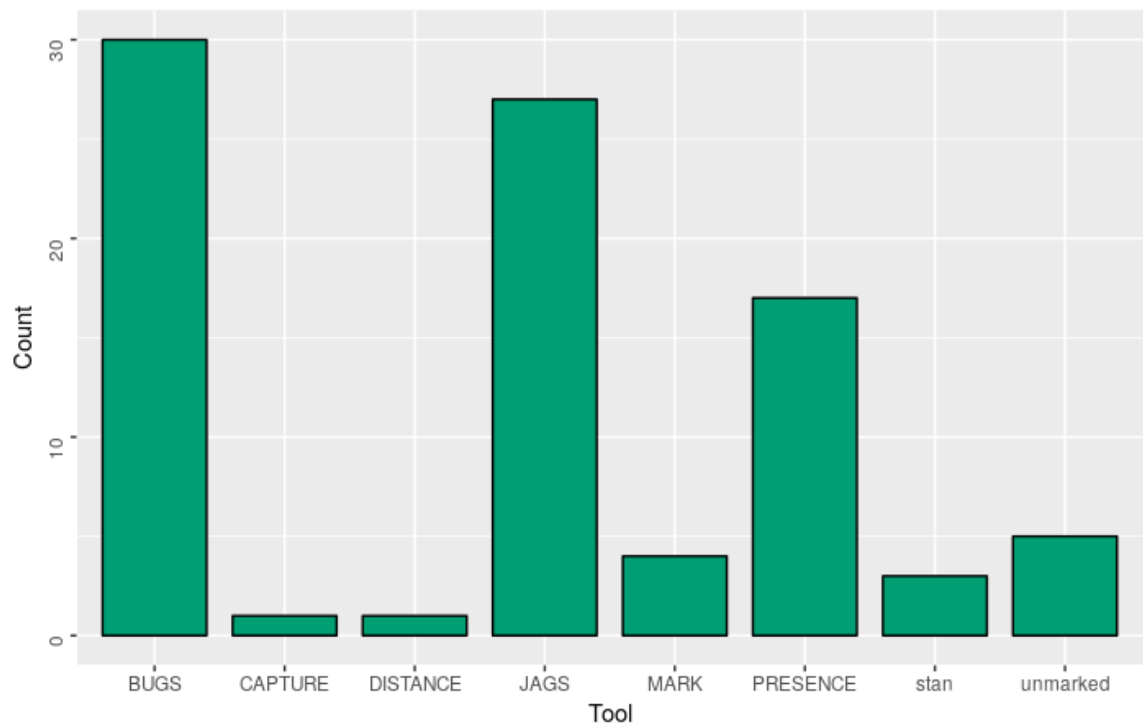


Figure A.5. Use of statistical tools for community occupancy across field site and taxa. The Bayesian framework seemed to be the most popular, with a majority of the studies using either BUGS or JAGS.

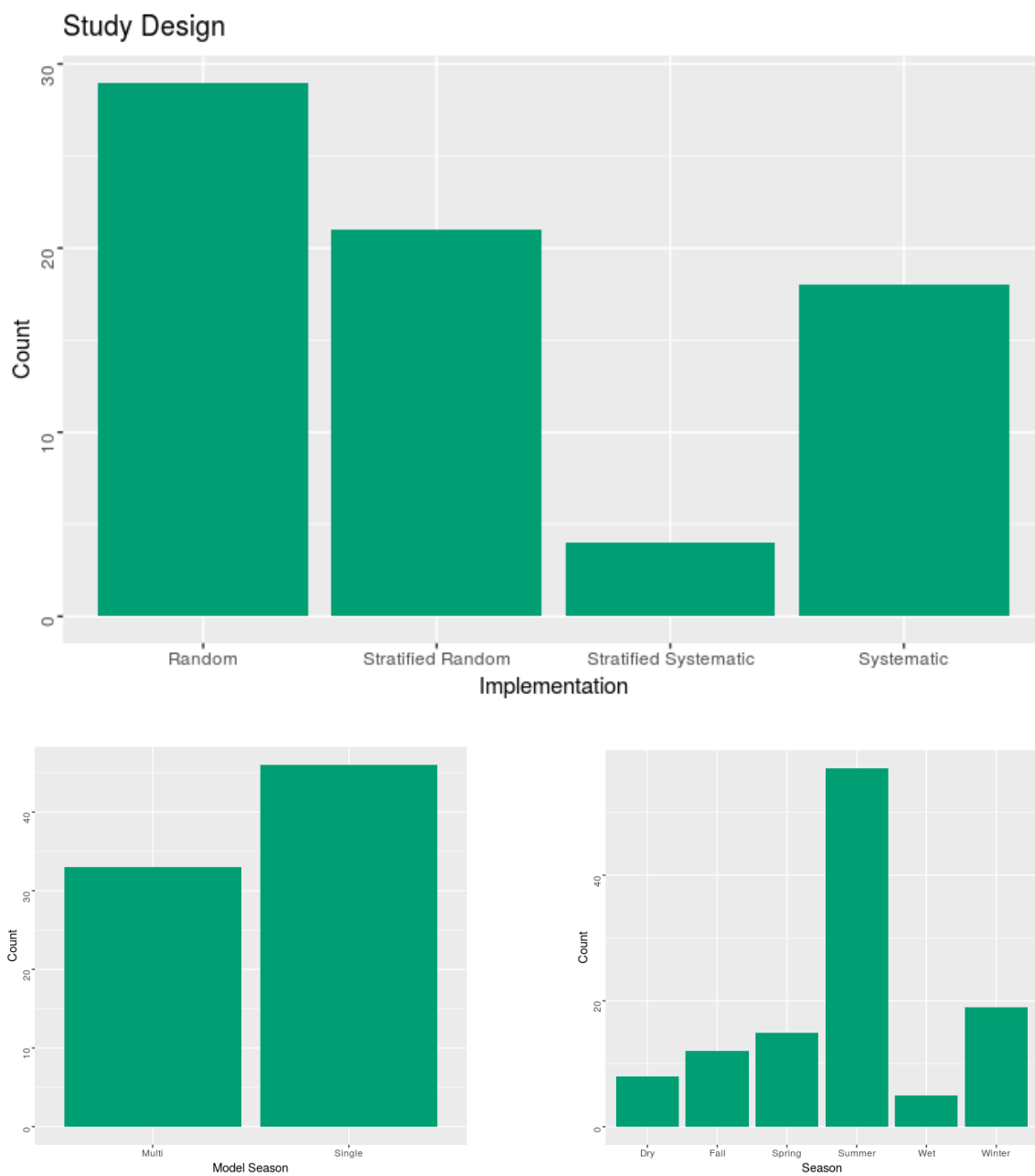


Figure A.6. Study designs and seasons.

APPENDIX B

CHAPTER TWO

Bioclimatic variables considered in this study for each of the major biogeographic regions in the global tropics and subtropics. The maps are of protected areas in each region color-coded with mean annual temperature and mean annual precipitation. Figures B.1 and B.11 correspond to the variation in species richness with latitude of protected areas in the Indomalayan region and Central and South America respectively, while figures B.5 and B.15 show the regional variation of all 19 bioclimatic variables considered here.

Table B.1. Bioclimatic variables considered for this study.

Variable code	Variable description
bio1	Modern Annual Mean Temperature
bio2	Modern Mean Diurnal Range (Mean of monthly (max temp - min temp))
bio3	Modern Isothermality (bio2/bio7) (* 100)
bio4	Modern Temperature Seasonality (standard deviation *100)
bio5	Modern Max Temperature of Warmest Month
bio6	Modern Min Temperature of Coldest Month
bio7	Modern Temperature Annual Range (bio5-bio6)
bio8	Modern Mean Temperature of Wettest Quarter
bio9	Modern Mean Temperature of Driest Quarter
bio10	Modern Mean Temperature of Warmest Quarter
bio11	Modern Mean Temperature of Coldest Quarter
bio12	Modern Annual Precipitation
bio13	Modern Precipitation of Wettest Month
bio14	Modern Precipitation of Driest Month
bio15	Modern Precipitation Seasonality (Coefficient of Variation)
bio16	Modern Precipitation of Wettest Quarter
bio17	Modern Precipitation of Driest Quarter
bio18	Modern Precipitation of Warmest Quarter
bio19	Modern Precipitation of Coldest Quarter

B.1 Indomalayan region

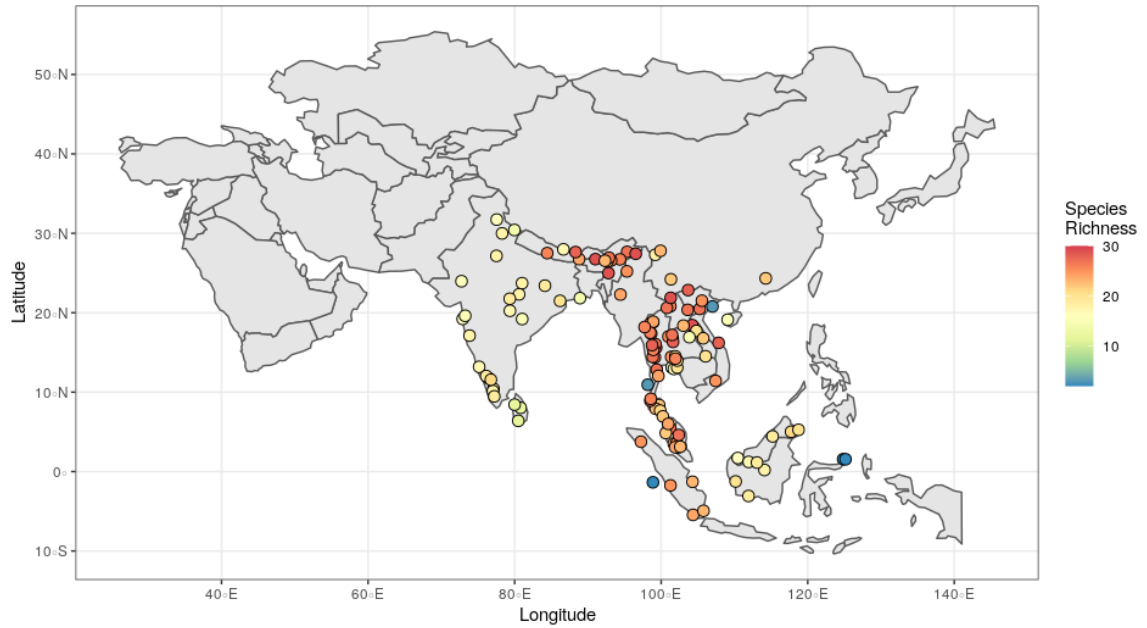


Figure B.1. Distribution of protected areas used in the study color-coded by carnivore community size in each Indomalayan protected area.

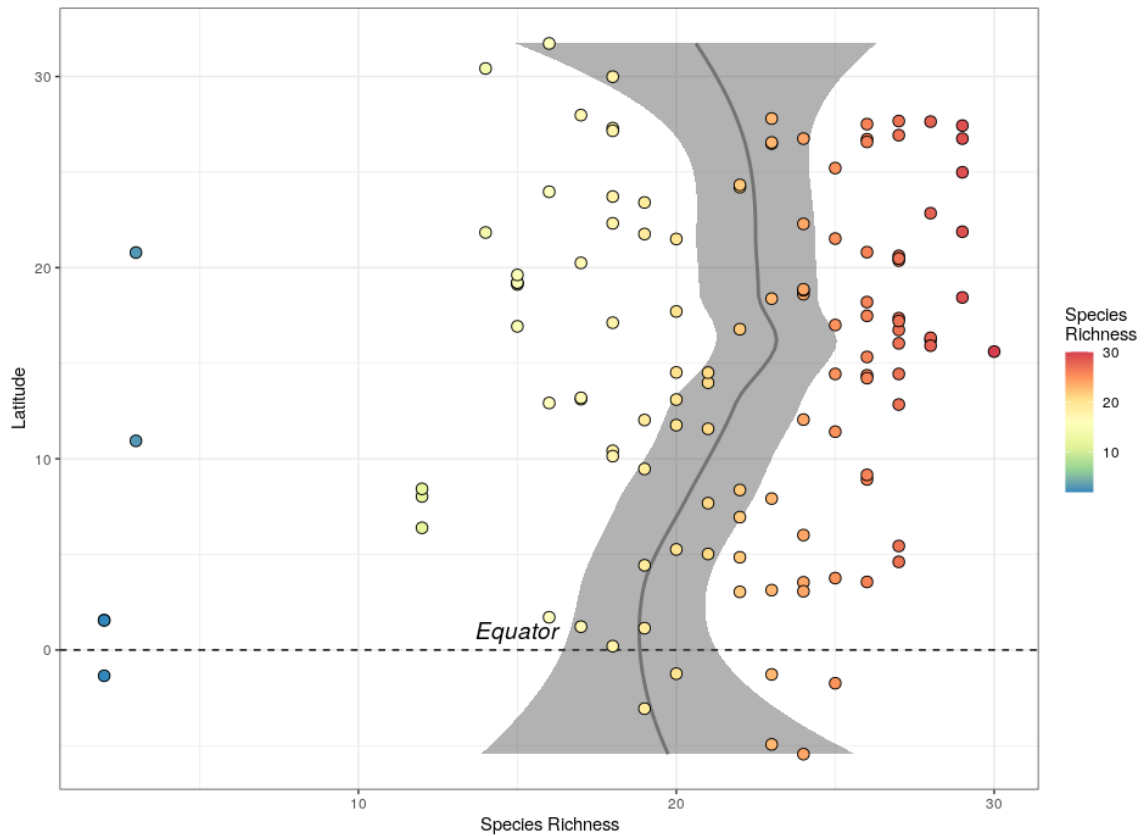


Figure B.2. Latitudinal gradient (variation of carnivore species richness with latitude) color-coded by community size for protected areas in the Indomalayan region.

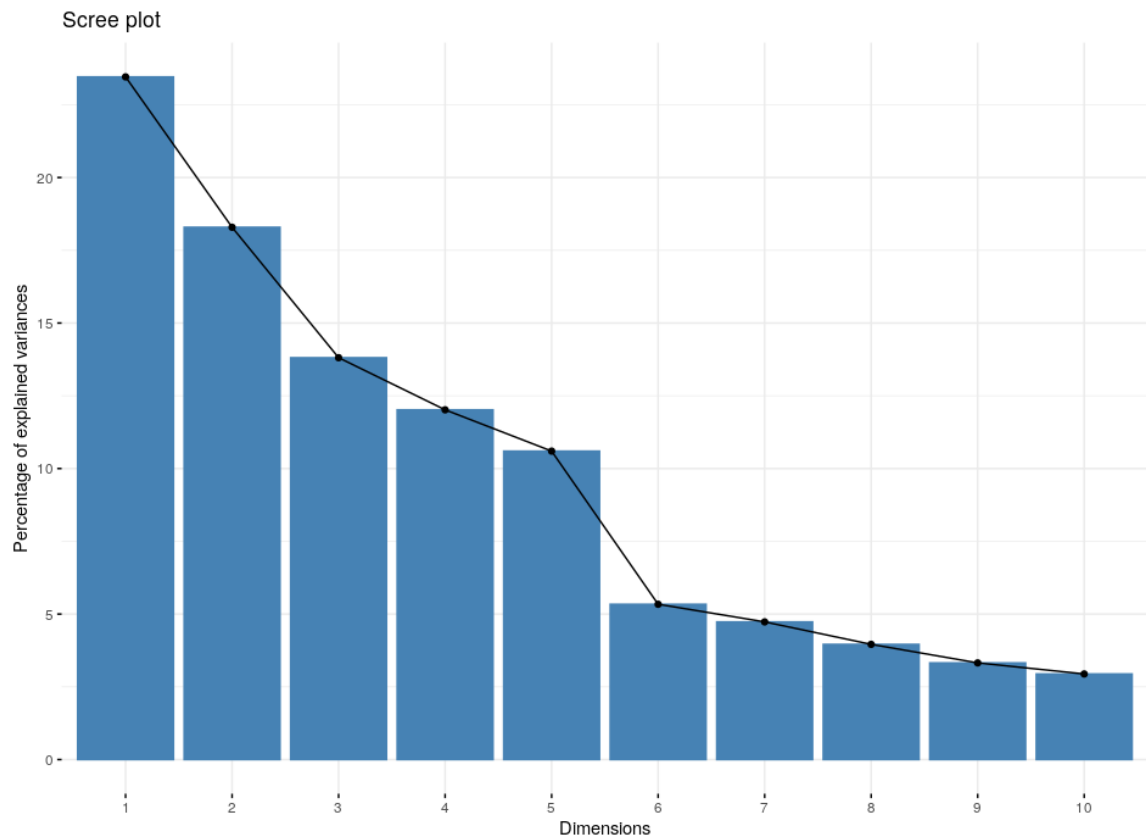


Figure B.3. Screeplot of dimensions with the highest percentage of explained variances for communities in the Indomalayan region based on Correspondence Analysis (CA) of carnivore community trait structure.

