Imperial College
London

Listening in on the Forest: Use of Bioacoustics to Preserve Soundscapes and Rare Species

Jenna Lawson

A thesis submitted for the degree of Doctor of Philosophy from the

Department of Life Sciences,

Imperial College London

2021

Funded by:

UKRI

Natural
Environment
Research Council

Under the supervision of

Dr. Cristina Banks-Leite (Imperial College London)

Dr. Andrew Whitworth (Osa Conservation and University of Glasgow)

Declaration of Originality

I hereby declare that all the work presented in this thesis is my own work, with the following acknowledgments:

Chapter Two

Dr. C. Banks-Leite and Dr. A. Whitworth provided support and editorial input

Chapter Three

Mr. George Rizos (Imperial College) assisted with the development of the machine learning algorithm for the Geoffroy’s Spider Monkey. I collected the data and compiled the labelled training database and Mr Rizos trained the model, which has been published as part of the Interspeech Challenge 2021.

Dr. C. Banks-Leite and Dr. A. Whitworth provided support and editorial input

Chapter Four

Dr. C. Banks-Leite and Dr. A. Whitworth provided support and editorial input

.

Copyright Declaration

Acknowledgements

First and foremost, I would like to thank my supervisor, Dr. Cristina Banks-Leite. Cristina, I came to you with a vision for my PhD, you believed in me and helped me to make it a reality. Without your support at this early stage, none of this would have been possible. Thank you for your continuous guidance, support and encouragement throughout the last four years, for pushing me to become a better scientist and especially for helping me to be more succinct in my writing! Finally, thank you for entering the world of bioacoustics with me, a new and challenging field for both of us. You have been a fantastic supervisor and I look forward to continued collaborations in the future. I would also like to thank my co-supervisor, Dr Andrew Whitworth, for supporting me whilst in the field, for your endless Osa specific knowledge and for your guidance in the writing process. I am also very grateful to the whole team at Osa Conservation, your support as a case partner helped to make this project a reality.

I would like to thank the members of my review panel, Prof. Rob Ewers and Prof. Tim Barraclough. Your insightful feedback during those early stages helped me to shape and improve my research.

A special thank you to Mr George Rizos, Mr Duncan Butler and Mr Zhuoda Han. Your specialised and technical support in training the machine learning algorithm for the spider monkey was invaluable and I am very grateful for all of your help and guidance.

Thank you to everyone at MINAE and SINAC in Costa Rica for your help with permits, ranger support and access to study sites in the national parks and fincas. A special thank you to Mr Guido Saborio Rodriguez, who has provided guidance and support from the very start. I remember our first conversation over five years ago when this project was just an idea! A big thank you to all the rangers and local people who guided me through challenging and often dangerous terrain in my quest to put up audio recorders. I would especially like to thank Marvin, Ronnie and Erlin, without your knowledge of the local area I would not have extended the network of recorders so far and wide.

Thank you to Dr. Gustavo Gutiérrez Espeleta for your support during the fieldwork process and for writing the crucial letters of support for my study visa.

Thank you to all of the landowners on the Osa Peninsula who allowed me to invade your privacy and put my recorders on your land; Terry and Katya, Cira, Derek, Danta Lodge, Luna Lodge, Lapa Rios, El Remanso, Osa Conservation and many more, without your support this project would not have been possible.

Thank you to Lana Wedmore and her amazing mother, Willie. You are my Osa mothers and a source of great friendship and support. Luna Lodge provided not just a study site, but a peaceful haven during the trying times that fieldwork brings.

Thank you to all the volunteers who helped me in the field; Suzi, Ellen, Rachel, Flora, Natalie, Claire, Will, Dana, Ellias, Nio and Mark. Your practical and moral support in the field was amazing and I will be eternally grateful for your hard work and dedication.

To all of the past and current members of cale lab, Drs. Jack Hatfield, Paula Vargas-Pellicer, Michelle Harrison, Edicson Parra and future Drs. Flavia Belloto, Elise Damstra, Ben Howes and Adam Fraser. Thank you for all of your help, support and most importantly, for your friendship, we really do have the best lab! I wish you all the luck in the world for your futures and I hope our paths collide once more.

A very special thank you to all of my fellow PhD students, Paula, Ana, Flavia, Chris, Andres, Joe, Ben, Danny, Deraj, Ceri, David, Hannah, Katie, Francis, Rachel, Jack, Lucas, Tom, Marie and Ewan. I have loved my time at Silwood and you guys made my experience complete!

Last but certainly not least, I would like to thank my family. My mum, Linda, the inspiration of my love of nature and the person who drives me yet grounds me every day. You have been my rock, my greatest source of support and my best friend. To my stepdad, Chris, thank you for your endless support and guidance, for your belief and just being and all round totally amazing person! To my dad, Dennis, thank you for your encouragement and support and to my brother, Josh, for always being there.

Main Abstract

Effective monitoring and protection of tropical ecosystems has the potential to conserve vast amounts of the earth's biodiversity. Yet logistical and technical challenges associated with species rarity, large distributions and home ranges, low detectability and inaccessibility of study sites can hinder monitoring efforts. If we are to mitigate against the threats to biodiversity and restore natural ecosystems, then we urgently need rapid and cost-effective methods to evaluate the current state of species, communities, ecosystems and the effectiveness of interventions. Here, we use passive acoustic monitoring (PAM) combined with computational approaches, as a method to effectively measure trends in biodiversity at a wide spatial scale across a biodiverse region in the tropics.

In Chapter Two we used soundscape analysis to evaluate changes in acoustic diversity across the diel cycle over a gradient of land use change. We aimed to assess if soundscape indices can reveal changes in the biological community across the diel cycle and whether loss of native forests affect acoustic diversity in tropical ecosystems. In disturbed habitats, we found a loss of the characteristic dawn and dusk peaks in the diel cycle; known as the dawn and dusk chorus. This was especially prominent in palm oil plantations and grasslands, which showed a complete loss of these peaks. This suggests that in disturbed ecosystems there is likely a loss of species diversity, a shift in species composition, where forest specialists are being replaced by disturbance tolerant species, or that there are modifications in species behaviour, reinforcing the value of native old growth forests in maintaining ecosystem functionality. This loss in dawn and dusk peaks was not apparent when analysing acoustic diversity at specific times during the diel cycle, showing that evaluating acoustic diversity at this temporal scale can be misleading, but in assessing trends across the diel cycle, we can gain a much better representation of changes to biotic communities.

In Chapter Three we determined if PAM and a newly developed automated detection and classification system was effective at retrieving information on the Geoffroy's spider monkey at a wide spatial scale. We assessed how this endangered primate responds to habitat loss and human influence across a gradient of disturbance. We found that the Geoffroy's spider monkey was absent below 80% forest cover and within 1 km of paved roads, yet was found to some extent in areas of secondary forest and near unpaved roads and buildings. The success of this methodology in the study of a vocal rare species suggests that similar rare species could be studied in the same way. Threshold values for percent forest cover and paved roads will be valuable in developing conservation strategies for the protection of this species.

In Chapter Four, we investigated the effectiveness of a sustainable use forest reserve in facilitating connectivity for the Geoffroy's Spider monkey between two National Parks. We specifically evaluated occurrence across the reserve, habitat suitability, barriers to connectivity and potential mitigation strategies to improve connectivity in the region. We found that the Golfo Dulce Forest Reserve is acting as a buffer to Corcovado National Park and is able to support populations of the Geoffroy's spider monkey, however, as occurrence was limited to the area surrounding Corcovado, it is possible that it is not facilitating connectivity as intended. Primary road and low forest cover were the most important predictors of poor habitat suitability, both acting as barriers to connectivity and potentially impeding the conservation of an endangered species. This is problematic since Piedras Blancas National Park serves as a connection between the Osa Peninsula and populations of the Geoffroy's spider monkey in other areas of Costa Rica.

In summary, we have shown how PAM, combined with computational approaches, can be used to effectively monitor trends at both fine temporal scales and wide spatial scales across a tropical ecosystem. PAM has provided an effective and rapid approach to monitor trends in biological communities across disturbance gradients, to study rare species across a challenging environment and to evaluate the effectiveness of current management interventions, overcoming many of the key logistical and technical challenges associated with biodiversity monitoring. These methods have revealed important information regarding how anthropogenic disturbance, related to land use change and human development, are threatening both species and communities, which can contribute to setting targets and developing conservation strategies for the protection of biodiversity in the Osa region and beyond.

Contents

List of Figures

List of Tables

Chapter One: Introduction

1.1. Biodiversity and Monitoring

1.1.1. Biodiversity Decline

Changes in land use and land cover due to agriculture, resource extraction and urban development are causing the loss and fragmentation of natural habitats, changing the type and amount of available land and its spatial configuration (Fahrig, 2003; Vallejos, Padial and Vitule, 2016; Arroyo-Rodríguez *et al.*, 2017b). It is well recognised that this is a major driver of biodiversity loss, as many species, communities and ecological functions rely on specific habitats, structures and environmental conditions (Rudnick et al, 2012). A recent study found that land use change and other human disturbance have had a significant effect on the reduction of biodiversity, with a loss of 13.7% of species globally and a further 41.5% predicted before 2100 (Newbold *et al.*, 2016). The availability and connectivity of natural habitats are central to sustaining viable populations of species, especially under the threat of climate change (Laurance, Carolina Useche, *et al.*, 2012; Stewart *et al.*, 2019).

Tropical forests make up just 2% of the earth's surface, yet hold over 50% of its biodiversity. As well as being the most biodiverse, tropical ecosystems are also among the most threatened in the world, mainly owing to anthropogenic disturbance. Over half of the world's tropical forests have been significantly altered and are threatened by fragmentation, logging and hunting, affecting the persistence of biodiversity (Laurance, Sayer and Cassman, 2014). Globally, we lack information on threatened species, ecosystems and the effectiveness of current management actions (Arroyo-Rodríguez and Fahrig, 2014; Browning *et al.*, 2017; Legge *et al.*, 2018; Bezanson and McNamara, 2019; Junker *et al.*, 2020), however this information gap is more apparent in tropical ecosystems (Browning *et al.*, 2017; Gibb *et al.*, 2019).

1.1.2. The Importance of Effective Monitoring

Rapid and cost-effective methods for monitoring and evaluating the current state of species, communities, ecosystems and the effectiveness of interventions are essential if we are to mitigate against anthropogenic disturbance (Stem *et al.*, 2005; Bennett *et al.*, 2018; Legge *et al.*, 2018; Dixon *et al.*, 2019; Gibb *et al.*, 2019). This information is critical for understanding what is driving changes in biodiversity, enables prioritisation of research and funding and feeds into policy frameworks for protection (Legge *et al.*, 2018). Despite decades of research, the status and trends for some of the worlds most threatened species and ecosystems are undefined and the effectiveness of our management actions remain unclear, impacting our ability to protect biodiversity (Arroyo-Rodríguez and Fahrig, 2014; Bennett *et al.*, 2018; Legge *et al.*, 2018; Dixon *et al.*, 2019; Junker *et al.*, 2020). This lack of information is often due to the logistical and technical challenges associated with species rarity, large distributions, low detectability and data collection across remote locations (Legge *et al.*, 2018). For example, there is no published literature for over 50% of primate species, with studies biased to specific, easier to access locations and more common species, impacting our ability to protect these species (Bezanson and McNamara, 2019; Junker *et al.*, 2020).