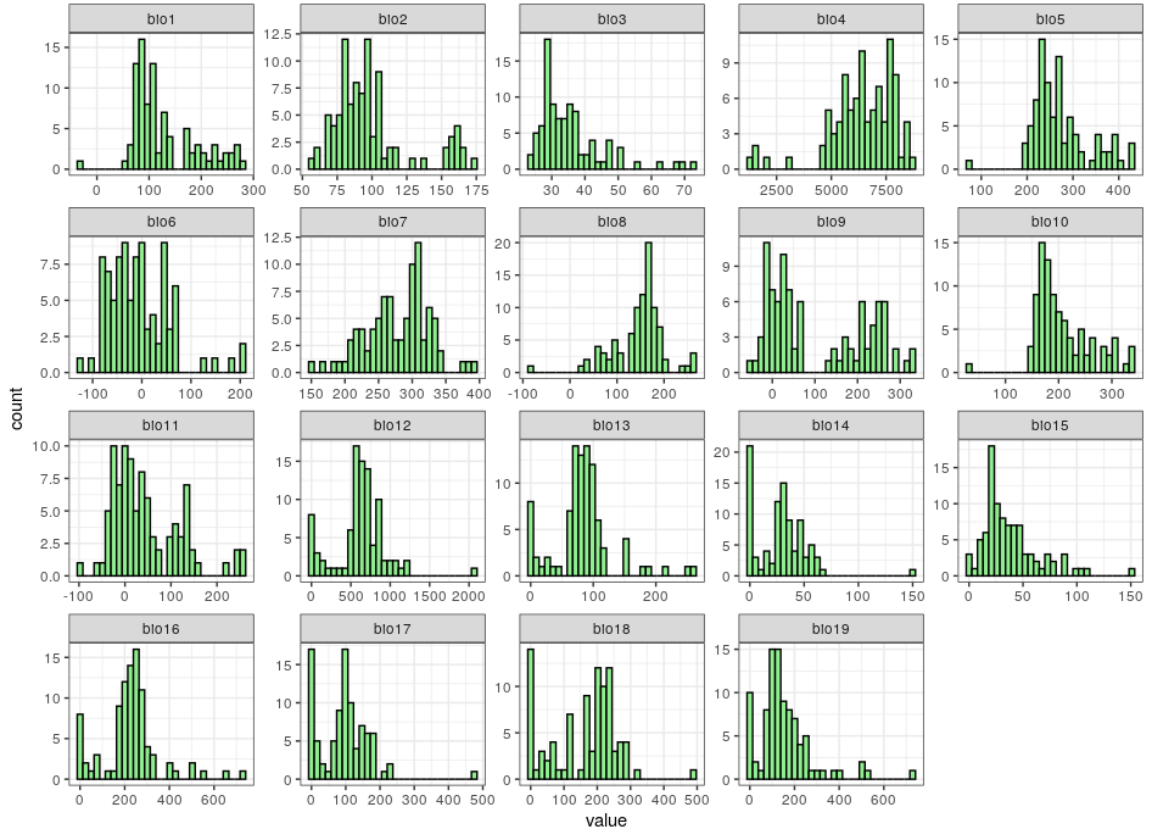


Figure B.5. Histograms of bioclimatic data for the Indomalayan region for variables in Table B.1.

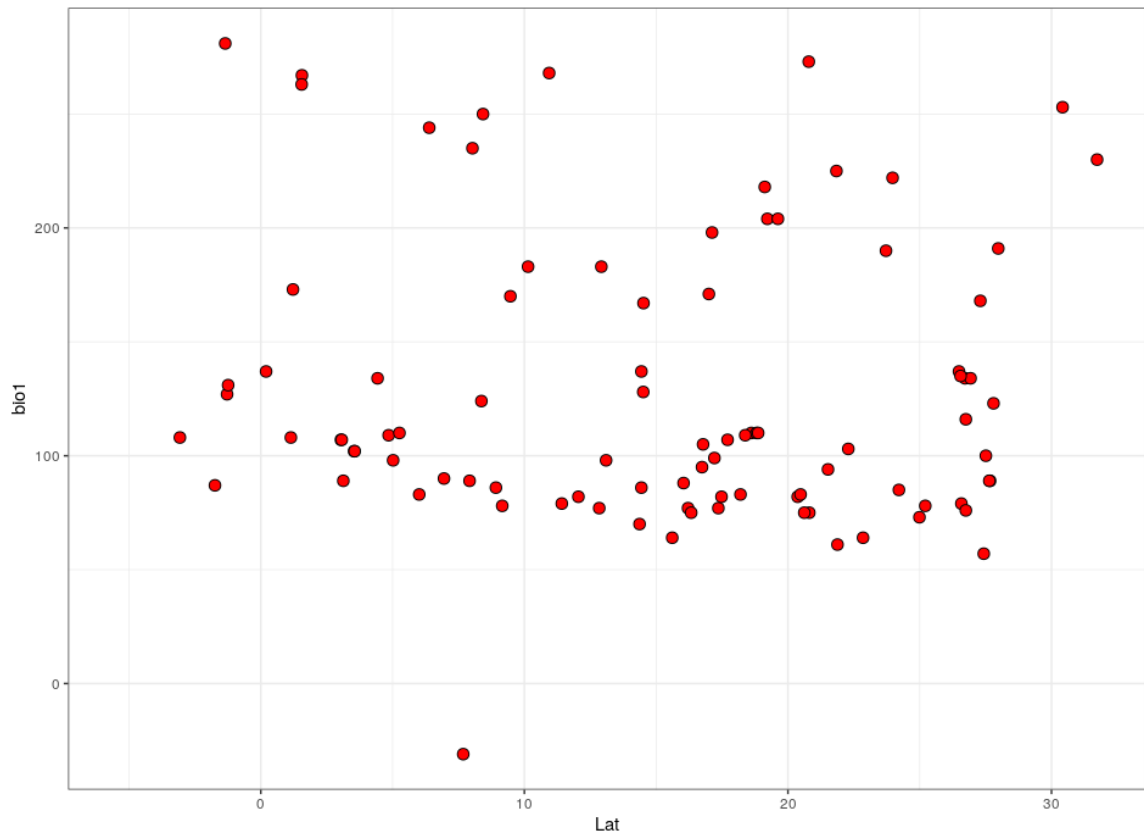


Figure B.6. Relationship between bio1 (modern annual mean temperature) and latitude for each protected area in the Indomalayan realm.

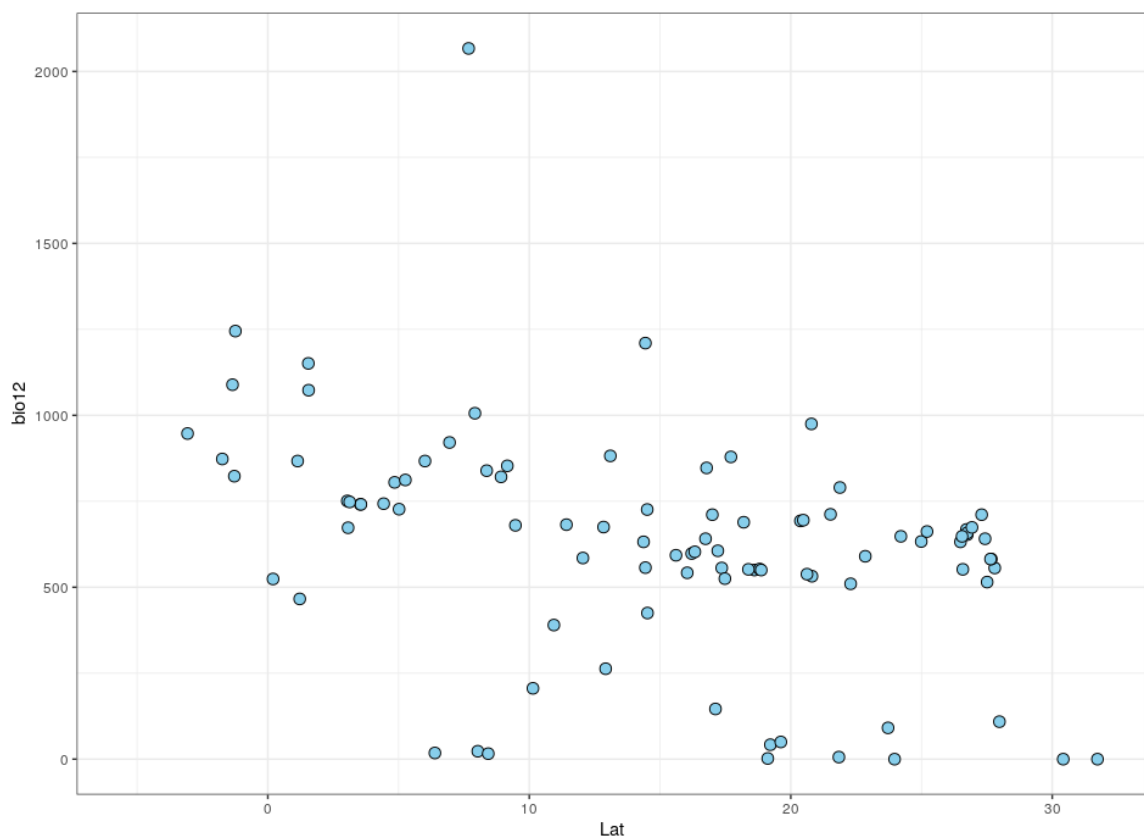


Figure B.7. Relationship between bio12 (modern annual precipitation) and latitude for each protected area in the Indomalayan realm.

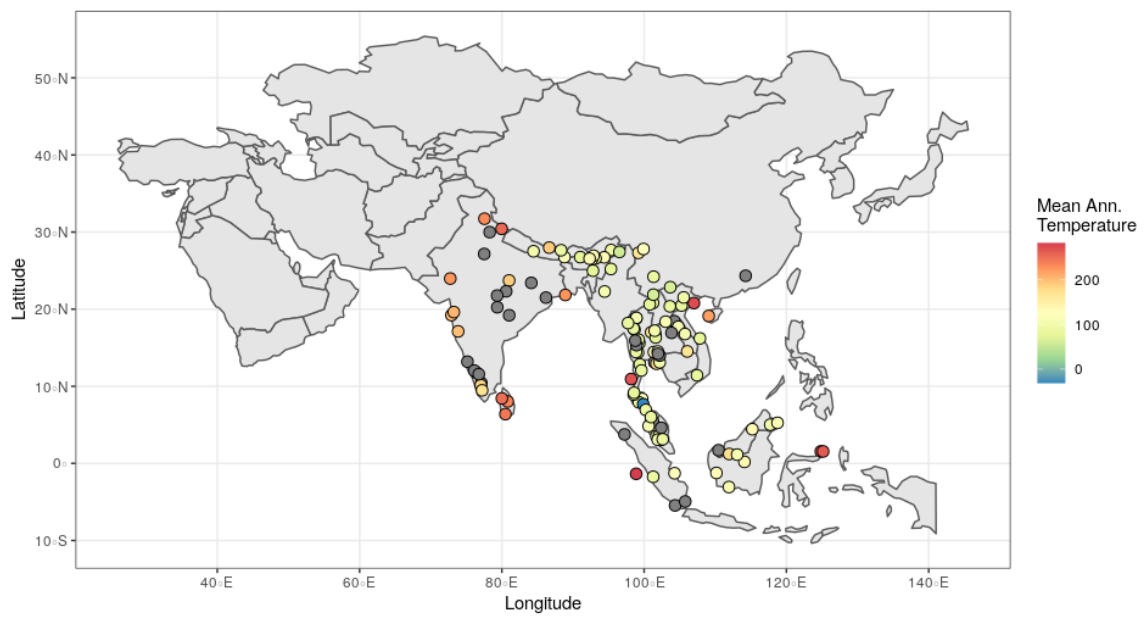


Figure B.8. Map of protected areas in the Indomalayan region color-coded by the mean annual temperature gradient.

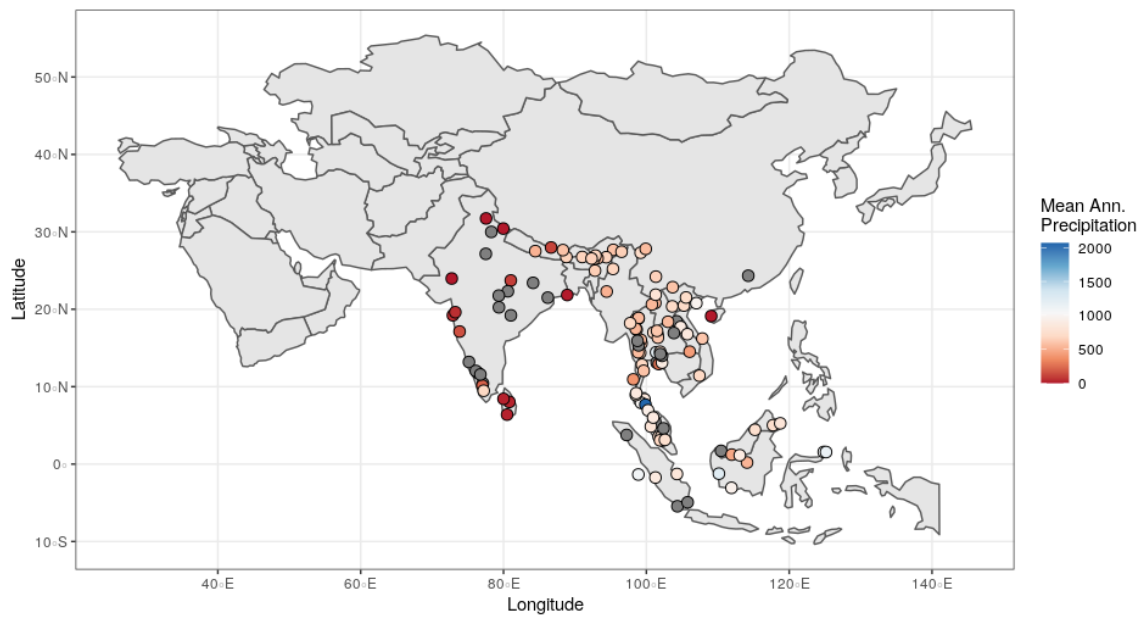


Figure B.9. Map of protected areas in the Indomalayan region color-coded by the mean annual precipitation gradient.

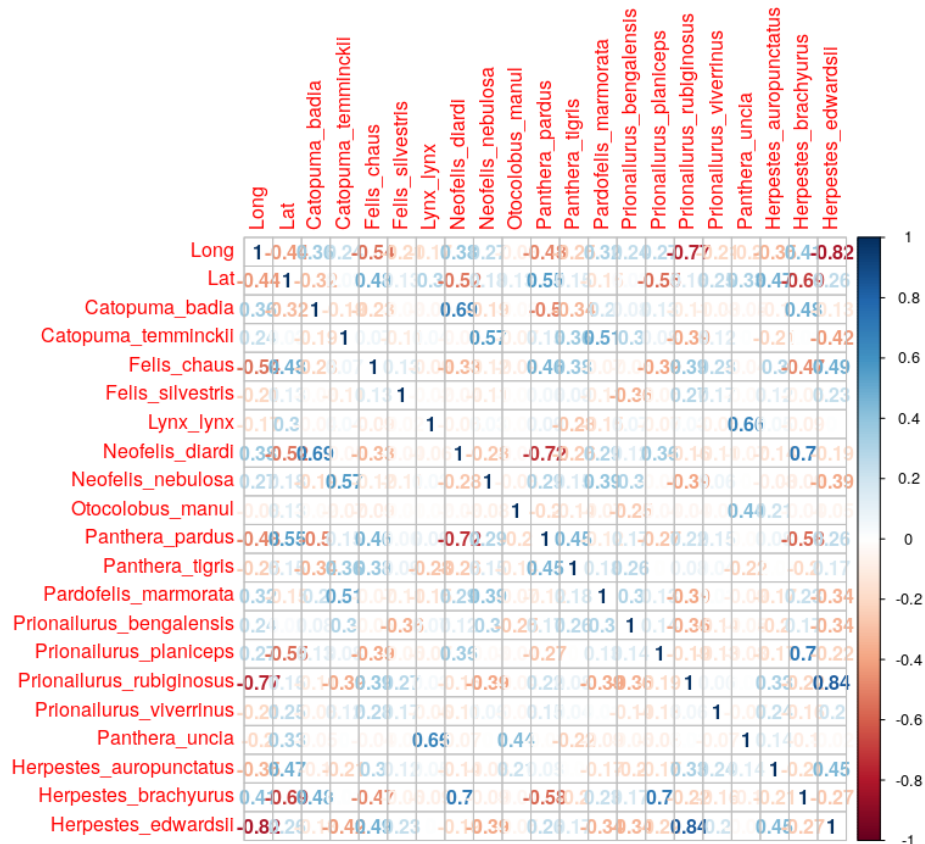


Figure B.10. Correlation plot of relationship between some of the carnivores in the Indomalayan region with protected area geography (latitude and longitude).

B.2 Central & South America

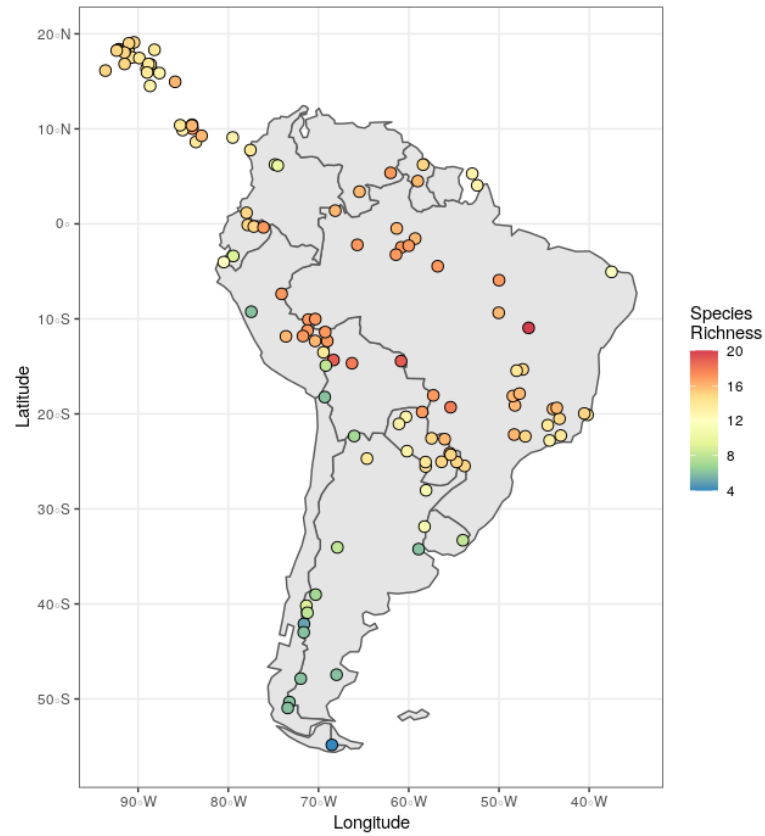


Figure B.11. Distribution of protected areas used in the study color-coded by carnivore community size in each protected area of Central and South America.

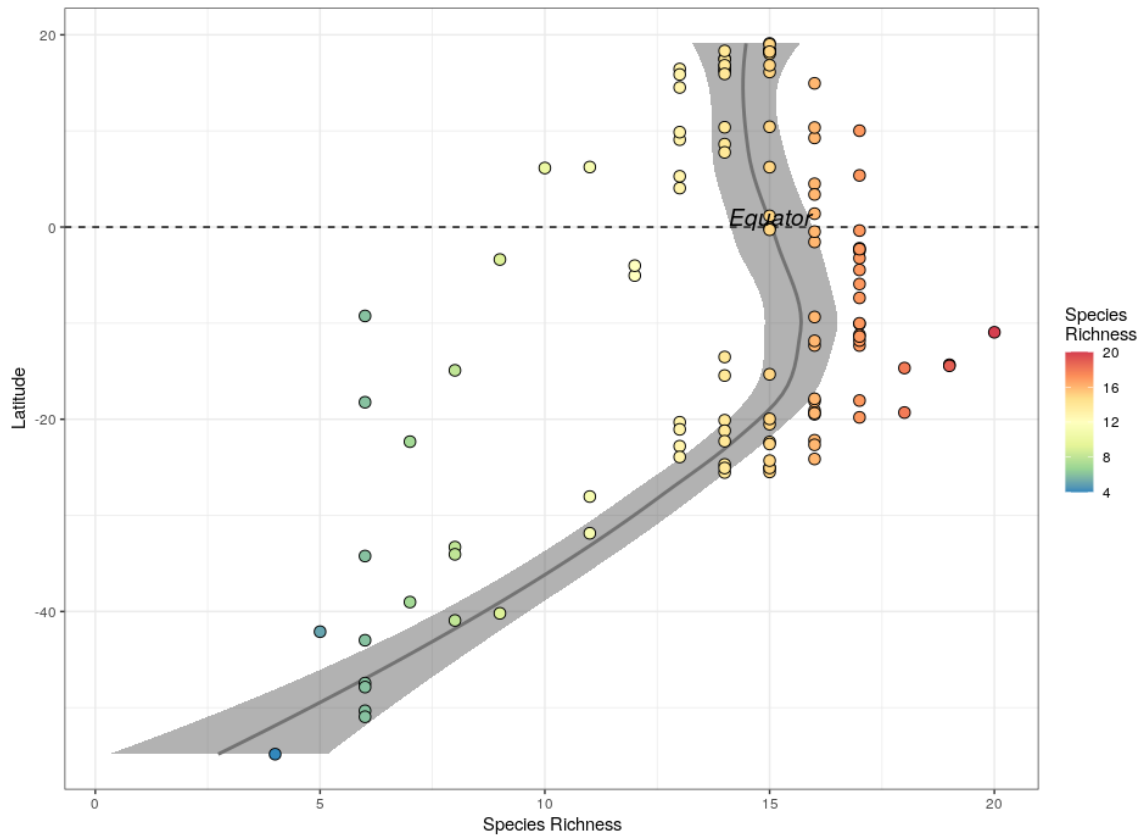


Figure B.12. Latitudinal gradient (variation of carnivore species richness with latitude) color-coded by community size for protected areas in Central and South America.

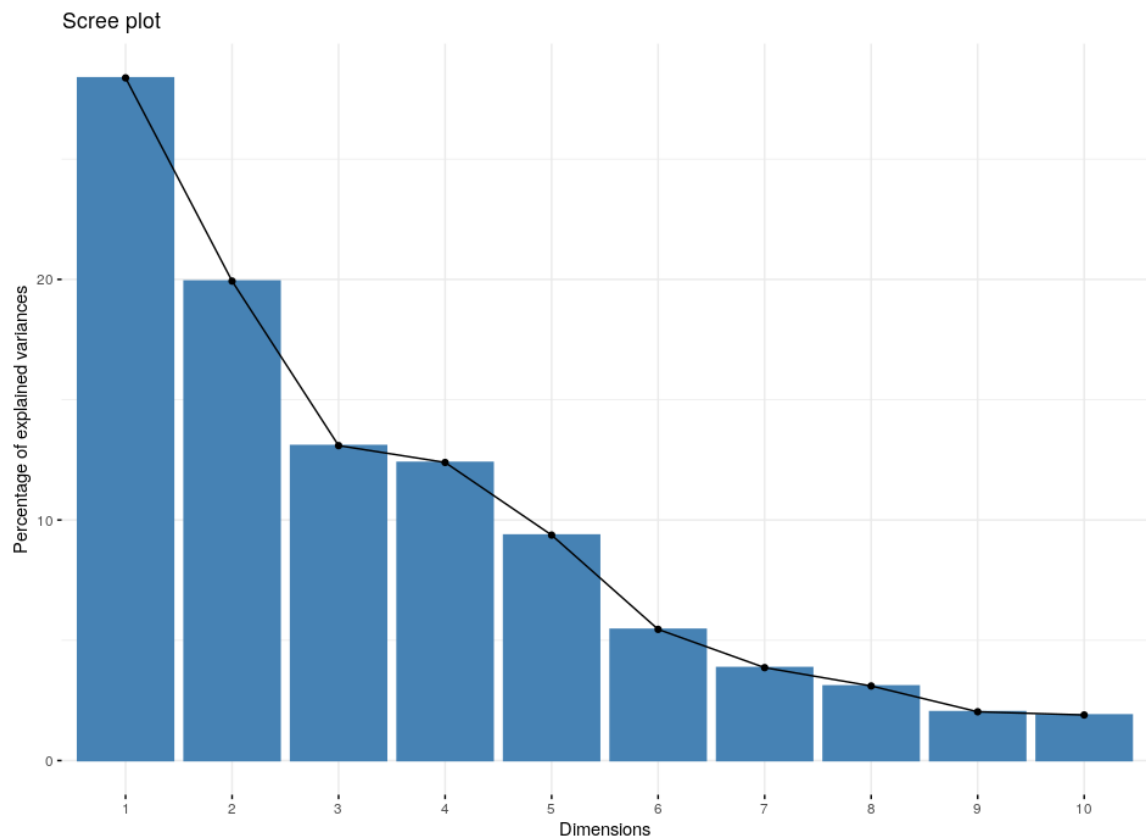


Figure B.13. Screeplot of dimensions with the highest percentage of explained variances for communities in Central and South America based on Correspondence Analysis (CA) of carnivore community trait structure.

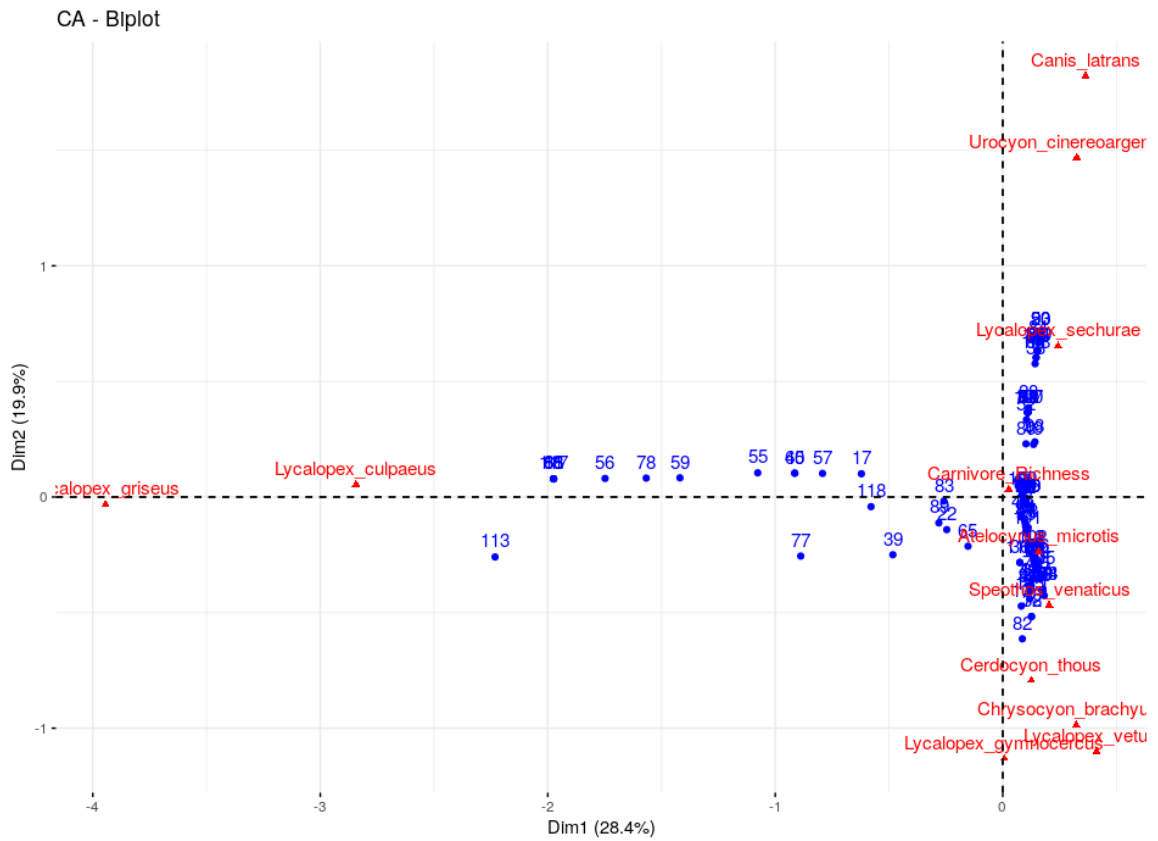


Figure B.14. Biplot of first two Correspondence Analysis (CA) axes obtained for the carnivores in Central and South America.

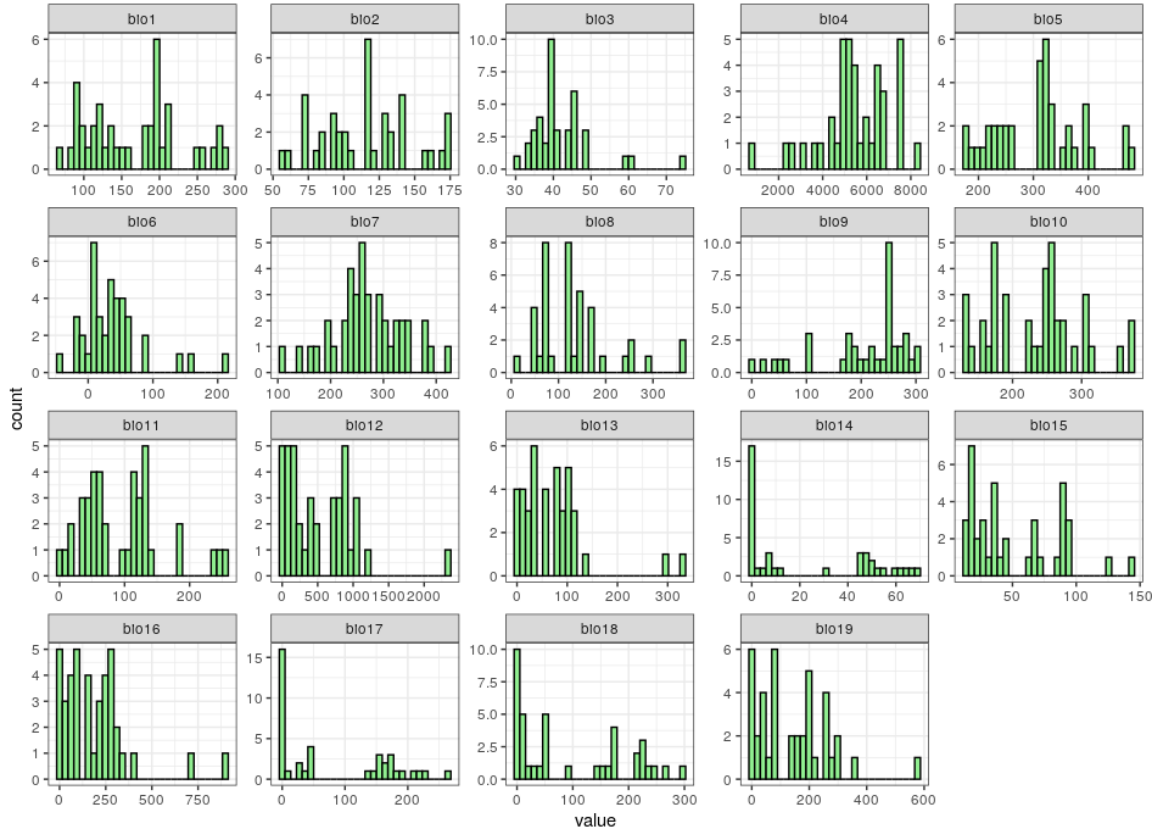


Figure B.15. Histograms of bioclimatic data for Central and South America for variables in Table B.1.