1.2. Passive Acoustic Monitoring

1.2.1. History and Application of Passive Acoustic Monitoring

Passive acoustic monitoring (PAM) in ecology involves the surveying of wildlife and ecosystems using sound recorders, where ecological data is then processed and extracted to answer questions of interest (Browning *et al.*, 2017). Ecological applications of PAM are similar to other survey methods and include abundance and density estimates, temporal or spatial trends, activity patterns, occupancy estimation and community composition (Gibb *et al.*, 2019). The field of PAM is rapidly advancing owing to the development of affordable, smaller devices, with increased storage capacity and longer battery life, which can be left unattended in the field for long periods and programmed according to specific schedules (Gibb *et al.*, 2019; Sugai *et al.*, 2019). For example, the recently developed AudioMoth is small, light, programmable and affordable, costing only $50 (Hill *et al.*, 2018). The benefits of these advancements can be seen in the exponential rise in the number of PAM studies published on terrestrial ecosystems since the 1990's (Sugai *et al.*, 2019). Despite this, terrestrial studies using PAM are currently biased towards northern temperate regions and concentrated around bat species, followed by birds, anurans and soundscapes, with the least studied groups being non-flying mammals and invertebrates and fewer studies in the tropics (<25%) (Sugai *et al.*, 2019).

1.2.2. Comparison to other Field Methods

In Chapters Three and Four, we focus on developing PAM methodology for primates. To date, most primate studies have used line transect methodology or scan sampling (van Roosmalen, 1980; Chapman, 1988; Defler, 1995; Sorensen and Fedigan, 2000; Pruetz and Leasor, 2002; Ramos-Fernandez and Ayala-Orozco, 2002; Zaldívar *et al.*, 2004; Wallace, 2005; Weghorst, 2007; Buckland *et al.*, 2010; Aquino *et al.*, 2013; Wood *et al.*, 2017). These methods are time consuming, practically challenging and require extensive person-power (Gibb *et al.*, 2019), and therefore generally, the spatial and temporal scale of studies are limited. This methodology is also invasive, especially when attempting to study species that react to human presence, meaning that we can alter the exact response that we are trying to measure simply by our presence (Penar, Magiera and Klocek, 2020). Camera trapping is receiving increasing interest because it is a relatively non-invasive method, effective for the study of elusive species and across challenging terrain (Whitworth *et al.*, 2019; Nguyen *et al.*, 2020), however, the detection space for this method is limited and installation can require specialist skills and climbing equipment for arboreal species, which adds to project expenses and practical challenges. The emerging field of PAM can overcome many of these constraints.

1.2.3. Benefits and Challenges of Passive Acoustic Monitoring

Passive Acoustic Monitoring has improved our ability to monitor landscapes at fine temporal resolutions and across large spatial scales, allowing the rapid and efficient collection of data to understand the status and trends of species and communities (Pijanowski, Farina, et al., 2011; Deichmann et al., 2018; Ross et al., 2018; Burivalova, Game and Butler, 2019; Sugai et al., 2019; Ducrettet et al., 2020). PAM shares many of the same benefits of camera trapping, acoustic sensors can be deployed in the field for long periods of time and can monitor continuously, and aside from initial deployment and collection, do not require the presence of the researcher (Kalan *et al.*, 2015; Sueur and Farina, 2015; Browning *et al.*, 2017; Gibb *et al.*, 2019). These benefits, combined with their feasibility in challenging terrain and increasing affordability of sensors, can increase the spatial-temporal extent of the study, reduce the effects of disturbance on individuals and increase the chance of detecting rarer species (Blumstein *et al.*, 2011; Mennill *et al.*, 2012; Kalan *et al.*, 2015; Sueur and Farina, 2015; Browning *et al.*, 2017; Gibb *et al.*, 2019; Sugai *et al.*, 2019; Penar, Magiera and Klocek, 2020). One major benefit of PAM when compared to camera trapping is the increased detection space, which can be hundreds of meters for PAM but just a few meters for camera trapping (Gibb *et al.*, 2019). PAM can therefore provide a favourable cost-benefit advantage when compared to traditional wildlife surveys (Wrege *et al.*, 2017; Sugai *et al.*, 2019).

Despite the benefits discussed above, PAM still faces many challenges. Firstly, larger PAM studies, and those that record at higher frequencies, have substantial data storage requirements, adding to the costs of any study (Gibb *et al.*, 2019). Secondly, whilst the costs associated with person-power may be reduced, projects must consider the initial and ongoing costs of purchasing and maintaining the recorders and associated equipment, which, for larger studies, can be substantial. However, with the development of increasingly affordable options these costs are becoming more manageable (Hill *et al.*, 2018). Thirdly, for long-term acoustic projects, ongoing redeployment of the recording units can involve significant time and economic costs. The development of affordable recorders that automatically transfer data to a central location will significantly reduce these costs (Browning *et al.*, 2017). Fourthly, as with more traditional wildlife surveys, PAM studies can still be challenging practically, with access issues and challenging terrain proving problematic. Finally, while PAM dramatically reduces the burden of collecting field data, the methods for extracting information from the recordings pose significant challenges. Large acoustic data sets are time consuming to analyse manually, often requiring automated detection and classification systems to extract sounds (Kalan *et al.*, 2015; Browning *et al.*, 2017; Gibb *et al.*, 2019). The development of these tools requires specialist skills and large labelled training datasets, which are difficult to collate, especially for rare species (Browning *et al.*, 2017). Automated systems should therefore be considered before undertaking any large-scale PAM study.

1.3. Soundscape Ecology and Acoustic Indices

1.3.1. What is Soundscape Ecology?

Soundscape ecology, or ecoacoustics, as it is also known, is a relatively new field of study, first formalised in 2011 (Pijanowski, Villanueva-Rivera, *et al.*, 2011; Sueur and Farina, 2015). Every landscape generates a diverse array of natural and anthropogenic sounds. Species that produce biotic sound collectively comprise the biophony. The geophony are those sounds originating from geophysical processes such as wind and water flow, and the anthrophony are those sounds generated from human-made objects such as vehicles. It is the combination of these sounds that is known as the soundscape (Pijanowski, Farina, *et al.*, 2011; Pijanowski, Villanueva-Rivera, *et al.*, 2011). Soundscape ecology is the study of the interaction between animals, humans and the environment and is useful for studying spatial-temporal patterns, interactions between different components of the soundscape and for ecosystem monitoring (Pijanowski et al, 2011). While soundscape ecology is used across all fields, ecoacoustics is devoted to the study of solely ecological questions (Sueur and Farina, 2015).

1.3.2. Acoustic Indices: Development and Application

Analysing all of the components in a soundscape can be challenging and automated analysis is becoming essential (Towsey *et al.*, 2014). To date, over 60 acoustic indices have been developed to automate this process (Bradfer-Lawrence *et al.*, 2019). Each index measures a different part of the soundscape, including pitch, saturation and amplitude across time and frequency bands, with most indices being sensitive to the characteristics of biophony (Sueur *et al.*, 2008; Bradfer-Lawrence *et al.*, 2019), thereby providing single measures of richness, evenness and heterogeneity of biotic sounds (Sueur *et al.*, 2014). Acoustic indices offer the potential to rapidly analyse acoustic datasets at wide temporal and spatial scales, which is beneficial for applied ecological studies and conservation management (Browning *et al.*, 2017; Bradfer-Lawrence *et al.*, 2019). Consequently, the number of studies using acoustic indices has grown exponentially over the last decade, providing information on the temporal and spatial variability of different soundscapes (Krause, Gage and Joo, 2011; Gottesman *et al.*, 2020; Francomano, Gottesman and Pijanowski, 2021) and the effects of anthropogenic sound and land use change on acoustic diversity (Sueur *et al.*, 2008; Tucker *et al.*, 2014; Burivalova *et al.*, 2021; Hao *et al.*, 2021; Holgate, Maggini and Fuller, 2021).

1.3.3. Acoustic Indices: Relationship with Traditional Biodiversity Metrics

Despite the growth in popularity of acoustic indices, the exact relationship between these indices and traditional biodiversity metrics remains questionable. Whilst some studies have demonstrated a correlation between index values and measures of species richness or the abundance of biological sounds in a recording (Boelman *et al.*, 2007; Sueur *et al.*, 2008; Joo, Gage and Kasten, 2011; Fairbrass *et al.*, 2017; Mammides *et al.*, 2017; Buxton, McKenna, *et al.*, 2018; Eldridge *et al.*, 2018; Bradfer-

Lawrence *et al.*, 2020; Smith *et al.*, 2020; Dröge *et al.*, 2021; Holgate, Maggini and Fuller, 2021) there is some inconsistency between results, with studies failing to find existing differences between landscapes (Mammides *et al.*, 2017; Ng, Butler and Woods, 2018) and others reporting opposing results using the same index (Bradfer-Lawrence *et al.*, 2019).

1.3.4. Acoustic Indices: Disadvantages

It is the inconsistencies in findings that generates the main disadvantages of using acoustic indices: the uncertainty surrounding if and how biotic sounds relate to the indices and what aspect of diversity they are measuring. Recent literature has suggested that this is due to the lack of a standardised approach across the field, with many indices being used, variance in the spatial and temporal configuration of studies (Bradfer-Lawrence *et al.*, 2019), and the inherent differences that exist across different ecosystems and geographically (Gibb *et al.*, 2019). Many indices are also sensitive to anthropogenic sounds, limiting their use in urban environments (Fairbrass *et al.*, 2017), and to abiotic factors resulting from rain and wind and poorly understood biotic sound; which is often not accounted for (Pijanowski *et al.*, 2011). For these reasons it is essential to be cautious in our interpretation of acoustic indices and develop standardised approaches to their use (Bradfer-Lawrence *et al.*, 2019). It is also important to recognise that many species do not produce sound and therefore the species captured within the field of bioacoustics may not be representative of overall biodiversity. To the best of my knowledge this relationship has not been tested in the published literature.