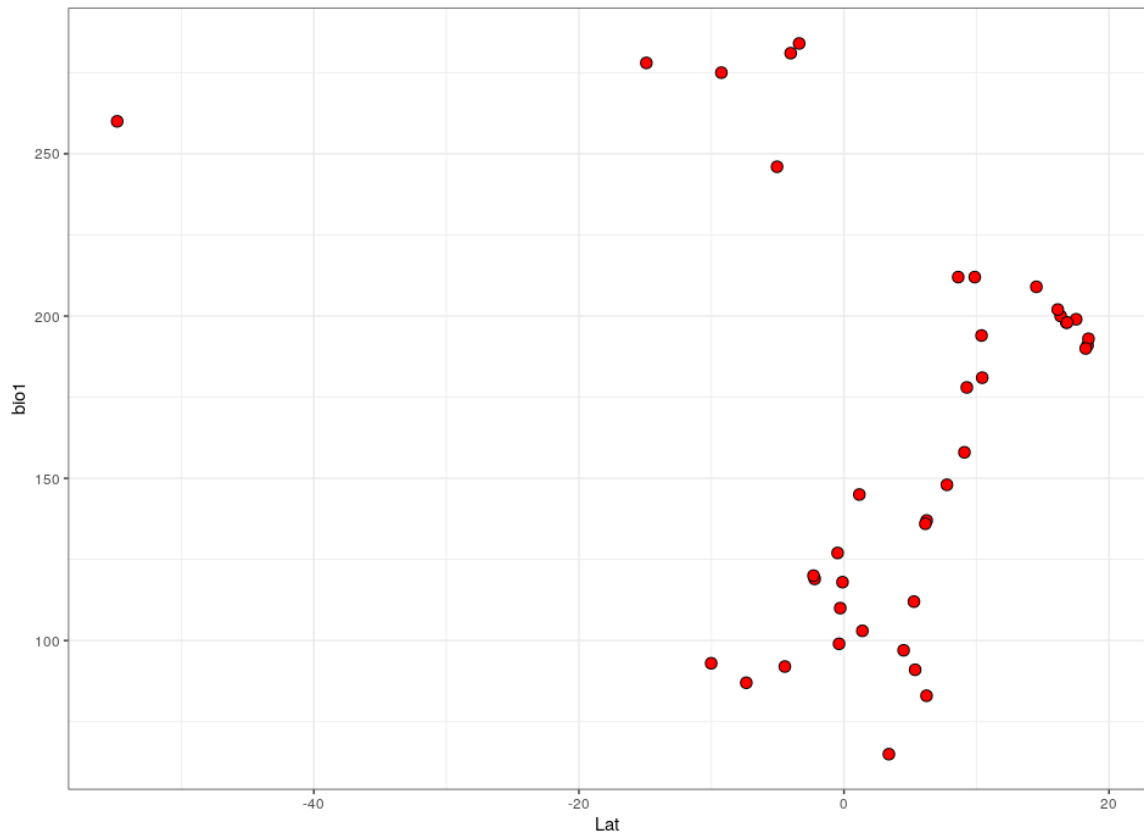


Figure B.16. Relationship between bio1 (modern annual mean temperature) and latitude for each protected area in Central and South America.

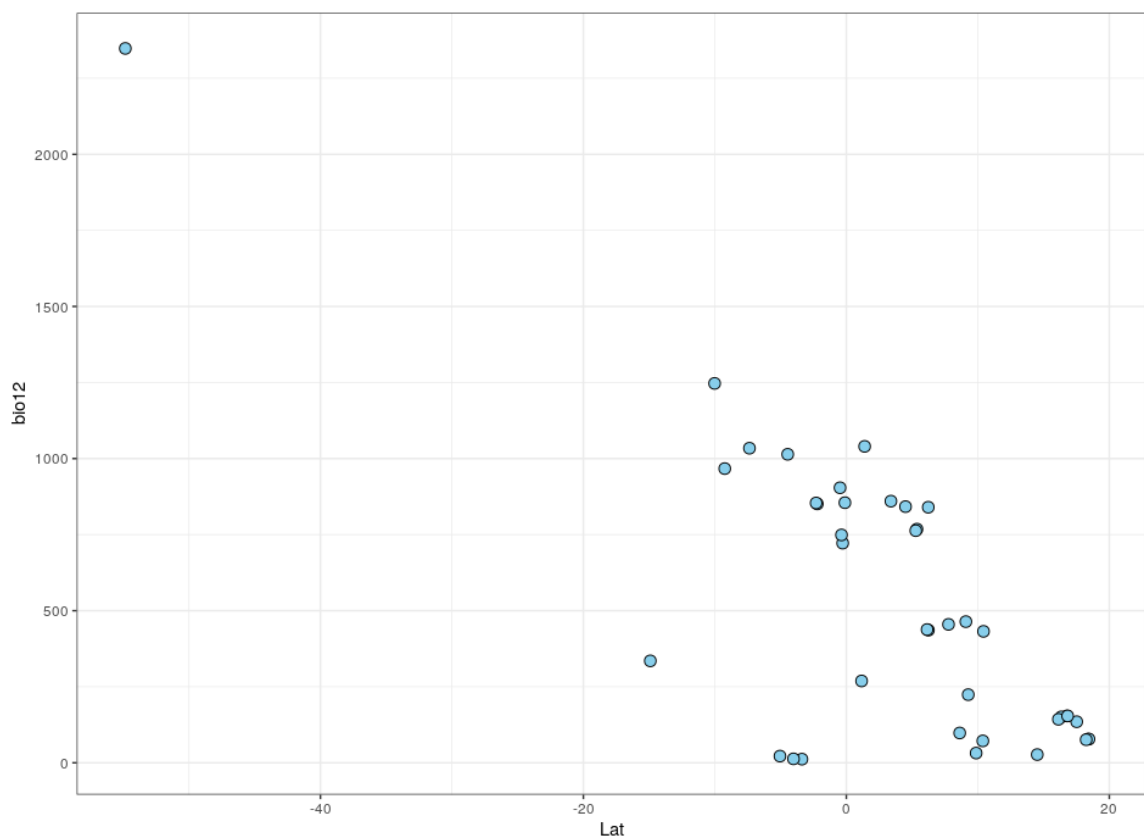


Figure B.17. Relationship between bio12 (modern annual precipitation) and latitude for each protected area in the Central and South America.

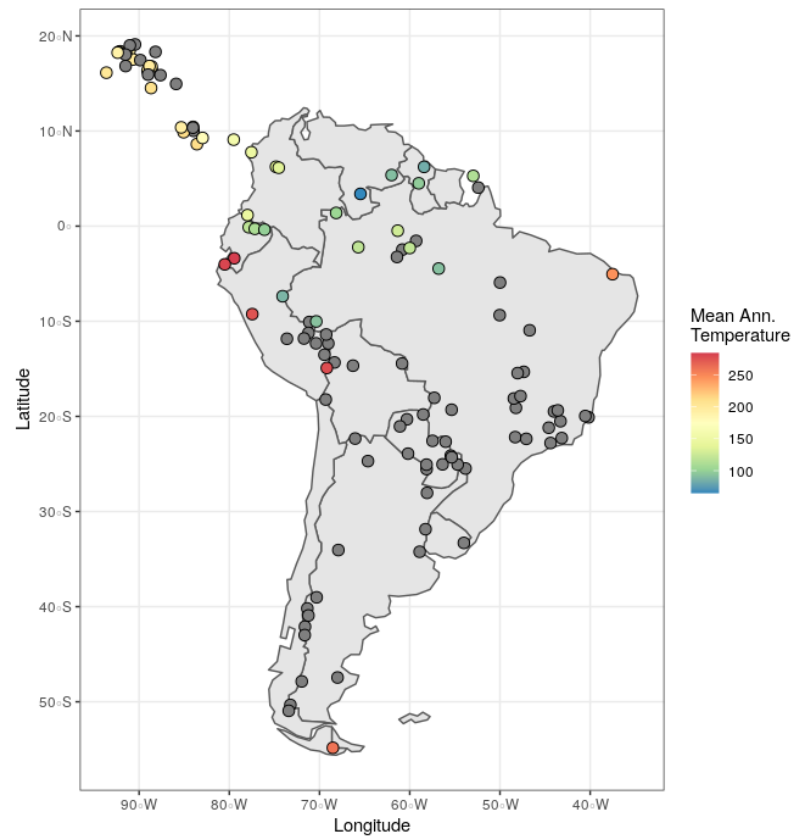


Figure B.18. Map of protected areas in Central and South America color-coded by the mean annual temperature gradient.

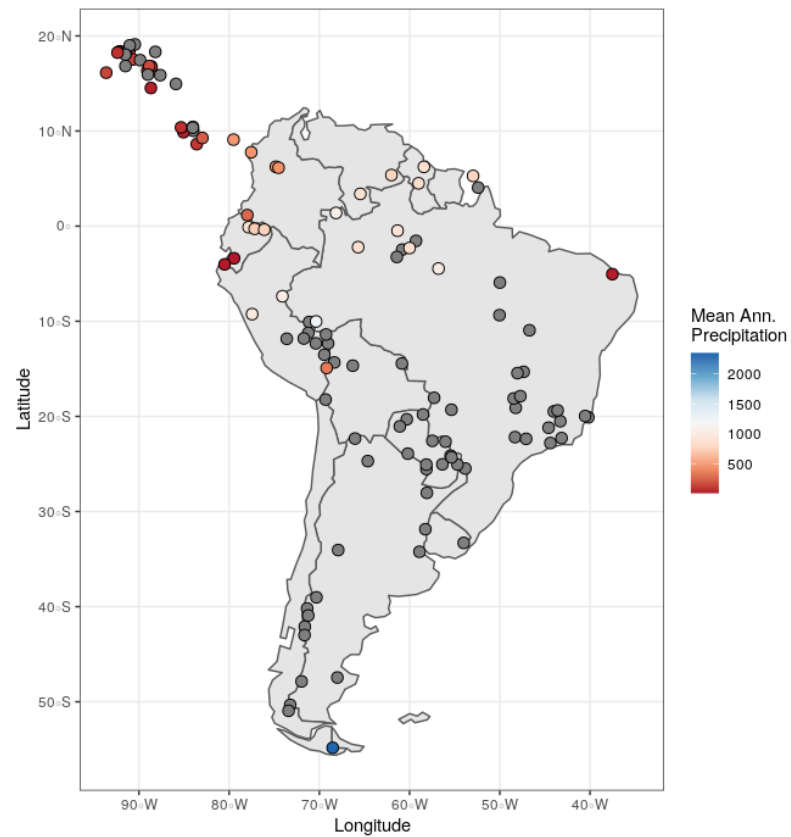


Figure B.19. Map of protected areas in Central and South America color-coded by the mean annual precipitation gradient.

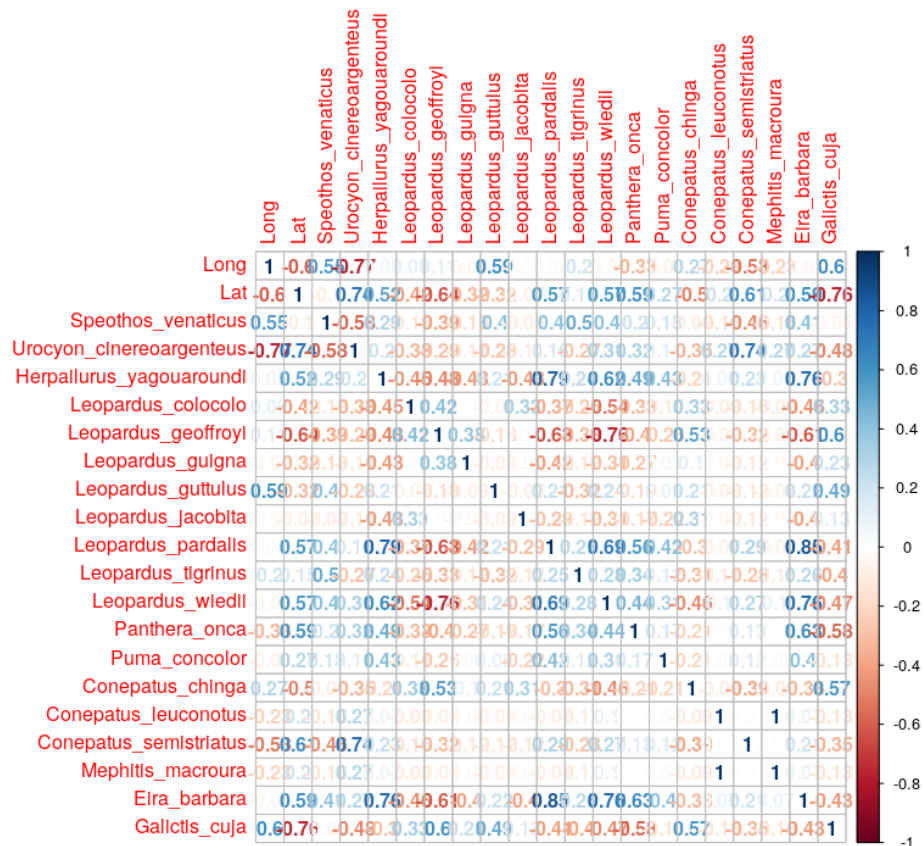


Figure B.20. Correlation plot of relationship between some of the carnivores in Central and South America with protected area geography (latitude and longitude).

B.3 Protected area size

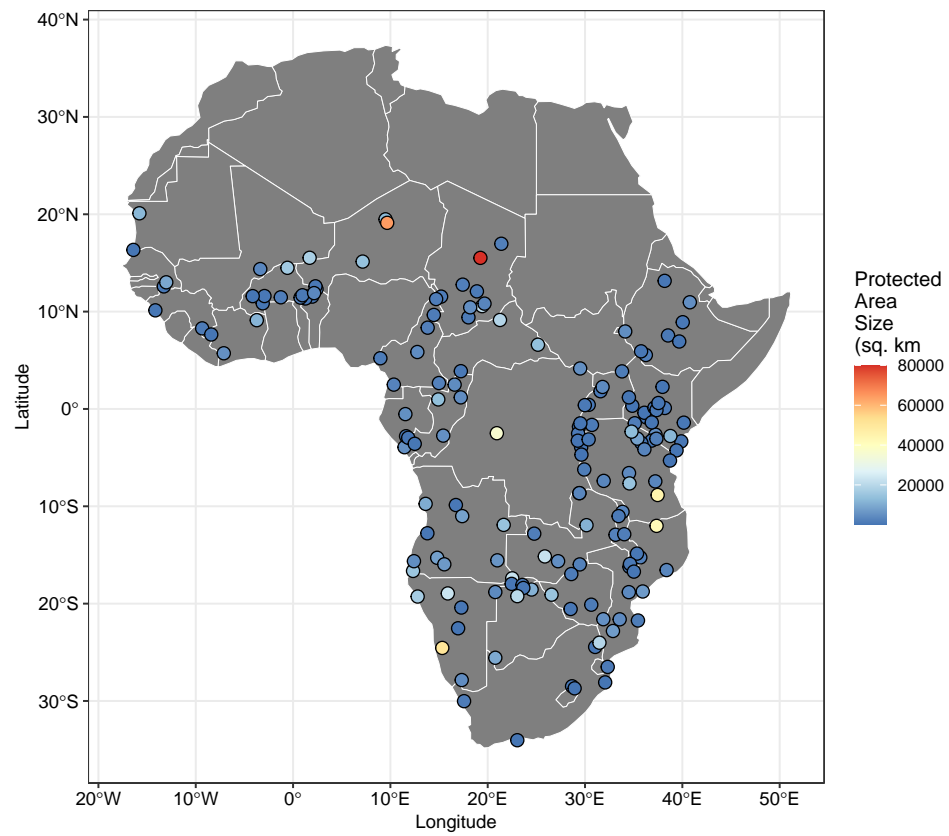


Figure B.21. Map of Africa color-coded by PA size.