1.4. Machine Learning Approaches

1.4.1. Application of Machine Learning in Passive Acoustic Monitoring

Depending on the objectives of the study, it may be preferable to monitor specific species and populations, rather than entire communities. The manual extraction of calls from large acoustic data sets is time consuming and for this reason it is common to use computational approaches to extract sounds (Kalan *et al.*, 2015; Browning *et al.*, 2017). To date, automated call classifiers have been used across a wide range of species including insects (Zilli *et al.*, 2014; Kiskin *et al.*, 2017) marine mammals (Jaramillo-Legorreta *et al.*, 2017), birds (Campos-Cerqueira and Aide, 2016; Jahn *et al.*, 2017; Znidersic *et al.*, 2021), bats (Jennings, Parsons and Pocock, 2008; Mac Aodha *et al.*, 2018), anurans (Crump and Houlahan, 2017; Lapp *et al.*, 2021) and non-flying mammals (Thompson *et al.*, 2010; Rocha *et al.*, 2015; Wrege *et al.*, 2017). Several automated analysis tools for primates have been developed across African and Asian species (Pozzi, Gamba and Giacoma, 2010; Mielke and Zuberbühler, 2013; Heinicke *et al.*, 2015; Kalan *et al.*, 2015, 2016; Spillmann *et al.*, 2015; Clink *et al.*, 2017; Dufourq *et al.*, 2021), but models for Neotropical species are lacking, with only one model created using calls from a small group of captive marmosets bred in a laboratory (Turesson *et al.*, 2016).

1.4.2. Advantages and Disadvantages of Machine Learning

Automated detection and classification systems can significantly reduce the time required for analysing acoustic datasets, providing information on presence, abundance and density of species, activity patterns, behaviour, phenology and responses to anthropogenic stressors (Kalan *et al.*, 2015; Browning *et al.*, 2017; Gibb *et al.*, 2019). Currently, the greatest barrier to the use of acoustics in ecology is the complexity of developing such computational approaches (Browning *et al.*, 2017). The creation of labelled training datasets can require extensive field work and many hours of manual analysis to find, extract and label calls for use in the training process. The subsequent development of machine learning algorithms also requires specialist knowledge and skills (Browning *et al.*, 2017). Although automated detection and classification systems have been developed for multiple species, they are currently biased to specific taxa (bats, birds and cetaceans) and geographic regions (Europe and North America) and their transferability to other datasets is questionable (Gibb *et al.*, 2019; Sugai *et al.*, 2019). The development of these approaches, especially for rare and endangered species in the tropics, are therefore considered a major gap in the field (Browning *et al.*, 2017). Classification algorithms are rarely perfect and performance is often reduced because of interference from background noise and other signals and failure to distinguish faint and distant calls (Gibb *et al.*, 2019). This means that the process is rarely fully automated, adding additional time costs to any project. Several companies have designed software with inbuilt algorithms, and, although user-friendly, they can act as a black-box in terms of analysis methods and expensive closed-source programmes further increase project costs (Gibb *et al.*, 2019). The future use of acoustics in ecology will partly depend on the development of open-source, reliable automated classifiers (Browning *et al.*, 2017).

1.5. Primates

1.5.1. The Importance of Primates

Of the 509 species of primate, 60% are threatened with extinction and 75% are declining as a result of human disturbance (Estrada *et al.*, 2017; Junker *et al.*, 2020). The conservation of primates is essential as they hold important functions in the ecosystem such as pollination and seed dispersal and, evidence suggests that local extinction can significantly alter floral structure and diversity, impacting other species that rely on the ecosystem (Chapman *et al.*, 2013; Wich and Marshall, 2016; Estrada *et al.*, 2017). In addition to their ecological benefits, primates can also have important economic benefits for local communities owing to nature tourism (Wich and Marshall, 2016). Their charismatic nature also makes them effective flagship species, helping to raise money for conservation that can protect entire ecosystems (Wich and Marshall, 2016). Despite decades of research, we still lack rapid and efficient methods to assess how primates respond to habitat changes across human-modified landscapes and the knowledge to implement conservation strategies to protect them (Estrada, 2006; Arroyo-Rodríguez and Fahrig, 2014; Junker *et al.*, 2020)

1.5.2. Ecology and Threats

Most primate species inhabit lowland moist tropical forests, yet they can also occur in tropical dry forests, montane and temperate forests, mangrove ecosystems, and even in savannahs, grasslands and deserts (Estrada *et al.*, 2017). Primates face a number of threats from habitat loss and fragmentation due to agriculture, logging, the development of urban areas and roads, mining and drilling, climate change and hunting (Wich and Marshall, 2016; Estrada *et al.*, 2017; Junker *et al.*, 2020). Whilst some species can persist in fragmented and degraded forests, those with specialist diets and forest specialists fare less well (Estrada *et al.*, 2017). The loss and fragmentation of forests can reduce population size and genetic diversity, weakening population fitness (Estrada *et al.*, 2017). The slow life histories and low reproductive rates of primates make recovery a challenge (Junker *et al.*, 2020). Primates also typically inhabit countries undergoing rapid development and growth, which further drives habitat loss, exploitation of resources and the exotic wildlife trade (Estrada *et al.*, 2017). The global demand for non-forest products and arboreal crops is driving deforestation across the tropics and expansion of these industries is predicted to significantly overlap with areas currently occupied by primates, making policies to avoid agricultural development in sensitive biodiverse regions essential (Estrada *et al.*, 2017).

1.5.3. Current Knowledge Gaps

Despite a wealth of primate studies in the literature, 75% of studies are based on Asian and African species and focus on just a small portion of the total species pool, making scientific data for the majority of primate species limited (Estrada *et al.*, 2017). Long-term monitoring studies are important for the study of primates due to their slow life histories. Owing to the short-lived nature of funding, long-term studies are rare (Junker *et al.*, 2020). Studies evaluating the response of primates to changes in habitat loss and fragmentation are mostly at the patch-scale. There is limited knowledge about how primates use the matrix or respond to heterogeneity of landscapes, which would be beneficial in designing conservation strategies (Arroyo-Rodríguez and Fahrig, 2014). In response it has been recommended that landscape scale studies are conducted (Arroyo-Rodríguez and Fahrig, 2014), however this requires extensive data collection, which, as discussed above, is expensive and can be challenging practically, especially at large spatial scales. A recent review of primate literature concluded that there is an urgent requirement for species and habitat specific knowledge on a range of threats, including habitat loss and fragmentation and climate change and an urgent need for species recovery plans (Estrada *et al.*, 2017), and it has been stated that we lack evidence-based strategies to effectively conserve primates (Estrada *et al.*, 2017; Junker *et al.*, 2020). New technology and methodologies for monitoring primates are essential to help overcome these knowledge gaps (Estrada *et al.*, 2017), and PAM could complement existing methods to bridge this gap.

1.6. The Geoffroy's Spider Monkey

1.6.1. Conservation Status and Importance

The Geoffroy's spider monkey *(Ateles geoffroyi*) is currently classified by the IUCN as Endangered and globally its population is known to be decreasing. It is estimated that this species will decline by 50% within a 45 year period (Cortes-Ortíz *et al.*, 2021). This is a cause for concern as this species has a critical function in the ecosystem. The Geoffroy's spider monkey has been found to disperse the seeds of over 150 species of tree, thereby increasing the chance of seed germination and establishment (Link and Di Fiore, 2006). Many of the dispersed seeds belong to hardwood species, which also have an important role in carbon storage (van Roosmalen, 1980; Whitworth et al., 2019).

1.6.2. Habitat and Dietary Requirements

The Geoffroy's spider monkey is found from sea level to 2200 m elevation (Zaldívar et al., 2004). They are reported to require continuous tracts of mature old growth forests to survive (van Roosmalen, 1980; Sorensen and Fedigan, 2000; Ramos-Fernández and Ayala-Orozco, 2003; Zaldívar *et al.*, 2004; Urquiza-Haas, Peres and Dolman, 2009), although they have been found to occur, albeit at lower levels, in secondary forest (Ramos-Fernández and Ayala-Orozco, 2003; Ramos-Fernandez *et al.*, 2013; Arroyo-Rodríguez *et al.*, 2017a) and forest fragments (Chaves, Stoner and Arroyo-Rodríguez, 2012; Galán-Acedo, Arroyo-Rodríguez and Chapman, 2021). For example, in Mexico, they were found at a density of 89.5/km^2 in mature forest and only 6.3/km^2 in secondary successional forests (Ramos-Fernández and Ayala-Orozco, 2003). Although not found to reside permanently in other land uses, infrequently, they have been found to use agroforestry plantations, isolated trees, and vegetation corridors for travelling and feeding (Estrada *et al.*, 2006; Estrada, Raboy and Oliveira, 2012; Arroyo-Rodríguez *et al.*, 2017a). They are mainly found in the mid and upper canopy, avoiding the lower canopy and rarely venturing to the forest floor (van Roosmalen, 1980; Weghorst, 2007).

The diet of the Geoffroy's spider monkey consists of 90% mature fruits, with the fruits of the fig family known to be particularly important (van Roosmalen, 1980; Sorensen and Fedigan, 2000; Wallace, 2008b). Their remaining diet comprises leaves, flowers and invertebrates, when fruits are less abundant (van Roosmalen, 1980; Sorensen and Fedigan, 2000; Weghorst, 2007; Felton *et al.*, 2008; Wallace, 2008b). Mainly due to their frugivorous diet, the Geoffroy's spider monkey requires larger areas of forest than other primates, with a home range of up to 4 km^2 and the ability to travel up to 4.5 km a day in search of food (Sorensen and Fedigan, 2000; Weghorst, 2007; Wallace, 2008b; Arroyo-Rodríguez *et al.*, 2017b). This means they are especially sensitive to habitat loss and fragmentation (Wallace, 2008b; Arroyo-Rodríguez *et al.*, 2017b). Ranging behaviour varies seasonally based on food and sleeping site availability, with travel being more limited during times of fruit scarcity (Wallace, 2008b). Ranging behaviour and choice of sleeping sites were also found to be based on predation risk, with the spider monkey avoiding areas of poor visibility and excessive noise (Wallace, 2008b).

In Costa Rica studies on the Geoffroy's spider monkey are limited, with most taking place in the dry forests of Santa Rosa National Park. Here, spider monkey density was positively correlated with forest age and continuity, reduced disturbance, higher fruit biomass (Sorensen and Fedigan, 2000) and the density of large mature sleeper trees (Chapman, 1989). On the Osa Peninsula, Costa Rica, one study located in Corcovado National Park, found high densities of the Geoffroy's spider monkey and no difference between use of old growth and secondary forests (Weghorst, 2007) and another, located in Pejepero wildlife refuge, characterised sleeping behaviour and its influence on other species, showcasing the importance of spider monkey latrines for biodiversity (Whitworth *et al.*, 2019).

1.6.3. Threats

The spider monkey is at risk from hunting across its range, for meat, the pet trade and in retaliatory killings. Spider monkeys have consistently been found at lower densities in areas where there is higher hunting pressure (van Roosmalen, 1980; Peres, 1990, 1997; Aquino et al., 2013; Cronin et al., 2016). For example, in Peru, spider monkey density was 70-80% lower in areas where they were hunted (Aquino *et al.*, 2013). In Costa Rica there are no formal assessments of hunting pressure, however it is known by rangers that the Geoffroy's spider monkey and other species are hunted using firearms (G.Saborio 2018, personal communication, 26 May). Due to their slow life history they are particularly slow to recover from hunting pressure and can take decades to respond to changes (Weghorst, 2007; Wich and Marshall, 2016).

Many species, especially medium-large bodied mammals, arboreal species and those who have high site fidelity or a transient nature, are vulnerable to the negative effects from roads (Coffin, 2007; Fahrig and Rytwinski, 2009; Taylor and Goldingay, 2010; da Rosa *et al.*, 2018; Pinto, Clevenger and Grilo, 2020). Whilst there are few studies looking specifically at primates, they are thought to be particularly affected by roads due to their arboreal nature, dependence on trees and sensitivity to habitat change (Asensio et al., 2017). To my knowledge only one study has addressed the effects of roads on spider monkeys (Asensio et al., 2017), finding that they avoided areas of their home range with roads and their ability to cross roads was based on the size of the opening in the canopy (Asensio *et al.*, 2017). Human population centres on the other hand appear to have mixed effects on the spider monkey. In Mexico human density was found to have no effect on spider monkey occurrence (Urquiza-Haas, Peres and Dolman, 2009) and a study in the north of Costa Rica concluded that they showed a preference for areas with less development, however this study did not separate the effects of roads, buildings or forest loss (Van Hulle and Vaughan, 2008).

1.6.4. Current Knowledge Gaps

As with other primate studies, previous studies of the Geoffroy's spider monkey have generally been limited in scale and/or coverage, with many studies focusing on just one or a few groups within a forested area (Chapman, 1987, 1989; Asensio, Schaffner and Aureli, 2012; Chaves and Stoner, 2012; Ramos-Fernandez *et al.*, 2013). Other studies have considered more individuals, however have only covered small regions of less than 10 km^2 (Luckett *et al.*, 2004; Weghorst, 2007). There have been several studies that covered larger regions, achieving a larger spatial scale, however these studies were still patch scale studies and coverage was limited to less than 50 forested sites (Sorensen and Fedigan, 2000; Boyle and Smith, 2010; Da Silva *et al.*, 2015; Galán-Acedo *et al.*, 2018; Spaan *et al.*, 2020; Galán-Acedo, Arroyo-Rodríguez and Chapman, 2021). It is therefore rare that previous studies have been at the recommended landscape scale and have achieved both high coverage and spatial scale. In addition to the lack of landscape scale studies, the Geoffroy's spider monkey experiences many of the same knowledge gaps as other primates, such as a lack of long term monitoring and large gaps in knowledge of distribution and density (Ramos-Fernández and Wallace, 2010). These knowledge gaps are partially a result of methodology constraints and the difficulties of surveying species with a high degree of fission-fusion dynamics and with large home ranges, which can be aided with new technologies (Spaan *et al.*, 2019).

1.7. Protected areas

1.7.1. Application and Benefits

Protected areas (PAs) are considered one of the key tools for mitigating biodiversity loss through protecting species and the habitat that they need to survive (Barrows, Fleming and Allen, 2011; Watson *et al.*, 2014; Gray *et al.*, 2016). The 2020 Strategic Plan for Biodiversity called for the protection of 17% of terrestrial land by 2020 (CBD, 2010) and it is expected that targets for 2030 will be set at 30% (Waldron *et al.*, 2020). Studies have shown that PAs can be effective in reducing land clearing and habitat loss (Bruner *et al.*, 2001) and protecting species, with higher levels of biodiversity found inside PAs than outside (Butchart *et al.*, 2012; Gray *et al.*, 2016; Geldmann *et al.*, 2019).

1.7.2. Protected Areas Under Threat

As the human population continues to expand and funding for management of PAs decreases, PAs are becoming increasingly threatened by habitat loss, illegal logging and hunting (Chazdon *et al.*, 2009; Laurance, Sayer and Cassman, 2014). As a consequence of habitat loss in the surrounding area, many are also isolated in a matrix of disturbed land (Chazdon *et al.*, 2009; Laurance, Sayer and Cassman, 2014). The effectiveness of PAs in protecting ecosystems and wildlife globally are questionable, and it is thought that as little as 20% of PAs are under effective protection (Laurance *et al.*, 2012; Watson *et al.*, 2014) and over 90% of PAs are currently not connected to each other via intact land (Ward *et al.*, 2020). Monitoring the effectiveness of protected areas is therefore essential to evaluate if they are functioning as intended, to measure the impact of investments, to allow for the reallocation of resources and adaptation of practices and to track targets and promote accountability and transparency (Geldmann *et al.*, 2021). Despite the value of monitoring, only 18% of the worlds PAs have had any assessment of effectiveness and there are no global standardised assessments (UNEP-WCMC and IUCN, 2016). This has led to calls to include indicators for measurement of effectiveness in future action plans, in addition to percentage cover targets (Geldmann *et al.*, 2021).

1.7.3. Passive Acoustic Monitoring as a Method for Monitoring Protected Areas

Geldmann *et al.*, (2021) recommended that to effectively monitor PAs, site-level field data, evaluating trends in species and ecosystems, should be collected at a fine scale, using an approach that can be implemented globally. The data required to make such assessments will be time consuming and expensive to obtain, especially for rare species, in challenging environments such as the tropics and for long term studies. Researchers are therefore searching for more efficient methods to evaluate conservation strategies (Wrege *et al.*, 2017). Passive acoustic monitoring could help fill this gap through providing information on multiple species and communities. As discussed above, PAM can also overcome some of the main constrains of using traditional wildlife survey methods, thereby allowing non-invasive, long term studies at greater spatial and temporal scales (Wrege *et al.*, 2017). There are few studies using PAM to evaluate the effectiveness of PAs, however, Campos *et al.*, (2021), showed that acoustic indices were able to successfully detect trends in acoustic diversity within PAs, and PAM has successfully been used to assess gun hunting inside PAs and evaluate the effectiveness of anti-poaching patrols (Astaras *et al.*, 2020).

1.8. Study Design

The initial sampling design for this study was developed to ensure a representative, independent and unbiased network of acoustic recorders across the study site. The study area was split into a grid of 240, 4 x 4 km^2 landscapes/squares, using a system developed by the Costa Rican government to aid the implementation of scientific research (Fig. 1.1). These squares also represented the maximum home range recorded for a group of spider monkeys (Wallace, 2008a). As the initial grid system did not cover the mangrove region, we expanded it using the fishnet tool in ArcGIS 10.8. High resolution 5 x 5 m land use maps were used to calculate the percentage cover of each land use in the study area (Fig. 1.1a) (Shrestha *et al.*, 2018), and GIS layers of protected areas were used to calculate the percentage cover of each protected area in the study region. Fifty-two squares were removed from the analysis as we were only interested in the area in between and surrounding the national parks. These squares represented the area to the east of Piedras Blancas national park. All squares to the east of and not directly bordering the park were not considered. From the remaining 188 squares, each square was designated to a particular land use and protection type based on the category with the highest proportion of cover in the square. Forty-five squares were then randomly chosen using a random number generator, ensuring a representative sample of each category. We aimed to install 8-10 recording devices in each square at a minimum distance of 500m apart. This is based on a maximum distance of 200 meters for most biotic sounds, ensuring independence in the samples and avoiding pseudo replication. (Figueira *et al.*, 2015). To identify the locations to place the recorders within each square we further divided the 4 x 4 km^2 grid into smaller $500m^2$ boxes and randomly chose 10 of those boxes as the installation locations.

We maintained this sampling strategy for four of the 4 x 4 km^2 squares, installing eight recording devices in each of the four target squares, however it quickly became apparent that access issues, owing to terrain and land ownership, would make this approach too challenging. The grid system was therefore abandoned and installation sites for the recording devices were selected on feasibility of access, whilst maintaining a representative number of recorders in each category of land use and protection and ensuring uniform coverage of the study region. To ensure non-bias in sampling locations, the first recorder in each accessible area was placed by walking 500 m in a random direction and the remaining placed at a minimum of 500 m apart. To avoid bias, trails were not used where possible, however, where this was not possible, devices were placed a minimum distance of 200 m perpendicular to a trail; as indicated by GPS.

Table 1.1 shows the target number of recording devices in each land use and protection category that we aimed to install, based on the percentage cover, against the achieved number of recorders installed. Old growth forest and large areas of Corcovado National Park were typically located in areas where access was a challenge and therefore, the optimal number of recorders were not achieved. Owners of private wildlife refuges were also very receptive to having the recorders installed on their land, consequently, there were additional recorders placed in these areas in order to achieve required numbers in old growth forests. Inaccessibility of locations may have introduced some bias as they are likely to be less prone to human disturbance and may therefore have higher levels of biodiversity, possibly leading to an underrepresentation of biodiversity levels across the study. Despite this difficulty it was possible to install many recording units in areas with little to no human disturbance and the sheer number of sampling sites should help mitigate any bias. Additionally, it is likely that access to some locations was refused due to illegal hunting and logging activity occurring, also potentially biasing the results.