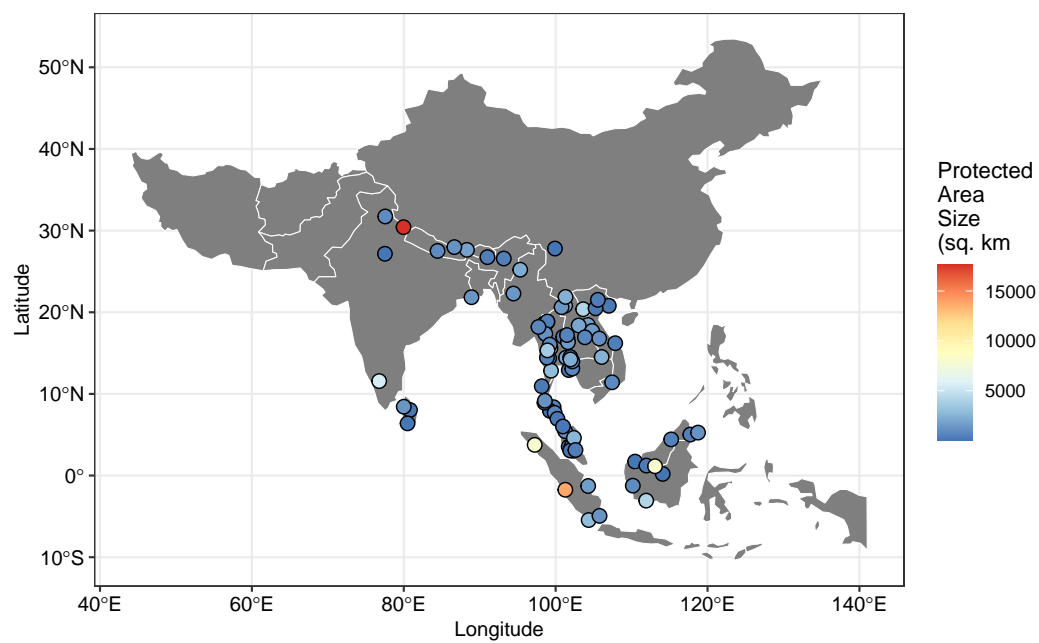


Figure B.22. Map of Indomalayan region color-coded by PA size.

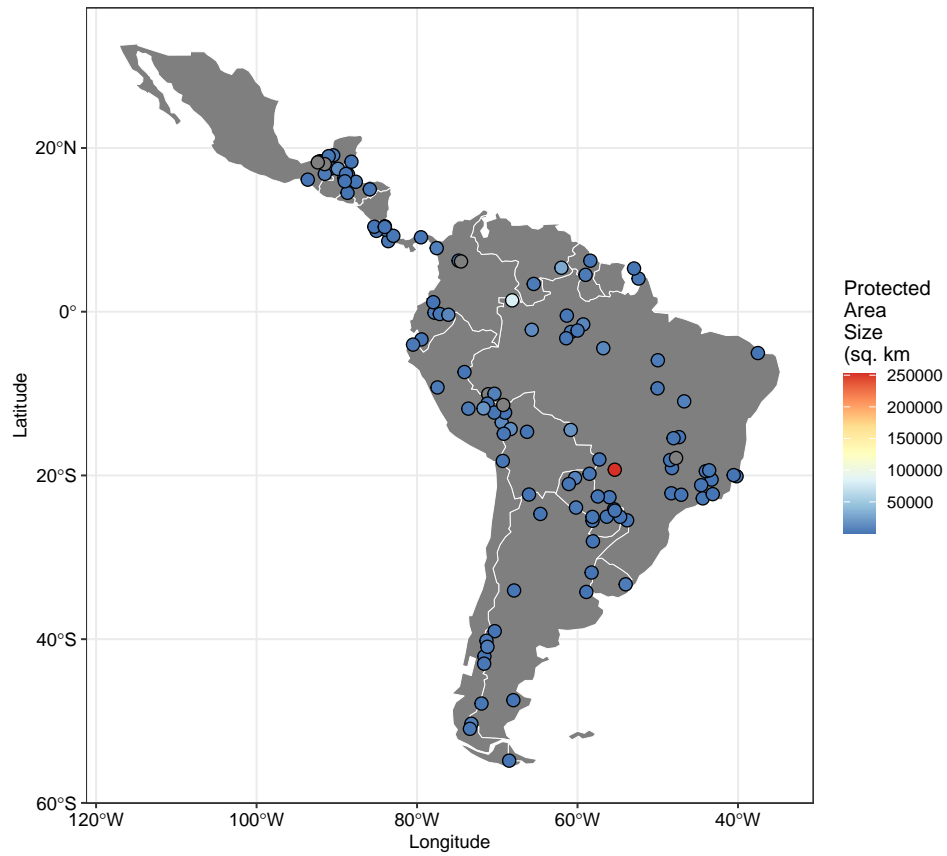


Figure B.23. Map of Central and South America color-coded by PA size.

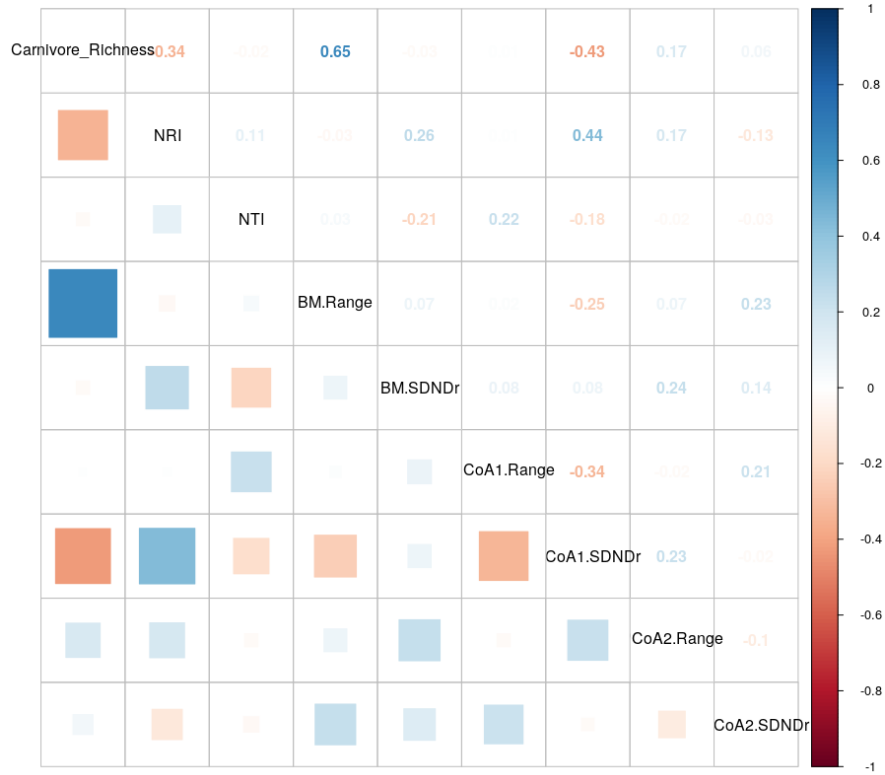


Figure B.24. Correlation matrices of multiple biodiversity metrics in relation to carnivore richness for Africa. *Carnivore_Richness*: Carnivore community size ; *NRI*: Net Relatedness Index ; *NTI*: Nearest Taxon Index ; *BM.Range*: Body mass range ; *BM.SDNDr*: Body mass SDNDr (standard deviation of neighbor distance divided by the overall range) ; *PCoA1.Range* and *PCoA2.Range*: Principal Coordinate Axes (PCoA) 1 and 2 of diet range ; *PCoA1.SDNDr* and *PCoA2.SDNDr*: PCoA 1 and 2 of diet SDNDr. The color gradient scale indicates the strength and direction of correlation.

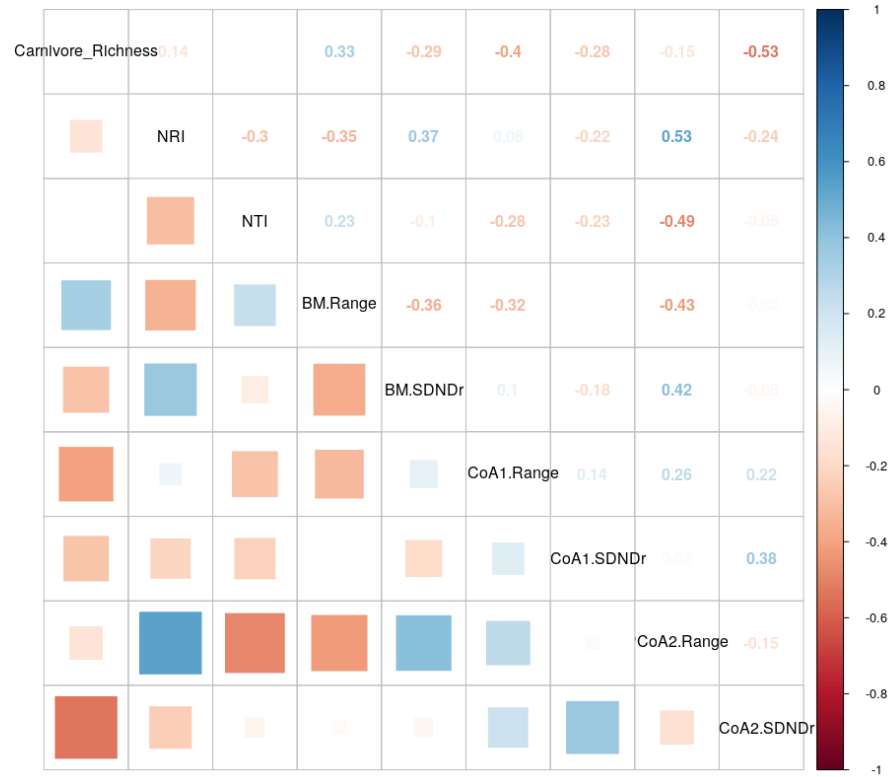


Figure B.25. Correlation matrices of multiple biodiversity metrics in relation to carnivore richness for Asia. *Carnivore_Richness*: Carnivore community size ; *NRI*: Net Relatedness Index ; *NTI*: Nearest Taxon Index ; *BM.Range*: Body mass range ; *BM.SDNDr*: Body mass SDNDr (standard deviation of neighbor distance divided by the overall range) ; *PCoA1.Range* and *PCoA2.Range*: Principal Coordinate Axes (PCoA) 1 and 2 of diet range ; *PCoA1.SDNDr* and *PCoA2.SDNDr*: PCoA 1 and 2 of diet SDNDr.

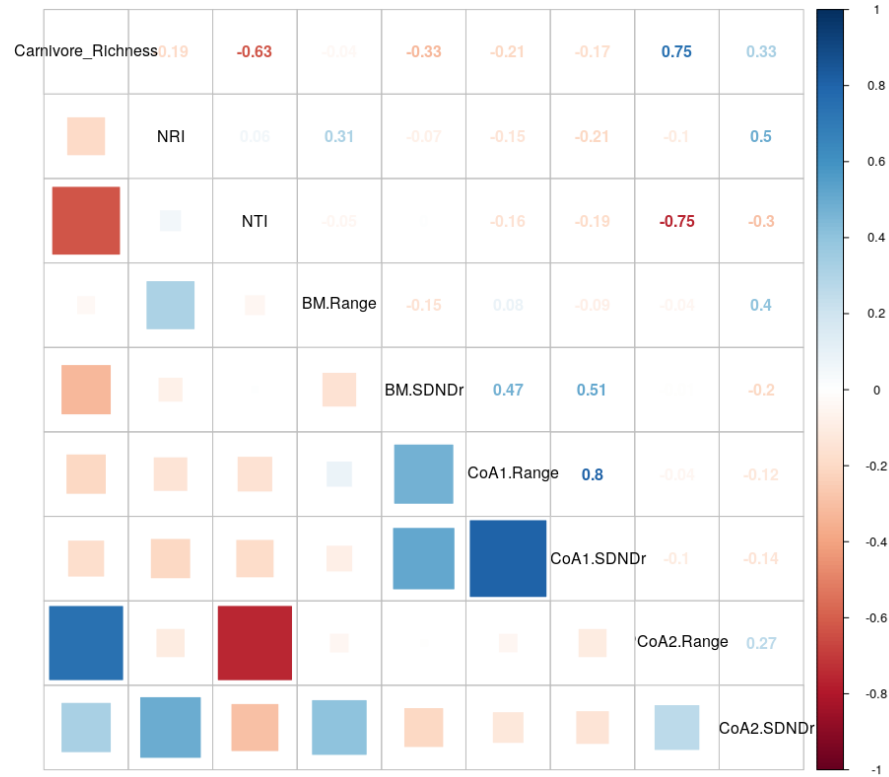


Figure B.26. Correlation matrices of multiple biodiversity metrics in relation to carnivore richness for Central and South America.

Carnivore_Richness: Carnivore community size ; *NRI*: Net Relatedness Index ; *NTI*: Nearest Taxon Index ; *BM.Range*: Body mass range ; *BM.SDNDr*: Body mass SDNDr (standard deviation of neighbor distance divided by the overall range) ; *PCoA1.Range* and *PCoA2.Range*: Principal Coordinate Axes (PCoA) 1 and 2 of diet range ; *PCoA1.SDNDr* and *PCoA2.SDNDr*: PCoA 1 and 2 of diet SDNDr.

APPENDIX C
CHAPTER THREE

C.1 Species occupancy maps

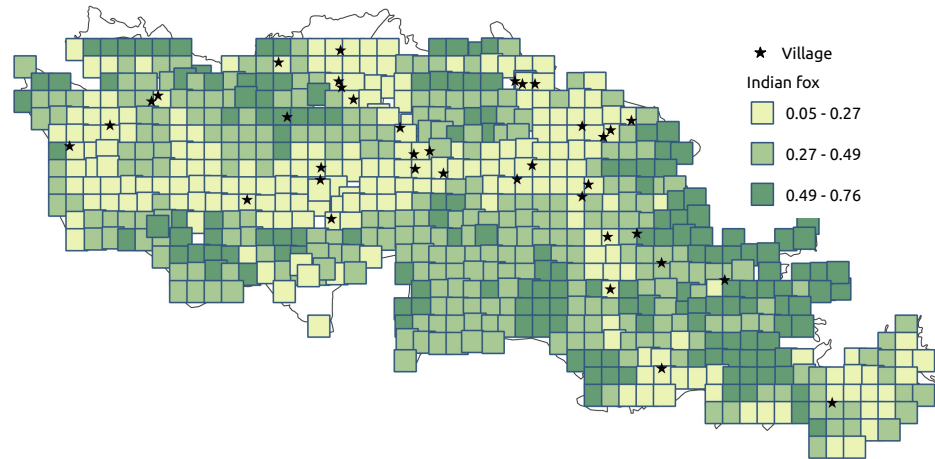


Figure C.1. Gradient map of estimated occupancy for Indian fox across the entire Banni landscape.

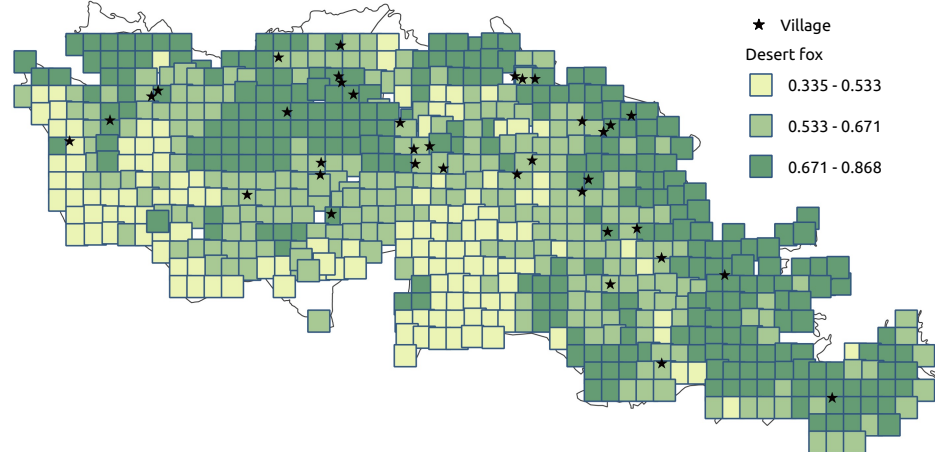


Figure C.2. Gradient map of estimated occupancy for desert fox across the entire Banni landscape.