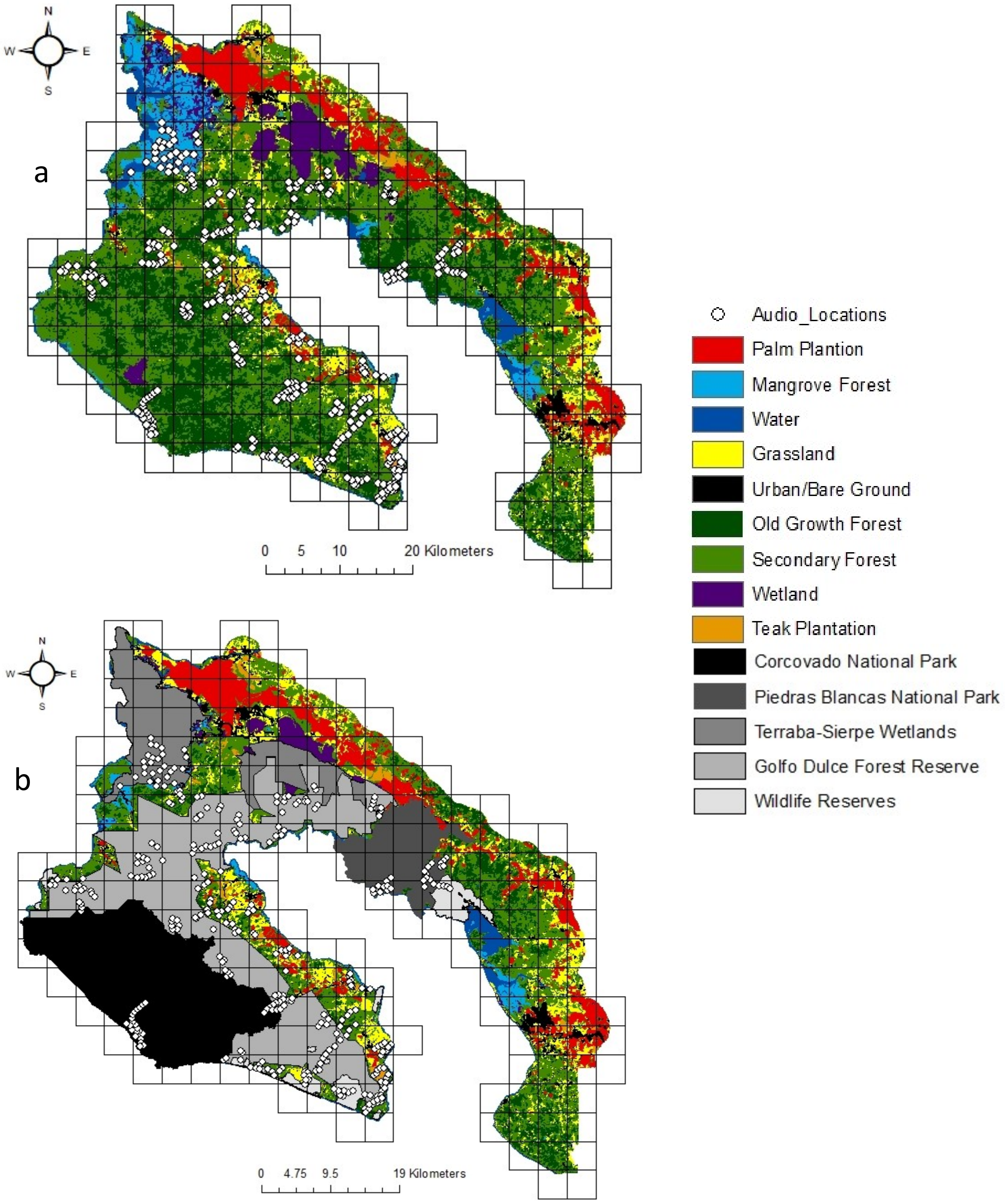


Figure 1.1.a. Land Use Map of the Osa Peninsula. Land use map showing the nine land use categories in the study site. Created at a resolution of 5 x 5 m using Landsat 5 Thematic Mapper (TM) and Landsat 8 Operational Land Imager (OLI) (Shrestha *et al.*, 2018). **b. Protected Area Map of the Osa Peninsula**. White circles represent the sample sites where each audio recorder was placed. The grid system in both maps contains 240 squares each 4 x 4 km^2.

Table 1.1. Audio Placement: Land Use. Target number of recording devices that we aimed to install in each land use category to achieve a representative number of recorders, based on the percentage (%) cover of each land use and the achieved number of recording devices that were installed.

Land Use Category	Percent Coverage (%)	Target No. of Devices	Achieved No. of Devices
Mangrove	4.8	18	28
Secondary	46.5	160	175
Agriculture	9.7	33	42
Palm	9.6	32	26
Old Growth forest	28	92	62
Teak	1.4	6	8
Total	**100**	**341**	**341**

Table 1.2. Audio Placement Protection. Target number of recording devices that we aimed to install in each protection category to achieve a representative number of recorders, based on the percentage (%) cover of each protection category and the achieved number of recording devices that were installed

Protected Area Category	Percent Coverage (%)	Target No. of Devices	Achieved No. of Devices
Corcovado National Park	21.9	71	30
Terraba-Sierpe National park	11	40	26
Piedras Blancas National Park	7.6	25	29
Golfo Dulce Forest Reserve	30.8	105	124
Private Wildlife Refuge	4	8	28
Non-protected Areas	24.8	92	104
Total	**100**	**341**	**341**

1.9. Pilot Study

Between December 2017 - May 2018 two pilot studies were conducted to test the feasibility of several methods for collecting data on the Geoffroy's spider monkey. Line transects, acoustic monitoring and monitoring with UAV's (Unmanned Aerial Vehicles) were tested as follows:

1. Line transects were trialled at five locations where it was known that spider monkeys were present, made up of old growth and secondary successional forest. The aim was to assess the feasibility and accessibility of potential sampling locations in the region. It became apparent very early on that access was going to be challenging due to topography, the density of the forest and land ownership. Cutting transects though forests was also not permitted on public or private lands and, therefore, access was restricted to pre-existing paths through the forest.
2. Several trial flights of a UAV were conducted to test whether spider monkeys could be seen in images if they were present in the canopy. The UAV was tested at two sites where spider monkeys were present, one open canopy secondary forest and one closed canopy old growth forest. On review, the spider monkeys could not be seen in any of the images taken, despite confirmation that they were present in the forest. This was due to both the density of the canopy and the height that the UAV was flown over the canopy because of inexperience and the UAV model.
3. Acoustic monitoring equipment was tested using the AudioMoth, a low-cost acoustic logger recently developed to allow high quality recordings at a fraction of the cost of current equipment on the market (Hill *et al.*, 2018). The devices were tested in eight locations, the same locations where line transects were conducted and were left up for 5-6 days each time. In between sessions, batteries were replaced and cards were cleared ready for the next recording period. The AudioMoth was placed in a bag for protection against environmental conditions, as recommended by the AudioMoth team, however, during periods of heavy rain, water leaked into the bag and the recorders stopped working. A specially designed waterproof case was

therefore used in the main study. For each day that the audio recorders were installed, attempts were made to walk line transects or to carry out timed searches, with the aim of comparing the detection capability of each method. The primary spider monkey call, the whinny, was successfully recorded on each of the audio devices, and, after analysing five recording days at one site, the spider monkeys were picked up every day. At this same site spider monkeys were only encountered on two out of five walks. Due to the success of the acoustic study it was decided that I would proceed with acoustic monitoring.

Chapter Framework

Across the field of ecology there remains a lack of information on threatened species and ecosystems and the effectiveness of current management actions (Estrada, 2006; Arroyo-Rodríguez and Fahrig, 2014; Browning *et al.*, 2017; Legge *et al.*, 2018; Bezanson and McNamara, 2019; Junker *et al.*, 2020). There is an urgent need for rapid and cost-effective methods to evaluate the current state of species, communities, ecosystems and the effectiveness of interventions. To help address this need I used passive acoustic monitoring (PAM), combined with computational approaches, to measure trends in biodiversity and the effectiveness of management actions at a wide spatial scale across a biodiverse region in the tropics.

Chapter Two

Fluctuations in the diel cycle can reveal key changes in the biological community and species behaviour (Bradfer-Lawrence *et al.*, 2019; Francomano, Gottesman and Pijanowski, 2021), yet few studies have addressed the effects of land use change on biodiversity across the diel cycle. The emergence of passive acoustic monitoring (PAM) allows us to monitor landscapes over far longer and more continuous periods, providing data on temporal variability (Francomano, Gottesman and Pijanowski, 2021). Due to limited resources, monitoring is still often conducted with long intervals between sampling periods and at a limited extent; providing only a snapshot of variables that can fluctuate greatly between samples. In this second chapter we assessed whether soundscape indices can reveal changes in the biological community across the diel cycle and if loss of native forests affect acoustic diversity across the diel cycle in tropical ecosystems. To do this we used a suite of nine acoustic indices to analyse differences in acoustic diversity across the diel cycle over a gradient of land use change. This chapter highlights the importance of using the diel cycle in soundscape studies to reveal changes in acoustic diversity and the disruption to the diel cycle in disturbed landscapes.

Chapter Three

As more land is altered by human activity and more species are threatened with extinction, it is essential that we understand how to conserve rare and threatened species across human-modified landscapes. Yet despite decades of research, we still lack rapid and efficient methods to assess how species respond to such disturbance and the knowledge to implement conservation strategies to protect them (Estrada, 2006; Arroyo-Rodríguez and Fahrig, 2014; Wrege *et al.*, 2017; Legge *et al.*, 2018; Bezanson and McNamara, 2019; Junker *et al.*, 2020). In this third chapter we determined if PAM and a newly developed automated detection and classification system, was effective at retrieving information on the Geoffroy's spider monkey across over 340 sites at a wide spatial scale. We then assessed how this endangered primate responds to habitat loss and human influence across a gradient of disturbance. Little is known about the distribution of this primate across the Osa region in Costa Rica and we addressed this for the first time at a landscape scale. This is important since the Osa Peninsula is considered a stronghold for this endangered species (Weghorst, 2007). Overall, this analysis shows how PAM, combined with machine learning approaches, can be an effective tool for the study of rare species and provides further evidence as to the sensitivity of this species to human disturbance.

Chapter Four

Protected areas (PAs) are a key method to prevent biodiversity loss and protect ecosystems, yet a large portion of PAs are not thought to be functioning as intended (Laurance, Useche, *et al.*, 2012; Watson *et al.*, 2014). Connectivity across a PA network is one of the essential aspects for sustaining viable populations of species, especially with the threat of climate change (Laurance, Carolina Useche, *et al.*, 2012; Stewart *et al.*, 2019), yet it is estimated that less than 10% of PAs are structurally connected via undisturbed land (Ward *et al.*, 2020) and any evaluation of connectedness is generally absent from reporting procedures (Ward *et al.*, 2020). Fine scale site-level field data is required to monitor protected areas, yet this information is difficult to obtain (Geldmann *et al.*, 2021) In Chapter Four, we investigated the effectiveness of a sustainable use PA in facilitating connectivity between two strictly protected PAs for an endangered forest specialist. Using PAM we assessed the occurrence of the Geoffroy's spider monkey across the PA network and used habitat suitability modelling to predict suitable habitat for the spider monkey and identify potential barriers to connectivity. Finally, we used least-cost analysis and Circuitscape analysis to determine an ideal biological corridor and highlight possible bottlenecks to connectivity. This chapter demonstrates the success of a PA in protecting forest and providing habitat for a threatened species, however, it also highlights the lack of connectivity in the region between PAs, mainly owing to a single paved road.

Chapter Two: Soundscapes Show Disruption across the Diel Cycle in Human Modified Tropical Landscapes

Abstract

Background: Fluctuations in the diel cycle, especially when compared across different land-use types, can reveal key changes in the biological community and species behaviour. Yet few studies have assessed the effects of land use change on biodiversity across the diel cycle. The emergence of passive acoustic monitoring (PAM) allows us to monitor landscapes over longer and more continuous periods, providing data on temporal variability across the diel cycle.

Methods: Using AudioMoth acoustic recorders we collected data at 170 sites on the Osa Peninsula, Costa Rica, across a gradient of land use change. Information was extracted from recordings using a suite of nine acoustic indices. Dimensionality reduction techniques reduced the indices into two indices of biotic and anthropogenic sound.

Results: In disturbed habitats, we found a loss of the characteristic dawn and dusk peaks across the diel cycle; known as the dawn and dusk chorus. Despite showing similar or higher levels of acoustic diversity when compared to native forests, palm oil plantations and grasslands sites showed a complete loss of these peaks, while teak plantations retained evidence of a small dawn and dusk chorus. Secondary forests showed slightly less pronounced peaks than did native forest. Changes in in acoustic diversity were less apparent when analysed at set points during the diel cycle.

Implications: While acoustic diversity may appear to be higher in grasslands, disturbed ecosystems did not present the usual pattern of a dawn and dusk chorus found in native forest habitats. This suggests that in disturbed ecosystems there is likely a loss of species diversity, a shift in species composition, or modifications in species behaviour, reinforcing the value of native old growth forests

in maintaining ecosystem functionality and the importance of reforestation and afforestation efforts that focus on native species rather than monoculture plantations. The lack of changes in acoustics diversity found when analysing the soundscape only at key times during the day suggests that evaluating acoustic diversity at specific times of the day is misleading, but by assessing trends across the diel cycle, we can gain a much better representation of changes to biotic communities.

2.1. Introduction

As we are facing a period of rapid biodiversity loss (Ceballos *et al.*, 2015), it is essential to monitor how ecosystems respond to both anthropogenic disturbance and management actions, so that we can effectively mitigate these threats and halt, or even reverse, biodiversity loss (Novacek and Cleland, 2001; Francomano, Gottesman and Pijanowski, 2021). It is only with the development of new technology and novel methods that we are able to effectively and efficiently monitor ecosystems at fine temporal resolutions and across large spatial scales (Deichmann *et al.*, 2018; Ross *et al.*, 2018; Burivalova, Game and Butler, 2019). The diel cycle is a complex organisation of species activity that can reveal important changes in the biological community and species behaviour resulting from anthropogenic activity (Francomano, Gottesman and Pijanowski, 2021). Yet due to limited resources, monitoring is often conducted with long intervals between sampling periods and at a limited extent; providing only a snapshot of variables that can fluctuate greatly between samples.

The activity patterns of species are generally classified into nocturnal, diurnal, crepuscular and cathemeral (Ikeda *et al.*, 2016). Animals' endogenous clocks are what control these activity patterns (Francomano, Gottesman and Pijanowski, 2021). The diel cycle is characterised by these changes in activity and the characteristic dawn and dusk peaks; known as the dawn and dusk chorus. Vocal communication, especially at these times, is generally associated with territorial, social and reproductive behaviour (Barnett and Briskie, 2007; Kleyn, da Cruz Kaizer and Passos, 2021). As proposed by the Acoustic Niche (Krause, 1987) and the Acoustic Adaptation Hypothesis (Sueur and Farina, 2015), species singing in the same temporal and spatial acoustic space, will often partition their song to minimise interference from other species and increase signal transmission (Planqué and Slabbekoorn, 2008; Luther, 2009).

The organisation of this acoustic space across the diel cycle has evolved over time and major disruptions to this system may alter species' ability to communicate (Francomano, Gottesman and Pijanowski, 2021). Effective intraspecies communication is directly linked to survival (Kleyn, da Cruz Kaizer and Passos, 2021), and inability to communicate can disrupt important behaviours such as mating, recognition, predator avoidance and territoriality, ultimately interfering with population fitness (Luther, 2009; Lee, MacGregor-Fors and Yeh, 2017). Changes across the diel cycle can also reveal differences in species behaviour and assemblage since loss of, or change in species composition, will alter activity and sounds produced (Bradfer-Lawrence *et al.*, 2019; Francomano, Gottesman and Pijanowski, 2021). Sampling at just one period in the day could lead to misrepresentation of or missing key changes in these patterns and processes. It is therefore recommended to sample at a fine temporal scale, across the diel cycle, to fully reveal differences in the biological community and species behaviour across ecosystems (Bradfer-Lawrence *et al.*, 2019; Francomano, Gottesman and Pijanowski, 2021; Hao *et al.*, 2021).

The emergence of new technology, such as passive acoustic monitoring (PAM), has improved our ability to monitor landscapes continuously, allowing the study of temporal variability at a fine scale, in a non-invasive way (Pijanowski *et al.*, 2011; Ducrettet *et al.*, 2020), paving the way for sampling across the diel cycle to be possible. Yet listening to and analysing this data can be challenging and automated analysis is becoming essential (Towsey *et al.*, 2014). Computational approaches from the field of soundscape ecology provide one method of automated analysis. Soundscape ecology, a branch of bioacoustics, is the study of the interaction between animals (biophony), humans (anthrophony) and the environment (geophony), and is useful for studying spatial-temporal patterns

(Pijanowski *et al.*, 2011). Soundscape ecology uses indices of acoustic diversity to determine measures of biotic and anthropogenic sound in the recordings across spatial and temporal scales (Pijanowski *et al.*, 2011; Sueur *et al.*, 2014). Each index measures a different part of the soundscape, including pitch, saturation and amplitude across time and frequency bands, with most indices being sensitive to the characteristics of biophony (Sueur *et al.*, 2008; Bradfer-Lawrence *et al.*, 2019), thereby providing measures of richness, evenness and heterogeneity of biotic sounds (Sueur *et al.*, 2014). By comparing acoustic diversity to diversity measured through standard sampling (e.g. point counts), a variety of indices are found to be related to the number of biological sounds in a recording, measures of species richness and abundance and functional diversity, mainly across avifauna (Boelman *et al.*, 2007; Joo, Gage and Kasten, 2011; Mammides *et al.*, 2017; Buxton, McKenna, *et al.*, 2018; Eldridge *et al.*, 2018; Bradfer-Lawrence *et al.*, 2020; Smith *et al.*, 2020; Dröge *et al.*, 2021), but also other taxa, including amphibians, orthopterans and mammals (Sueur *et al.*, 2008; Fairbrass *et al.*, 2017; Holgate, Maggini and Fuller, 2021).

Few studies have used PAM to analyse acoustic diversity across the diel cycle, with relatively little focus on biodiverse tropical regions, but those that did consistently found higher acoustic diversity during the day than at night (Villanueva-Rivera *et al.*, 2011; Pieretti *et al.*, 2015; Gage *et al.*, 2017; Bradfer-Lawrence *et al.*, 2019; Dröge *et al.*, 2021; Francomano, Gottesman and Pijanowski, 2021). Changes in the diel cycle over a gradient of land use change, however, are even less studied. Dröge *et al.,* (2021) found that some biotic index values were lower during the day in more disturbed land uses, such as agroforestry and rice fields, but remained high in forested areas. Villanueva-Rivera *et al.* (2011) analysed recordings for 15 minutes per hour and found higher acoustic biotic diversity and evenness with increasing habitat quality; especially at dawn. Spatial patterns in other studies were either not considered (Gage *et al.*, 2017; Francomano, Gottesman and Pijanowski, 2021), or no clear effects were found (Bradfer-Lawrence *et al.*, 2019).

A number of other acoustic studies have used indices of acoustic diversity to demonstrate the effects of land use change on biodiversity, most taking measures during specific points of the day. For instance, Hao *et al., (*2021) found higher biophony in areas with more complex vegetation structure and a taller, denser canopy and Burivalova *et al.,* (2021) found that biophony dropped when forested areas had been logged. In general, studies have found that biophony increases and anthrophony decreases with increasing habitat quality (Sueur *et al.*, 2008; Tucker *et al.*, 2014; Burivalova *et al.*, 2021; Hao *et al.*, 2021; Holgate, Maggini and Fuller, 2021).

Despite evidence that acoustic indices correlate to species richness and diversity, and can reveal changes in biodiversity across different land uses, there is some inconsistency in results, with some studies failing to find any differences between landscapes (Mammides *et al.*, 2017; Ng, Butler and Woods, 2018) and others reporting opposite results using the same index (Bradfer-Lawrence *et al.*, 2019). This is perhaps due to lack of a standardised approach across the field, with over 60 different indices being used across very different temporal sampling regimes (Bradfer-Lawrence *et al.*, 2019) and the inherent differences that exist across different environments and geographically (Gibb *et al.*, 2019). Indices are also sensitive to abiotic factors resulting from rain and wind and poorly understood biotic sound; which is often not accounted for (Pijanowski *et al.*, 2011).

To avoid these inconsistencies several recommendations have been proposed. As each index detects different spatial-temporal features, it is recommended to use multiple indices to represent the soundscape, especially to capture changes across land use types (Bradfer-Lawrence *et al.*, 2019; Dröge *et al.*, 2021; Hao *et al.*, 2021). It is also recommended to record continuously, for long enough to capture temporal variability, to reliably describe fine scale temporal patterns in the soundscape that can reveal important changes in the ecosystem (Bradfer-Lawrence *et al.*, 2019; Dröge *et al.*, 2021; Francomano, Gottesman and Pijanowski, 2021).

This study aims to address this research gap by using a suite of nine acoustic indices to analyse differences in acoustic diversity across the diel cycle, over a gradient of land use change, to reveal potential changes in ecosystem patterns and processes. Here we ask: 1. Can soundscape indices reveal changes in the biological community across the diel cycle. 2. Does loss of native forests affect acoustic diversity across the diel cycle in tropical ecosystems.

2.2. Methods

2.2.1. Study Site

Our study area covers 1093 km^2 on the South Pacific coast of Costa Rica. The terrain is generally low-lying, with a maximum elevation of 792 meters. Mean annual rainfall ranges from 3,000-6,500 mm and mean yearly temperature is 27 ^{o}C, with high levels of humidity throughout the year. There are two distinct seasons, wet and dry season, with the highest rainfall occurring September through December (Gilbert *et al.*, 2016).

The peninsula contains the last remnants of tropical broadleaf evergreen lowland rainforest on the Central American Pacific (Gilbert *et al.*, 2016), imbedded within a mosaic of pasture, plantations and urban centres (Figure 2.1). Due to the geology and geography of the area, the peninsula contains high levels of biodiversity and endemism (Sánchez-Azofeifa *et al.*, 2002). There are three national parks (Corcovado, Piedras Blancas and the Terrebe-Sierpe Wetlands) and one forest reserve, the Golfo Dulce. The Terreba-Sierpe wetlands (30,654 ha) were declared a national park in 1997, Corcovado (42, 560ha) in 1975, Piedras Blancas (14,019ha) in 1991 and the forest reserve (60,000ha) in 1979 (Sánchez-Azofeifa *et al.*, 2002; Osa Conservation, 2016; Gutierrez *et al.*, 2019).