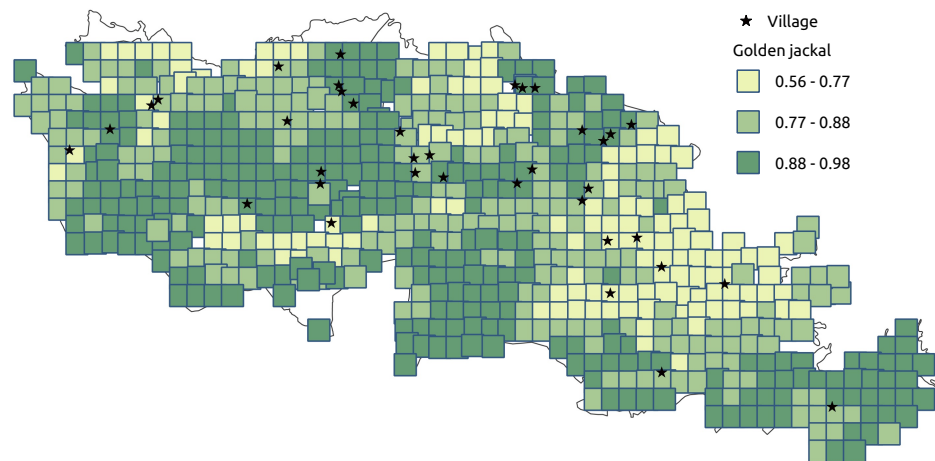


Figure C.3. Gradient map of estimated occupancy for golden jackal across the entire Banni landscape.

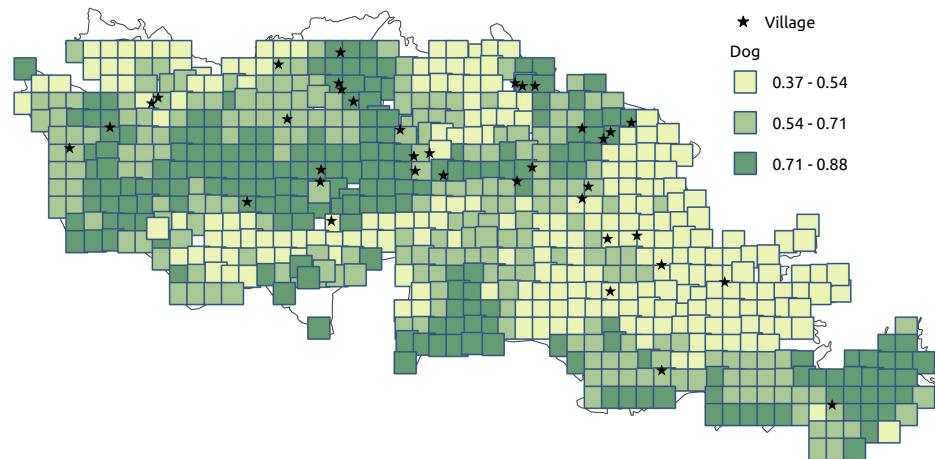


Figure C.4. Gradient map of estimated occupancy for free-ranging domestic dog across the entire Banni landscape.

C.2 Field methods and sampling protocol

C.2.1 Objectives

Set camera traps across the 2500 km² Banni grasslands landscape in northwest India with a systematic sampling study design involving 2×2 km² grids for subsequent multi-species occupancy modeling of canid species.

C.2.2 Equipment list

- GPS unit
- Binoculars
- Clipboard with data sheets
- Printed map with study grids
- Non-smudge pen/marker/pencil
- Trail cameras
- Camera mounts
- AA Batteries (8 per camera trap, 2 for GPS unit + a few extra)
- Hammer (for hammering camera mounts into the ground)
- Camera locks and keys
- Memory cards
- Card reader
- Scented lure
- Permanent markers
- Laptop with charger

- Battery chargers (if using rechargeable batteries)
- Checkerboard

C.2.3 Sampling Protocol

[illegible]

Figure C.5. Data sheet used for sampling.

C.2.3.1 General Protocol

- Each camera trap location ('site') is surveyed for 4 consecutive days ('visits') during a single season (post-monsoon, dry season)
- Each camera site is separated from the neighboring site by 2 km
- The camera traps are set up in a study design following 2×2 km² grid area



Figure C.7. The canid species considered in this study.

- After collecting the camera trap (on day 5), turn off the camera, and record date and time at which trail camera was retrieved



Figure C.8. Setting up a camera trap in Kutch.
Photo credit: Pankaj Joshi

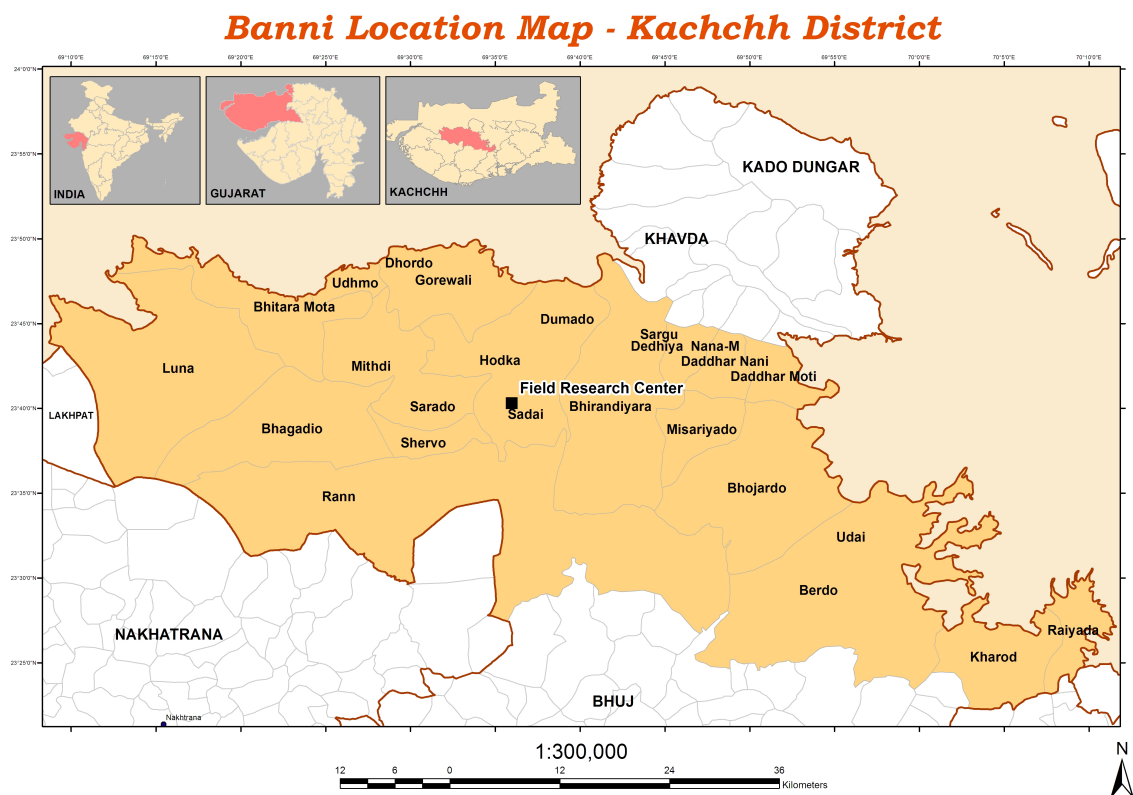


Figure C.9. Map of the Banni region.
Source: K-Link

APPENDIX D
CHAPTER FOUR

D.1 Field methods and sampling protocol

D.1.1 Objectives

Set camera traps across the Kasanka National Park (Zambia) with a systematic sampling study design involving 2×2 km² grids for subsequent multi-species occupancy modeling of carnivores.



Figure D.1. Equipment set up for extracting videos from the trail cameras.

D.1.2 Equipment list

- GPS unit
- Binoculars
- Clipboard with data sheets



Figure D.2. Setting up a camera trap in miombo woodland.

Photo credit: Geraldine Claire Taylor

- Printed map with study grids
- Non-smudge pen/marker/pencil
- Trail cameras
- Bicycle cable locks and keys
- Grass slasher (to clear vegetation around the camera traps)
- Canopy densiometer
- Scented lure
- External hard disk
- Ruler



Figure D.3. Camera trap set up near a waterhole.

- Permanent markers
- Trail camera straps
- Memory cards
- AA Batteries (8 per camera trap, 2 for GPS unit)
- Memory card reader
- Laptop with charger
- Battery chargers (if using rechargeable batteries)
- Small locks (number or with keys)

D.1.3 Sampling Protocol

D.1.3.1 General Protocol

- Each camera trap location ('site') is surveyed for 5 consecutive days ('visits') during a single season (dry season)
- Each camera site is separated from the neighboring site by 2 km
- The camera traps are set up in a study design following $2 \times 2 \text{ km}^2$ grid area

D.1.3.2 Field Protocol

- Navigate to site coordinates using GPS
- Hammer the camera trap into the ground (tie to a tree if available), set to record temperature, confirm required settings (date, time, name), ensure memory card is inserted, leave the camera on, and lock the trail camera's outer case
- Record grid ID, camera ID, lat/long from GPS, date set, time set, weather, habitat in the data sheet
- After collecting the camera trap (on day 6), turn off the camera, and record date and time at which trail camera was retrieved



(a) Setting up trail camera.



(b) Recording information in data sheet.

Figure D.4. Setting up camera traps and entering data with the field crew in Kasanka.

Photo credits: Geraldine Claire Taylor

[illegible]

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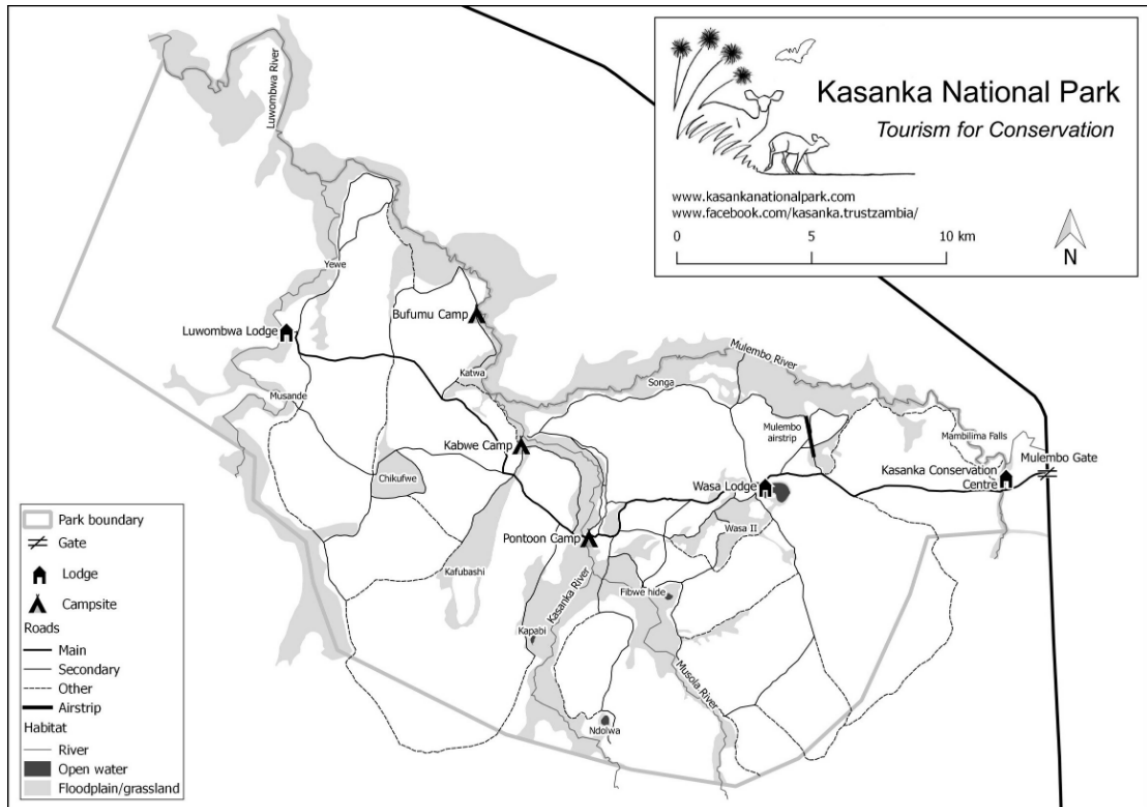


Figure D.6. Map of Kasanka National Park with roads.
Source: Kasanka Trust Ltd

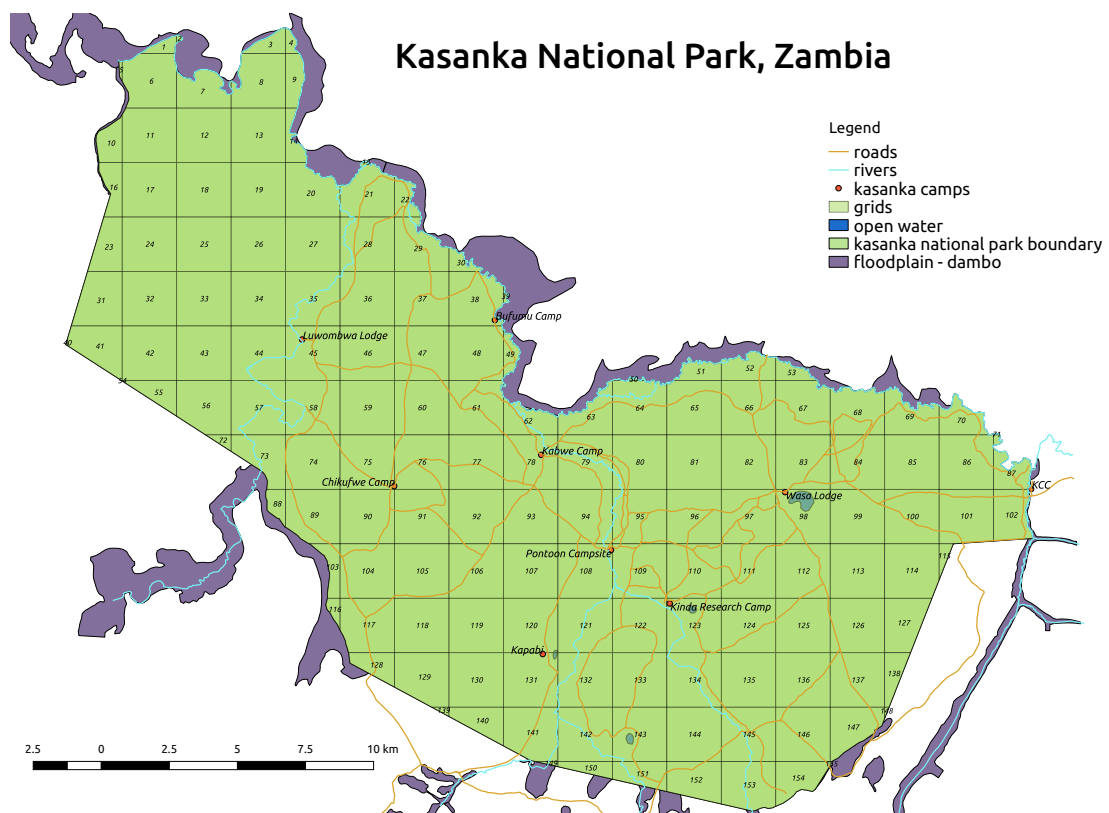


Figure D.7. Map of Kasanka National Park with grids demarcated.

BIBLIOGRAPHY

- Aiyadurai, A. & Jhala, Y.V. (2006) Foraging and habitat use by golden jackals (*Canis aureus*) in the Bhal Region, Gujarat, India. *Journal of the Bombay Natural History Society*, **103**, 5.
- Anderson, S.C., Elsen, P.R., Hughes, B.B., Tonietto, R.K., Bletz, M.C., Gill, D.A., Holgerson, M.A., Kuebbing, S.E., McDonough MacKenzie, C., Meek, M.H. *et al.* (2021) Trends in ecology and conservation over eight decades. *Frontiers in Ecology and the Environment*.
- Barnosky, A.D. (2001) Distinguishing the effects of the Red Queen and Court Jester on Miocene mammal evolution in the northern Rocky Mountains. *Journal of Vertebrate Paleontology*, **21**, 172–185.
- Basset, A. (1995) Body size-related coexistence: an approach through allometric constraints on home-range use. *Ecology*, **76**, 1027–1035.
- Battistini, R. & Richard-Vindard, G. (2013) *Biogeography and ecology in Madagascar*, volume 21. Springer Science & Business Media.
- Beaudrot, L., Ahumada, J.A., O'Brien, T., Alvarez-Loayza, P., Boekee, K., Campos-Arceiz, A., Eichberg, D., Espinosa, S., Fegraus, E., Fletcher, C. *et al.* (2016) Standardized assessment of biodiversity trends in tropical forest protected areas: the end is not in sight. *PLoS Biology*, **14**, e1002357.
- Blanchet, F.G., Cazelles, K. & Gravel, D. (2020) Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, **23**, 1050–1063.
- Bouley, P., Paulo, A., Angela, M., Du Plessis, C. & Marneweck, D.G. (2021) The successful reintroduction of African wild dogs (*Lycaon pictus*) to Gorongosa National Park, Mozambique. *PloS One*, **16**, e0249860.
- Broms, K.M., Hooten, M.B. & Fitzpatrick, R.M. (2016) Model selection and assessment for multi-species occupancy models. *Ecology*, **97**, 1759–1770.
- Brown, J.H. (1971) Mammals on mountaintops: nonequilibrium insular biogeography. *The American Naturalist*, **105**, 467–478.
- Bubnicki, J.W., Churski, M. & Kuijper, D.P.J. (2016) TRAPPER: An open source web-based application to manage camera trapping projects. *Methods in Ecology and Evolution*, **7**, 1209–1216.

- Cardillo, M. (2011) Phylogenetic structure of mammal assemblages at large geographical scales: linking phylogenetic community ecology with macroecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 2545–2553.
- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R., Sechrest, W., Orme, C.D.L. & Purvis, A. (2005) Multiple causes of high extinction risk in large mammal species. *Science*, **309**, 1239–1241.
- Carroll, C. & Noss, R.F. (2021) Rewilding in the face of climate change. *Conservation Biology*, **35**, 155–167.
- Carroll, S.B. (2016) *The Serengeti rules: the quest to discover how life works and why it matters*. Princeton University Press.
- Cartagena-Matos, B., Gregório, I., Morais, M. & Ferreira, E. (2017) Trends in the extinction of carnivores in Madagascar. *Animal Biodiversity and Conservation*, **40**, 103–114.
- Caswell, H. (1982) Optimal life histories and the maximization of reproductive value: a general theorem for complex life cycles. *Ecology*, **63**, 1218–1222.
- Chambert, T., Kendall, W.L., Hines, J.E., Nichols, J.D., Pedrini, P., Waddle, J.H., Tavecchia, G., Walls, S.C. & Tenan, S. (2015) Testing hypotheses on distribution shifts and changes in phenology of imperfectly detectable species. *Methods in Ecology and Evolution*, **6**, 638–647.
- Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004) The mid-domain effect and species richness patterns: what have we learned so far? *The American Naturalist*, **163**, E1–E23.
- Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.
- Cunningham, S.J., Gardner, J.L. & Martin, R.O. (2021) Opportunity costs and the response of birds and mammals to climate warming. *Frontiers in Ecology and the Environment*.
- Davis, C.L., Rich, L.N., Farris, Z.J., Kelly, M.J., Di Bitetti, M.S., Blanco, Y.D., Albanesi, S., Farhadinia, M.S., Gholikhani, N., Hamel, S. *et al.* (2018) Ecological correlates of the spatial co-occurrence of sympatric mammalian carnivores worldwide. *Ecology Letters*, **21**, 1401–1412.
- Devarajan, K. (2020a) Banni canid dataset. Figshare. Dataset. <https://doi.org/10.6084/m9.figshare.13075097.v1>.
- Devarajan, K. (2020b) Canid MSOM JAGS model and output. Figshare. Dataset. <https://doi.org/10.6084/m9.figshare.13089140.v1>.

- Devarajan, K., Morelli, T.L. & Tenan, S. (2020) Multi-species occupancy models: review, roadmap, and recommendations. *Ecography*.
- Devarajan, K. & Ramachandran, P. (2020) View eXtract aNnotate (ViXeN) media files: A project manager for multimedia data. *2020 ESA Annual Meeting (August 3-6)*. ESA.
- Devarajan, K. & Vanak, A.T. (2020) The company canids confront: Spatiotemporal partitioning at local scales facilitates carnivore coexistence at the landscape level. *bioRxiv*.
- Dorazio, R.M. (2007) On the choice of statistical models for estimating occurrence and extinction from animal surveys. *Ecology*, **88**, 2773–2782.
- Dorazio, R.M., Gotelli, N.J. & Ellison, A.M. (2011) Modern methods of estimating biodiversity from presence-absence surveys. *Biodiversity Loss in a Changing Planet*, pp. 277–302.
- Dorazio, R.M. & Royle, J.A. (2005) Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, **100**, 389–398.
- Dorazio, R.M., Royle, J.A., Söderström, B. & Glimskär, A. (2006) Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology*, **87**, 842–854.
- Dunn, R.R., Harris, N.C., Colwell, R.K., Koh, L.P. & Sodhi, N.S. (2009) The sixth mass coextinction: are most endangered species parasites and mutualists? *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3037–3045.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B. *et al.* (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–306.
- Farris, Z., Gerber, B., Karpanty, S., Murphy, A., Andrianjakarivelo, V., Ratelolahy, F. & Kelly, M. (2015) When carnivores roam: temporal patterns and overlap among Madagascar’s native and exotic carnivores. *Journal of Zoology*, **296**, 45–57.
- Farris, Z., Kelly, M., Karpanty, S. & Ratelolahy, F. (2016) Patterns of spatial co-occurrence among native and exotic carnivores in north-eastern Madagascar. *Animal Conservation*, **19**, 189–198.
- Faurby, S., Davis, M., Pedersen, R.Ø., Schowanek, S.D., Antonelli, A. & Svenning, J.C. (2018) PHYLACINE 1.2: The phylogenetic atlas of mammal macroecology. *Ecology*, **99**, 2626.
- Faurby, S. & Svenning, J.C. (2015) A species-level phylogeny of all extant and late Quaternary extinct mammals using a novel heuristic-hierarchical Bayesian approach. *Molecular Phylogenetics and Evolution*, **84**, 14–26.

- Fisher, J.T., Anholt, B., Bradbury, S., Wheatley, M. & Volpe, J.P. (2013) Spatial segregation of sympatric marten and fishers: the influence of landscapes and species-scapes. *Ecography*, **36**, 240–248.
- Fleagle, J.G. & Gilbert, C.C. (2006) The biogeography of primate evolution: the role of plate tectonics, climate and chance. *Primate Biogeography*, pp. 375–418. Springer.
- Gómez, S. & Harris, N.C. (2020) Living in the concrete jungle: carnivore spatial ecology in urban parks. *bioRxiv*.
- Garrote, G., Gil-Sánchez, J.M., McCain, E.B., de Lillo, S., Tellería, J.L. & Simón, M.Á. (2012) The effect of attractant lures in camera trapping: a case study of population estimates for the Iberian lynx (*Lynx pardinus*). *European Journal of Wildlife Research*, **58**, 881–884.
- Gaston, K.J. (2009) Geographic range limits: achieving synthesis. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1395–1406.
- Gause, G.F. *et al.* (1934) Experimental analysis of Vito Volterra’s mathematical theory of the struggle for existence. *Science*, **79**, 16–17.
- Geijzendorffer, I.R., Regan, E.C., Pereira, H.M., Brotons, L., Brummitt, N., Gavish, Y., Haase, P., Martin, C.S., Mihoub, J.B., Secades, C. *et al.* (2016) Bridging the gap between biodiversity data and policy reporting needs: An Essential Biodiversity Variables perspective. *Journal of Applied Ecology*, **53**, 1341–1350.
- Gelman, A., Rubin, D.B. *et al.* (1992) Inference from iterative simulation using multiple sequences. *Statistical Science*, **7**, 457–472.
- Genet, K.S. & Sargent, L.G. (2003) Evaluation of methods and data quality from a volunteer-based amphibian call survey. *Wildlife Society Bulletin*, pp. 703–714.
- Gerber, B.D., Karpanty, S.M. & Kelly, M.J. (2012a) Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. *Population Ecology*, **54**, 43–54.
- Gerber, B.D., Karpanty, S.M. & Randrianantenaina, J. (2012b) The impact of forest logging and fragmentation on carnivore species composition, density and occupancy in Madagascar’s rainforests. *Oryx*, **46**, 414–422.
- Gittleman, J.L. (2019) *Carnivore behavior, ecology, and evolution*. Cornell University Press.
- Gittleman, J.L., Funk, S.M., MacDonald, D.W. & Wayne, R.K. (2001) *Carnivore conservation*. Cambridge University Press Cambridge.

- Gompper, M.E., Lesmeister, D.B., Ray, J.C., Malcolm, J.R. & Kays, R. (2016) Differential habitat use or intraguild interactions: what structures a carnivore community? *PloS One*, **11**, e0146055.
- Grant, P.R. & Grant, B.R. (2014) *40 years of evolution: Darwin's finches on Daphne Major Island*. Princeton University Press.
- Guillera-Aroita, G. (2017) Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. *Ecography*, **40**, 281–295.
- Guillera-Aroita, G., Kéry, M. & Lahoz-Monfort, J.J. (2019) Inferring species richness using multispecies occupancy modeling: Estimation performance and interpretation. *Ecology and Evolution*, **9**, 780–792.
- Guillera-Aroita, G., Ridout, M.S. & Morgan, B.J. (2010) Design of occupancy studies with imperfect detection. *Methods in Ecology and Evolution*, **1**, 131–139.
- Hacker, S.D. & Gaines, S.D. (1997) Some implications of direct positive interactions for community species diversity. *Ecology*, **78**, 1990–2003.
- Hampton, S.C., Strasser, C.A., Tewksbury, J.J., Gram, W.K., Budden, A.E., Batcheller, A.L., Duke, C.S. & Porter, J.H. (2013) Big data and the future of ecology. *Frontiers in Ecology and the Environment*, **11**, 156–162.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S., Goetz, S.J., Loveland, T.R. *et al.* (2013) High-resolution global maps of 21st-century forest cover change. *Science*, **342**, 850–853.
- Hanson, J.O. (2020) *wdpar: Interface to the World Database on Protected Areas*. R package version 1.0.6.
- Hardin, G. (1960) The competitive exclusion principle. *Science*, **131**, 1292–1297.
- Herrera, J.P. (2017) Prioritizing protected areas in Madagascar for lemur diversity using a multidimensional perspective. *Biological Conservation*, **207**, 1–8.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, **25**, 1965–1978.
- Hines, G., Swanson, A., Kosmala, M. & Lintott, C.J. (2015) Aggregating user input in ecology citizen science projects. *Innovative Applications of Artificial Intelligence*, pp. 3975–3980.
- Holt, R.D., Grover, J. & Tilman, D. (1994) Simple rules for interspecific dominance in systems with exploitative and apparent competition. *The American Naturalist*, **144**, 741–771.

- Home, C., Bhatnagar, Y.V. & Vanak, A.T. (2018) Canine conundrum: domestic dogs as an invasive species and their impacts on wildlife in India. *Animal Conservation*, **21**, 275–282.
- Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography (MPB-32)*. Princeton University Press.
- Huston, M. (1979) A general hypothesis of species diversity. *The American Naturalist*, **113**, 81–101.
- Huston, M.A. (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos*, pp. 393–401.
- Hutchinson, G.E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*, **93**, 145–159.
- Hutchinson, G.E. (1961) The paradox of the plankton. *The American Naturalist*, **95**, 137–145.
- Iknayan, K.J., Tingley, M.W., Furnas, B.J. & Beissinger, S.R. (2014) Detecting diversity: emerging methods to estimate species diversity. *Trends in Ecology & Evolution*, **29**, 97–106.
- Isaac, N.J., Turvey, S.T., Collen, B., Waterman, C. & Baillie, J.E. (2007) Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PloS One*, **2**, e296.
- IUCN (2021) The IUCN Red List of Threatened Species. Version 2021-1. *see* <https://www.iucnredlist.org>.
- Ives, A.R. & Carpenter, S.R. (2007) Stability and diversity of ecosystems. *Science*, **317**, 58–62.
- Jaksić, F.M., Feinsinger, P. & Jiménez, J.E. (1993) A long-term study on the dynamics of guild structure among predatory vertebrates at a semi-arid Neotropical site. *Oikos*, pp. 87–96.
- Jarzyna, M.A. & Jetz, W. (2016) Detecting the multiple facets of biodiversity. *Trends in Ecology & Evolution*, **31**, 527–538.
- Jensen, E.L., Mooers, A.Ø., Cacccone, A. & Russello, M.A. (2016) I-HEDGE: determining the optimum complementary sets of taxa for conservation using evolutionary isolation. *PeerJ*, **4**, e2350.
- Jiménez, J., Nuñez-Arjona, J.C., Rueda, C., González, L.M., García-Domínguez, F., Muñoz-Igualada, J. & López-Bao, J.V. (2017) Estimating carnivore community structures. *Scientific Reports*, **7**, 1–10.
- Johnson, R.A. (1986) Intraspecific resource partitioning in the bumble bees *Bombus ternarius* and *B. pennsylvanicus*. *Ecology*, **67**, 133–138.

- Kamler, J.F., Ballard, W.B., Lemons, P.R. & Mote, K. (2004) Variation in mating system and group structure in two populations of swift foxes, *Vulpes velox*. *Animal Behaviour*, **68**, 83–88.
- Kamler, J.F., Stenkewitz, U., Klare, U., Jacobsen, N.F. & Macdonald, D.W. (2012) Resource partitioning among cape foxes, bat-eared foxes, and black-backed jackals in South Africa. *The Journal of Wildlife Management*, **76**, 1241–1253.
- Karanth, K.U., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R. & Kumar, N.S. (2017) Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proceedings of the Royal Society B: Biological Sciences*, **284**, 20161860.
- Karenyi, N., Nel, R., Altwegg, R. & Sink, K. (2016) Incorporating species detectability into conservation targets based on species – area relationship. *Diversity and Distributions*, **22**, 758–769.
- Kendall, W.L., Hines, J.E., Nichols, J.D. & Grant, E.H.C. (2013) Relaxing the closure assumption in occupancy models: staggered arrival and departure times. *Ecology*, **94**, 610–617.
- Kéry, M. & Schaub, M. (2012) *Bayesian Population Analysis Using WinBUGS*. Elsevier, London.
- Kéry, M. & Royle, J.A. (2015) *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1: Prelude and Static Models*. Academic Press.
- Kissling, W.D., Walls, R., Bowser, A., Jones, M.O., Kattge, J., Agosti, D., Amengual, J., Basset, A., Van Bodegom, P.M., Cornelissen, J.H. *et al.* (2018) Towards global data products of essential biodiversity variables on species traits. *Nature Ecology & Evolution*, **2**, 1531–1540.
- Kissling, W.D., Dalby, L., Fløjgaard, C., Lenoir, J., Sandel, B., Sandom, C., Trøjelsgaard, K. & Svenning, J.C. (2014) Establishing macroecological trait datasets: digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecology and Evolution*, **4**, 2913–2930.
- Kleijnen, J.P. (1998) Experimental design for sensitivity analysis, optimization, and validation of simulation models. *Handbook of Simulation*, **1998**, 173–223.
- Kraft, N.J. & Ackerly, D.D. (2010) Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological Monographs*, **80**, 401–422.
- Krishnappa, Y.S. & Turner, W.C. (2014) Software for minimalistic data management in large camera trap studies. *Ecological Informatics*, **24**, 11–16.
- Lawton, J.H. (1999) Are there general laws in ecology? *Oikos*, pp. 177–192.

- Levin, S.A. (1970) Community equilibria and stability, and an extension of the competitive exclusion principle. *The American Naturalist*, **104**, 413–423.
- Levin, S.A. (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology*, **73**, 1943–1967.
- Linden, D.W., Fuller, A.K., Royle, J.A. & Hare, M.P. (2017) Examining the occupancy–density relationship for a low-density carnivore. *Journal of Applied Ecology*, **54**, 2043–2052.
- Lindenmayer, D.B., Wood, J., McBurney, L., Blair, D. & Banks, S.C. (2015) Single large versus several small: The SLOSS debate in the context of bird responses to a variable retention logging experiment. *Forest Ecology and Management*, **339**, 1–10.
- Linnell, J.D. & Strand, O. (2000) Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity and Distributions*, **6**, 169–176.
- Linnell, J.D., Swenson, J.E. & Anderson, R. (2001) Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation*, **4**, 345–349.
- Loiseau, N., Mouquet, N., Casajus, N., Grenié, M., Guéguen, M., Maitner, B., Mouillot, D., Ostling, A., Renaud, J., Tucker, C. *et al.* (2020) Global distribution and conservation status of ecologically rare mammal and bird species. *Nature Communications*, **11**, 1–11.
- Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K. & Rodríguez-Schettino, L. (1998) Contingency and determinism in replicated adaptive radiations of island lizards. *Science*, **279**, 2115–2118.
- Losos, J.B., Leal, M., Glor, R.E., de Queiroz, K., Hertz, P.E., Schettino, L.R., Lara, A.C., Jackman, T.R. & Larson, A. (2003) Niche lability in the evolution of a Caribbean lizard community. *Nature*, **424**, 542–545.
- Loyola, R.D., De Oliveira, G., Diniz-Filho, J.A.F. & Lewinsohn, T.M. (2008) Conservation of Neotropical carnivores under different prioritization scenarios: mapping species traits to minimize conservation conflicts. *Diversity and Distributions*, **14**, 949–960.
- MacKenzie, D.I., Bailey, L.L. & Nichols, J.D. (2004) Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology*, **73**, 546–555.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.

- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L. & Hines, J.E. (2017) *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier.
- Mateo-Tomás, P., Olea, P.P., Moleón, M., Selva, N. & Sánchez-Zapata, J.A. (2017) Both rare and common species support ecosystem services in scavenger communities. *Global Ecology and Biogeography*, **26**, 1459–1470.
- May, R.M. (1974) On the theory of niche overlap. *Theoretical Population Biology*, **5**, 297–332.
- Mayor, S.J., Schneider, D.C., Schaefer, J.A. & Mahoney, S.P. (2009) Habitat selection at multiple scales. *Ecoscience*, **16**, 238–247.
- Mazel, F., Guilhaumon, F., Mouquet, N., Devictor, V., Gravel, D., Renaud, J., Cianciaruso, M.V., Loyola, R., Diniz-Filho, J.A.F., Mouillot, D. *et al.* (2014) Multi-faceted diversity–area relationships reveal global hotspots of mammalian species, trait and lineage diversity. *Global Ecology and Biogeography*, **23**, 836–847.
- Mccain, C.M. & King, S.R. (2014) Body size and activity times mediate mammalian responses to climate change. *Global Change Biology*, **20**, 1760–1769.
- McClintock, B.T., Bailey, L.L., Pollock, K.H. & Simons, T.R. (2010) Unmodeled observation error induces bias when inferring patterns and dynamics of species occurrence via aural detections. *Ecology*, **91**, 2446–2454.
- McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C. & Cushman, S.A. (2016) Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology*, **31**, 1161–1175.
- McGill, B.J. (2010) Matters of scale. *Science*, **328**, 575–576.
- McKenna, M.C. & Bell, S.K. (1997) *Classification of mammals: above the species level*. Columbia University Press.
- McKinney, W. (2015) Pandas, python data analysis library. *see <http://pandas.pydata.org>*.
- McNew, L.B. & Handel, C.M. (2015) Evaluating species richness: biased ecological inference results from spatial heterogeneity in detection probabilities. *Ecological Applications*, **25**, 1669–1680.
- Mendiratta, U., Osuri, A.M., Shetty, S.J. & Harihar, A. (2021) Mammal and bird species ranges overlap with armed conflicts and associated conservation threats. *Conservation Letters*, p. e12815.
- Menge, B.A. & Sutherland, J.P. (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist*, **130**, 730–757.

- Meyer, A. (1993) Phylogenetic relationships and evolutionary processes in East African cichlids. *Trends in Ecology and Evolution*, **8**, 279–284.
- Morcatty, T.Q., Bausch Macedo, J.C., Nekaris, K.A.I., Ni, Q., Durigan, C.C., Svensson, M.S. & Nijman, V. (2020) Illegal trade in wild cats and its link to Chinese-led development in Central and South America. *Conservation Biology*, **34**, 1525–1535.
- Morelli, T.L., Smith, A.B., Mancini, A.N., Balko, E.A., Borgerson, C., Dolch, R., Farris, Z., Federman, S., Golden, C.D., Holmes, S.M. *et al.* (2020) The fate of Madagascar’s rainforest habitat. *Nature Climate Change*, **10**, 89–96.
- Niedballa, J., Sollmann, R., Courtiol, A. & Wilting, A. (2016) camtrapR: An R package for efficient camera trap data management. *Methods in Ecology and Evolution*, **7**, 1457–1462.
- Oliphant, T.E. (2007) Python for scientific computing. *Computing in Science & Engineering*, **9**, 10–20.
- Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T. & Abrego, N. (2017) How to make more out of community data? a conceptual framework and its implementation as models and software. *Ecology Letters*, **20**, 561–576.
- Paine, R.T. (1966) Food web complexity and species diversity. *The American Naturalist*, **100**, 65–75.
- Palomares, F. & Caro, T.M. (1999) Interspecific killing among mammalian carnivores. *The American Naturalist*, **153**, 492–508.
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global ecology and biogeography*, **12**, 361–371.
- Pease, B., Pacifici, K. & Collazo, J. (2021) Survey design optimization for monitoring wildlife communities in areas managed for federally endangered species. *Animal Conservation*.
- Peck, S.L. (2004) Simulation as experiment: a philosophical reassessment for biological modeling. *Trends in Ecology & Evolution*, **19**, 530–534.
- Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R., Scholes, R.J., Bruford, M.W., Brummitt, N., Butchart, S., Cardoso, A. *et al.* (2013) Essential biodiversity variables. *Science*, **339**, 277–278.
- Peters, D.P., Bestelmeyer, B.T. & Turner, M.G. (2007) Cross-scale interactions and changing pattern–process relationships: consequences for system dynamics. *Ecosystems*, **10**, 790–796.

- Peterson, G., Allen, C.R. & Holling, C.S. (1998) Ecological resilience, biodiversity, and scale. *Ecosystems*, **1**, 6–18.
- Pimm, S.L. (2021) What is biodiversity conservation? *Ambio*, **50**, 976–980.
- Pollock, K.H. (1982) A capture-recapture design robust to unequal probability of capture. *The Journal of Wildlife Management*, **46**, 752–757.
- Pollock, L.J., Thuiller, W. & Jetz, W. (2017) Large conservation gains possible for global biodiversity facets. *Nature*, **546**, 141.
- Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O’Hara, R.B., Parris, K.M., Vesk, P.A. & McCarthy, M.A. (2014) Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, **5**, 397–406.
- Pollock, M.M., Naiman, R.J. & Hanley, T.A. (1998) Plant species richness in riparian wetlands—a test of biodiversity theory. *Ecology*, **79**, 94–105.
- Powers, S.M. & Hampton, S.E. (2019) Open science, reproducibility, and transparency in ecology. *Ecological Applications*, **29**, e01822.
- QGIS Development Team (2021) *QGIS Geographic Information System*. QGIS Association.
- R Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>. ISBN 3-900051-07-0.
- Ramachandran, P. & Devarajan, K. (2018) ViXeN: An open-source package for managing multimedia data. *Methods in Ecology and Evolution*, **9**, 785–792.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P. *et al.* (2014) Status and ecological effects of the world’s largest carnivores. *Science*, **343**.
- Rota, C.T., Ferreira, M.A., Kays, R.W., Forrester, T.D., Kalies, E.L., McShea, W.J., Parsons, A.W. & Millspaugh, J.J. (2016) A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution*, **7**, 1164–1173.
- Rota, C.T., Fletcher Jr, R.J., Dorazio, R.M. & Betts, M.G. (2009) Occupancy estimation and the closure assumption. *Journal of Applied Ecology*, **46**, 1173–1181.
- Roughgarden, J. (1974) Niche width: biogeographic patterns among Anolis lizard populations. *The American Naturalist*, **108**, 429–442.
- Rowan, J., Beaudrot, L., Franklin, J., Reed, K.E., Smail, I.E., Zamora, A. & Kamilar, J.M. (2020) Geographically divergent evolutionary and ecological legacies shape mammal biodiversity in the global tropics and subtropics. *Proceedings of the National Academy of Sciences*, **117**, 1559–1565.

- Royle, J.A., Karanth, K.U., Gopalaswamy, A.M. & Kumar, N.S. (2009) Bayesian inference in camera trapping studies for a class of spatial capture–recapture models. *Ecology*, **90**, 3233–3244.
- Royle, J.A. & Link, W.A. (2006) Generalized site occupancy models allowing for false positive and false negative errors. *Ecology*, **87**, 835–841.
- Royle, J.A. & Young, K.V. (2008) A hierarchical model for spatial capture–recapture data. *Ecology*, **89**, 2281–2289.
- RStudio Team (2018) RStudio: Integrated Development for R.
- Sale, P.F. (1977) Maintenance of high diversity in coral reef fish communities. *The American Naturalist*, **111**, 337–359.
- Schneider, D.C. (2001) The rise of the concept of scale in ecology: The concept of scale is evolving from verbal expression to quantitative expression. *BioScience*, **51**, 545–553.
- Schuetz, P., Wagner, A.P., Wagner, M.E. & Creel, S. (2013) Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation*, **158**, 301–312.
- Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009) Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 415–436.
- Shurin, J.B. (2001) Interactive effects of predation and dispersal on zooplankton communities. *Ecology*, **82**, 3404–3416.
- Sillero-Zubiri, C., Laurenson, M., Gittleman, J., Funk, S., Macdonald, D. & Wayne, R. (2001) *Carnivore conservation*. Cambridge: Cambridge University Press.
- Sillero-Zubiri, C., Hoffmann, M. & Macdonald, D.W. (2004) *Canids: foxes, wolves, jackals, and dogs: status survey and conservation action plan*. IUCN Gland, Switzerland.
- Simons, T.R., Alldredge, M.W., Pollock, K.H. & Wettroth, J.M. (2007) Experimental analysis of the auditory detection process on avian point counts. *The Auk*, **124**, 986–999.
- Smith, D.W. & Peterson, R.O. (2021) Intended and unintended consequences of wolf restoration to Yellowstone and Isle Royale National Parks. *Conservation Science and Practice*, **3**, e413.
- Sodhi, N.S., Koh, L.P., Brook, B.W. & Ng, P.K. (2004) Southeast Asian biodiversity: an impending disaster. *Trends in Ecology & Evolution*, **19**, 654–660.

- Sollmann, R., Furtado, M.M., Gardner, B., Hofer, H., Jácomo, A.T., Tôrres, N.M. & Silveira, L. (2011) Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biological Conservation*, **144**, 1017–1024.
- Sousa, W.P. (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, **60**, 1225–1239.
- Steenweg, R., Hebblewhite, M., Whittington, J. & McKelvey, K. (2019) Species-specific differences in detection and occupancy probabilities help drive ability to detect trends in occupancy. *Ecosphere*, **10**, e02639.
- Sun, C.C., Fuller, A.K. & Royle, J.A. (2019) Incorporating citizen science data in spatially explicit integrated population models. *Ecology*, p. e02777.
- Svenning, J.C., Eiserhardt, W.L., Normand, S., Ordonez, A. & Sandel, B. (2015) The influence of paleoclimate on present-day patterns in biodiversity and ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **46**, 551–572.
- Team, R.C. *et al.* (2013) R: A language and environment for statistical computing.
- Team, R. (2020) *RStudio: Integrated Development Environment for R*. RStudio, PBC., Boston, MA.
- Tenan, S., O’Hara, R.B., Hendriks, I. & Tavecchia, G. (2014) Bayesian model selection: the steepest mountain to climb. *Ecological Modelling*, **283**, 62–69.
- Thompson, D.B., Brown, J.H. & Spencer, W.D. (1991) Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. *Ecology*, **72**, 852–863.
- Thomson, R., Potgieter, G.C. & Bahaa-el din, L. (2018) Closing the gap between camera trap software development and the user community. *African Journal of Ecology*, **56**, 721–739.
- Tikhonov, G., Opedal, Ø.H., Abrego, N., Lehikoinen, A., de Jonge, M.M., Oksanen, J. & Ovaskainen, O. (2020) Joint species distribution modelling with the R-package HMSC. *Methods in Ecology and Evolution*, **11**, 442–447.
- Tilman, D. (1980) Resources: a graphical-mechanistic approach to competition and predation. *The American Naturalist*, **116**, 362–393.
- Tilman, D. (1987) The importance of the mechanisms of interspecific competition. *The American Naturalist*, **129**, 769–774.
- Tobler, M.W., Kéry, M., Hui, F.K., Guillera-Arroita, G., Knaus, P. & Sattler, T. (2019) Joint species distribution models with species correlations and imperfect detection. *Ecology*, p. e02754.

- Tobler, M.W., Zúñiga Hartley, A., Carrillo-Percestequi, S.E. & Powell, G.V. (2015) Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. *Journal of Applied Ecology*, **52**, 413–421.
- Udy, K., Fritsch, M., Meyer, K.M., Grass, I., Hanß, S., Hartig, F., Kneib, T., Kreft, H., Kukunda, C.B., Pe’er, G. *et al.* (2021) Environmental heterogeneity predicts global species richness patterns better than area. *Global Ecology and Biogeography*, **30**, 842–851.
- UNEP-WCMC & IUCN (2020) *Protected Planet: The World Database on Protected Areas (WDPA)*.
- Van Rossum, G. & Drake, F.L. (2009) *Python 3 Reference Manual*. CreateSpace, Scotts Valley, CA.
- Van Rossum, G. & Drake Jr, F.L. (1995) *Python tutorial*. Centrum voor Wiskunde en Informatica Amsterdam, The Netherlands.
- Vance, R.R. (1978) Predation and resource partitioning in one predator–two prey model communities. *The American Naturalist*, **112**, 797–813.
- Virtanen, P., Gommers, R., Oliphant, T.E., Haberland, M., Reddy, T., Cournapeau, D., Burovski, E., Peterson, P., Weckesser, W., Bright, J. *et al.* (2020) SciPy 1.0: fundamental algorithms for scientific computing in Python. *Nature Methods*, **17**, 261–272.
- Waddle, J.H., Dorazio, R.M., Walls, S.C., Rice, K.G., Beauchamp, J., Schuman, M.J. & Mazzotti, F.J. (2010) A new parameterization for estimating co-occurrence of interacting species. *Ecological Applications*, **20**, 1467–1475.
- Warton, D.I., Blanchet, F.G., O’Hara, R.B., Ovaskainen, O., Taskinen, S., Walker, S.C. & Hui, F.K. (2015) So many variables: joint modeling in community ecology. *Trends in Ecology & Evolution*, **30**, 766–779.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.
- Whittaker, R.H., Levin, S.A. & Root, R.B. (1973) Niche, habitat, and ecotope. *The American Naturalist*, **107**, 321–338.
- Wickham, H. (2016) ggplot2–Elegant Graphics for Data Analysis. Springer International Publishing. Cham, Switzerland.
- Wickham, H. (2010) ggplot2: elegant graphics for data analysis. *Journal of Statistical Software*, **35**, 65–88.
- Wickham, H. & Chang, W. (2008) ggplot2: An implementation of the Grammar of Graphics. *R package version 07*, URL: <http://CRAN.R-project.org/package=ggplot2>.

- Wickham, H., Chang, W. *et al.* (2016) An implementation of the grammar of graphics. WWW: <http://ggplot2.org>.
- Wilkinson, D.M. (1999) The disturbing history of intermediate disturbance. *Oikos*, pp. 145–147.
- Wilkinson, M.D., Dumontier, M., Aalbersberg, I.J., Appleton, G., Axton, M., Baak, A., Blomberg, N., Boiten, J.W., da Silva Santos, L.B., Bourne, P.E. *et al.* (2016) The FAIR guiding principles for scientific data management and stewardship. *Scientific Data*, **3**.
- Wolf, C. & Ripple, W.J. (2017) Range contractions of the world’s large carnivores. *Royal Society Open Science*, **4**, 170052.
- Wright, W.J., Irvine, K.M. & Rodhouse, T.J. (2016) A goodness-of-fit test for occupancy models with correlated within-season revisits. *Ecology and Evolution*, **6**, 5404–5415.
- Young, S., Rode-Margono, J. & Amin, R. (2018) Software to facilitate and streamline camera trap data management: A review. *Ecology and Evolution*, **8**, 9947–9957.
- Zipkin, E.F., DeWan, A. & Royle, A.J. (2009) Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. *Journal of Applied Ecology*, **46**, 815–822.
- Zipkin, E.F., Royle, A.J., Dawson, D.K. & Bates, S. (2010) Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation*, **143**, 479–484.
- Ziv, Y. (1998) The effect of habitat heterogeneity on species diversity patterns: a community-level approach using an object-oriented landscape simulation model (SHALOM). *Ecological Modelling*, **111**, 135–170.