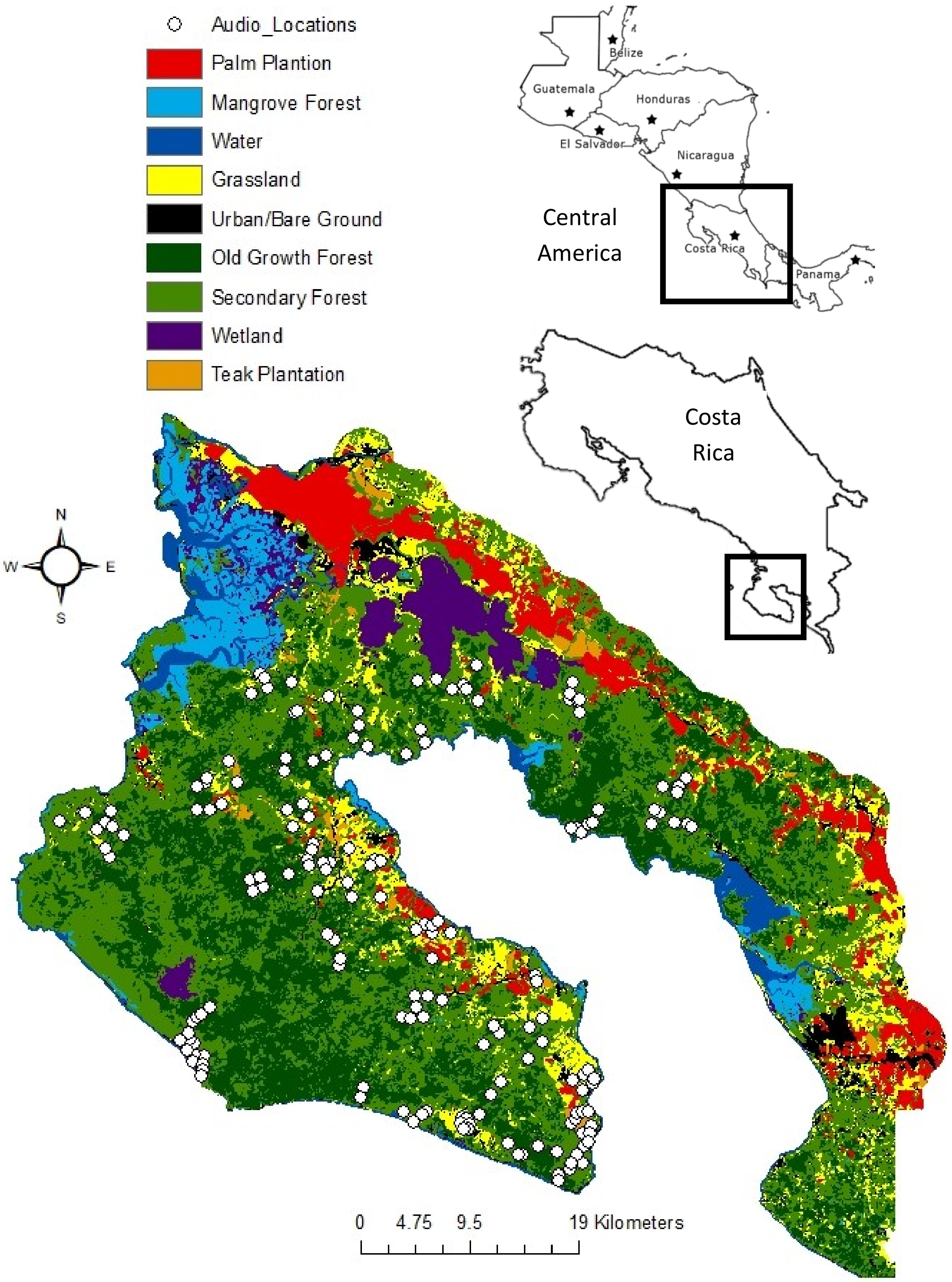


Figure 2.1. Land Use Map of the Osa Peninsula. Shows the nine land use categories, created at a scale of 5 x 5 m using Landsat 5 Thematic Mapper (TM) and Landsat 8 Operational Land Imager (OLI) (Shrestha *et al.*, 2018). White circles represent the sample sites where each audio recorder was placed.

2.2.2. Sampling Design

Land use at each site was calculated using land use maps provided by NASA, created at a scale of 5 x 5 m using Landsat 5 Thematic Mapper (TM) and Landsat 8 Operational Land Imager (OLI) (Shrestha *et al.*, 2018) (Figure 2.1). The map was classified into nine land use categories (Figure 2.1), with recordings taken in old growth and secondary forests, palm and teak plantations, mangroves and grassland sites (Figure 2.1). Wetlands, water and urban areas were excluded from the analysis due to inaccessibility.

To ensure a representative number of sampling sites were chosen across each land use category, we used a stratified sampling approach. We calculated the percentage cover of each land use category across the region and placed a representative number of recorders in each category. To ensure even coverage of the study region we selected sampling locations in a uniform distribution across the area. Due to access issues it was not possible to randomly choose sampling locations in all areas, therefore, to ensure independence among sampling locations, the first recorder in each area was placed by walking 500 m in a random direction and the remaining placed at a minimum of 500 m apart. Where possible, trails were not used to avoid bias, however, where this was not possible, devices were placed a minimum distance of 200 m perpendicular to a trail; as indicated by GPS. Non-audio data were collected for each point including GPS location, elevation and land use, to verify data from NASA land use maps. For more information on sampling design please see Chapter One.

Of the 341 data points sampled, 170 were included in the final analysis, again ensuring a representative number of points were chosen across land use, levels of protection and to ensure even coverage of the study site. Given that biotic sounds generally travel a maximum distance of 200 m (Figueira *et al.*, 2015), we used a minimum distance of 500 m between recorders, ensuring independence in the samples and avoiding pseudo-replication. Recording devices were also placed at a minimum distance of 200 m from habitat boundaries, to ensure sounds were solely from the classified habitat.

Recordings were obtained using Audio Moth devices (Open Acoustics Devices, UK). Recorders ran for seven consecutive days to allow for variability in activity across different days and to allow for sufficient sampling effort. The devices recorded on a schedule of 05:00-09:30, 14:00-18:30 and 21:00- 03:00, to ensure data were collected across the diel cycle. We recorded constantly over the recording schedule at a sample rate of 48000 kHz based on best practice guidelines (Bradfer-Lawrence *et al.*, 2019). Sampling was conducted within the dry season (December-August) to avoid extreme seasonal differences and due to restricted access to many areas of the study site during wet season. Birds generally tend to migrate to the area during the North American winter between November and March (Desante *et al.*, 2005). To avoid bias from these events we included sampling month as a random effect in our models.

2.2.3. Environmental Variables

Land use at each site was calculated using land use maps provided by NASA in ArcGIS software v.10.6. Maps were created at a scale of 5 x 5 m using Landsat 5 Thematic Mapper (TM) and Landsat 8 Operational Land Imager (OLI) (Nasa Develop, 2018) (Figure 2.1).

Time of day was used as an explanatory variable to understand changes in biotic and anthropogenic sound throughout the diel cycle. The cycle was split into 30 categories corresponding to each 30-minute period during the recording schedule.

2.2.4. Acoustic Indices

To extract acoustic information from the raw data we used a suite of nine complementary acoustic indices which, depending on study design, can be used together to provide a comprehensive picture of the soundscape (Towsey, 2018). These indices were chosen, as together, they capture the spatial-temporal variation that exists across the soundscape (Towsey, 2018), avoiding incorrect interpretations that may occur due to competing explanations or sensitivities in different environments for a particular index value (Bradfer-Lawrence *et al.*, 2019). The indices are designed to represent various components of biotic sound, except for NDSI, which calculates anthrophony. Larger index values are correlated to increased diversity, abundance, entropy or evenness of biotic sounds. Table 2.1 describes each index, for a full description of how indices are calculated refer to Towsey (2018)**.**

Table 2.1. Description of Acoustic Indices. Description of each acoustic index used, together with the reference to papers where indices were first developed and presented

Index	Measure	Reference
Acoustic Complexity Index (ACI)	A spectral index that calculates the difference between two adjacent values of amplitude. It measures fluctuations in amplitude, with larger differences and information contained indicating a more complex and variable environment	Pieretti, Farina and Morri, 2011
Temporal Entropy (ENT)	Measures the entropy of energy values of the signal waveform to provide a measure of energy concentration.	Towsey, 2018
Normalised Difference Soundscape Index (NDSI)	This index is based on the difference between anthropogenic and biotic sounds. It produces a value between 0 and 1 based on the proportion of these sounds in the recordings, with a value of 1 being pure biotic sounds	Kasten *et al.*, 2012
Events per Second (EVN)	Calculates the number of acoustic events per second above 3 dB	Towsey, 2018
Low Frequency Cover (LFC)	The number of spectrogram cells exceeding 3 dB in the low frequency band (1-1000Hz)	Towsey, 2018
Mid Frequency Cover (MFC)	The number of spectrogram cells exceeding 3 dB in the mid frequency band (1000-8000Hz)	Towsey, 2018
High Frequency Cover (HFC)	The number of spectrogram cells exceeding 3 dB in the high frequency band (8000-11025Hz).	Towsey, 2018
Cluster Count (CLS)	Calculates the number of distinct spectral clusters in the mid frequency band. This index measures the amount of internal acoustic structure within the mid frequency band.	Towsey, 2018
Three Gramm Count (ThreeG)	Derived from calculation of spectral clusters in the mid frequency band and the number of sequences that occur more than once.	Towsey, 2018

2.2.5. Statistical Analysis

2.2.5.1. Pre-processing

Geophony is known to inflate the values of some indices and reduce others (Bradfer-Lawrence *et al.*, 2019). We selected 20 sites, four from each land use, and reviewed the response of the indices to geophony in the recordings by simultaneously listening to the recordings and viewing the spectrograms and associated indices. To do this we generated Long Duration False Colour Spectrograms (LDFC Spectrograms) using Analysis Programmes software developed by Towsey *et al.,* (2018)**.** This process combines the spectral data from six indices, ACI, EVN, ENT, BGN, PMN and EVN, to visually summarise the content of 24 hours of audio recording, allowing sections of geophony, such as rain and wind, to be identified visually. We determined that geophony inflates the NDSI index and reduces indices of biotic sound. For each site, geophony was therefore isolated and removed before calculating index values. To do this we used the LDFC spectrograms to determine roughly where geophony was located across each 24-hr period and then matched these times to the associated index values to pinpoint the exact time that the index values either increased or decreased. In total 4% of data were lost to Geophony.

Using Windows PowerShell 6.0 all data were processed using Analysis Programmes software and a value calculated for each of the nine indices for each 1-minute file (Towsey *et al*, 2018). These data were then averaged across the seven days and then again for each 30-minute period.

2.2.5.2. Principal Component Analysis (PCA)

We used PCA to reduce the dimensionality of the nine acoustic indices using the *vegan* package (Oksanen *et al.*, 2019) to find the best summary of the data in the Principal Components (PC's). Eigenvalues were extracted to determine the number of PC's to retain. PC's were retained if their eigenvalue was > 1 and until approximately 70% cumulative variance was reached (James *et al.*, 2013).

To determine which combinations of indices are represented across the PC's, we used the loadings values for each index, with higher values indicating a larger effect from the index on that particular PC. PC scores were then extracted for use in regression analysis (For a more detailed explanation of PCA analysis please see Supplementary Information. 1.1).

2.2.5.3. Generalised Additive Mixed Models

Generalised additive mixed models (GAMM's) were fitted using a thin plate regression spline smoother chosen for optimum RMSE performance. REML-restricted maximum likelihood method was used for smoothness selection (Wood, 2017), and degree of smoothness was tested by fitting different basis functions and assessing fit, both visually, and using AIC. The optimum number of basis functions for PC1 GAMM was 12 ('Gam_k12'). Model AIC increased for 15 and 20 basis functions ('Gam_k15', 'Gam_k20'), but on visual inspection it was confirmed the model was overfitting to biologically irrelevant patterns. Optimum basis functions for PC2 GAMM was nine ('Gam_k9'), as chosen by the mgcv package. Increasing the basis functions to 12, 15 or 20 ('Gam_k12', 'Gam_k15', Gam_k20') did not improve model AIC (Supplementary Information 1.2- Table. 1.3) or change the smooth plots.

GAMM's were fitted using the *mgcv* package (Wood, 2017). Models were fitted with a Gaussian error structure using an identity link function. All outliers that fell outside the Inter-Quartile Range were tested. They were removed if, on inspection, they were considered abnormal.

GAMM's were used to assess how the soundscape varied across the diel cycle between land use type. We conducted two separate GAMM's, using PC1 and PC2 as the response variables, as together they captured almost 70% of the cumulative variance and both had eigenvalues of > 1 (Supplementary Information 1.1- Table. 1.1). We included a smooth term to model changes across the diel cycle and an interaction term between time and land use to test whether the effect of time was dependent on land use. The variable month, to account for temporal variation across the sampling period, reduced model AIC and significantly improved loglikelihood for PC1, and was therefore added to the final model (Supplementary Information 1.2- Table. 1.3).

Temporal autocorrelation was expected due to the nature of diel time-series analysis. We tested our model for autocorrelation of the residuals using the autocorrelation function (ACF), which calculates the degree of correlation associated with increasing lags. When there is no autocorrelation, lags should all be close to 0, when present, there will be a pattern across time lags, with values significantly different from 0. Where autocorrelation was found, we included an autocorrelation structure in the model. We tested three autocorrelation structures, auto-regressive model order 1(AR-1), continuous auto-regressive (corCAR) and auto-regressive moving average (ARMA) (Pinheiro and Bates, 2000). The best model for both PC1 and PC2, ‘Gamm_Final’, included a corCAR autocorrelation structure, producing time lags generally below the line of significance (Supplementary Information 1.2- Figure. 1.3) and improving model AIC and loglikelihood (Supplementary Information 1.2- Table. 1.3).

Due to the nested structure in the data, we also tested for spatial autocorrelation. We created a distanced based weight matrix using model residuals and sampling site coordinates. Using *gstat* package (v2.0-6; Pebesma, 2004) we then produced a variogram plot to visually determine the presence of autocorrelation. Points should roughly run along a horizontal line across the y-axis if there is no auto-correlation present. Finally, we calculated the Moran’s I statistic in *ape* package (v5.4; Paradis and Schliep, 2019). If no autocorrelation is present, then the p-value should be insignificant and the observed and expected values very similar. Moran’s I Statistic and variogram plots indicated that there was no significant spatial autocorrelation in the final models for PC1 or PC2 (Supplementary Information 1.2- Table 1.4 & Figure 1.4).

2.2.5.4. Linear Mixed Models (LMM's)

To quantify the difference in PC1 and PC2 between land use types at different points during the day, LMM's were used, assuming a gaussian distribution for normally distributed data. We fitted models in the *nlme* (Pinheiro, Bates and DebRoy, 2020) and *lme4* package (Bates, Maechler and Bolker, 2015). We chose four points, corresponding to dawn (06:30-07:00), mid-afternoon (14:00-14:30), dusk (16:30-17:00), and night (00:00-00:30). Two models were created for each time period using PC1 and PC2 as response variables. Fixed covariate was land use. Bonferroni's correction for multiple pairwise comparisons was applied to adjust p-values and reduce the risk of type I errors. Model assumptions were verified by inspecting residual plots for normality and temporal and spatial dependency. Temporal autocorrelation between months were tested using ACF plots and spatial autocorrelation using variograms and the Moran's I statistic, as detailed above. ACF plots showed no significant temporal autocorrelation across months for PC1 or PC2 (Supplementary Information 1.2- Figure 1.5). Moran's I statistic and variogram plots suggest no significant spatial autocorrelation in model residuals (Supplementary Information 1.2- Figure 1.6 & Table 1.5).

2.2.5.5. Model Selection

Model performance was evaluated using Akaike Information Criteria (AIC) to select the model with the best fit and the likelihood ratio test (LRT) to test for goodness of fit (Zuur *et al.*, 2009a). Diagnostic plots for all models indicate model assumptions are met. All statistical analysis were carried out in R 3.6.0 (R Core Team, 2020).

2.3. Results

2.3.1. Dimensionality Reduction

The variable correlation plot shows that the biotic indices are correlated, apart from the HFC index and the NDSI index, which represents anthropogenic sound (Figure. 2). From inspection of high frequency areas of the LDFC spectrograms (Supplementary Information 1.3- Figure. 1.7), we conclude that across our landscape, HFC index is dominated by anthropogenic sounds from vehicles and, to a lesser extent, by insect sounds, which is likely why we see little correlation to other biotic indices and more correlation to the NDSI index. The biotic indices are represented across PC1 (56.1% variance), with ThreeG, MFC, CLS and ENT indices showing a stronger effect and NDSI and HFC indices are represented across PC2 (12.8% variance) (Figure 2.2). From this result we can conclude that PC1 can be considered an index of biotic sound and PC2 an index of anthropogenic sound. Some caution must be taken with interpretation of PC2 since HFC does represent both anthropogenic and biotic sounds.

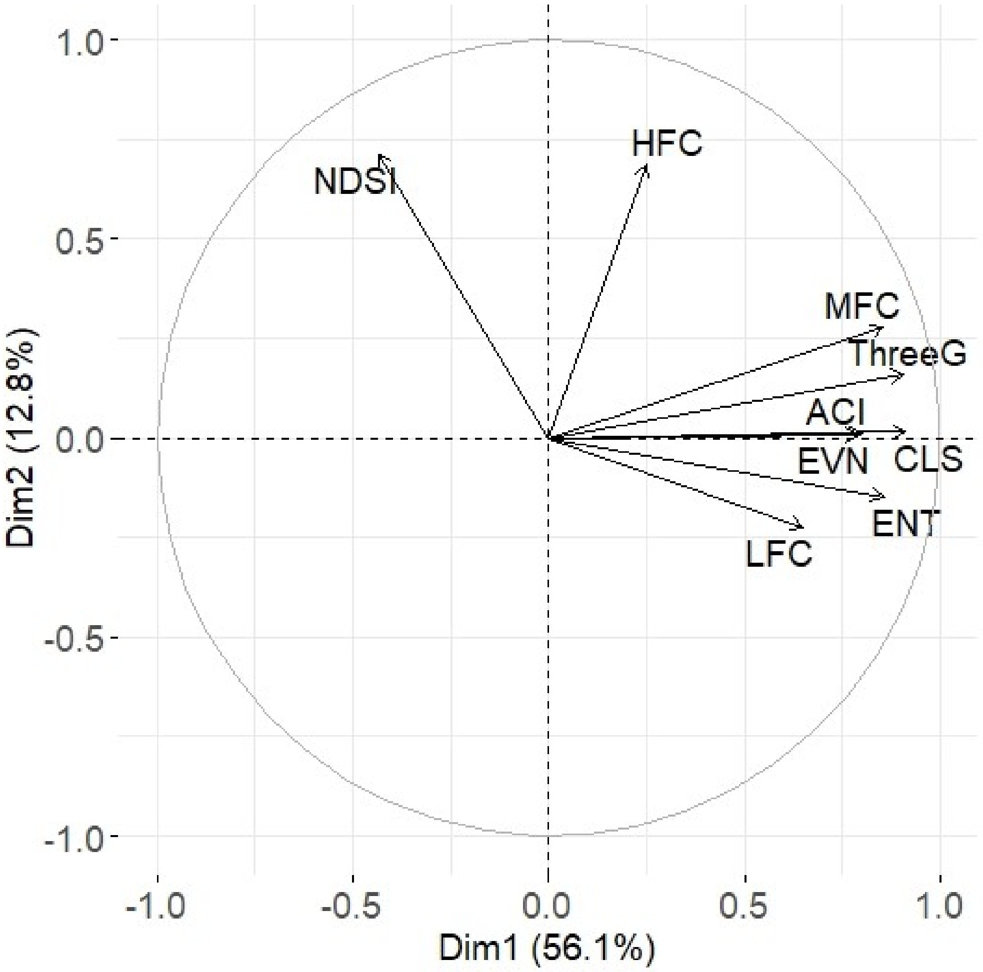


Figure 2.2. Variable Correlation Plot. Variable correlation plot showing the relationship between the indices and the PC's. Closer vectors are more highly correlated, those on opposite quadrants are negatively correlated and indices with longer vectors indicate increased strength on that PC. The x-axis represents PC1, represented by biotic indices and y-axis PC2, represented by NDSI and HFC index, with % of variance explained.

2.3.2. Changes in Acoustic Diversity Across the Diel Cycle

The best models, with time and land use as predictor variables, month as a random effect and a corCAR1 correlation structure, explained a large proportion of the variation in the data (R^2=0.544) across PC1 and less so across PC2 (R^2=0.166) (Supplementary Information 1.2- Table. 1.3). Diagnostic plots showed normality and homoscedasticity in the residuals.

2.2.2.1. Index of Biotic Sound: PC1

Effective degrees of freedom (edf) are given for each smooth term, which describe the level of structure and pattern in the relationship between the response and explanatory variables. A score of 1 is a linear fit and anything over 8 is considered to have a strong non-linear pattern (Zuur *et al.*, 2009b). Edf were higher in forested habitats and grassland, compared with palm and teak plantations, indicating that biotic sound varied more across the diel cycle in native forests and grasslands (Figure 2.3 & Supplementary Information 1.3- Table. 1.6). Although edf values are similar between old growth and secondary forests, we can see more defined dawn and dusk peaks in old growth forests (Figure 2.3). The relationship between biotic sound and time is significant in all land use types ($p<0.001$), showing that biotic sound varied non-linearly throughout the day. F-value is lower in plantations, suggesting a weaker association between time and biotic sound (Figure 2.3 & Supplementary Information 1.3- Table. 1.6).

GAMM plots of biotic sound (PC1) across the diel cycle in different land use types show a strong pattern in forested habitats, with clear dawn and dusk peaks that are more prominent in old growth than secondary forests. Grassland habitat shows much higher levels of biotic sound during the day, but loss of dawn and dusk peaks. Palm and teak plantations show a small increase in biotic sound during the day, but with less clear or non-existent dawn and dusk peaks (Figure 2.3). Whilst it is difficult to pinpoint the onset of the dawn chorus, the peak of activity is earlier in teak plantations, compared to native forests, being at 5:45 instead of 6:30.

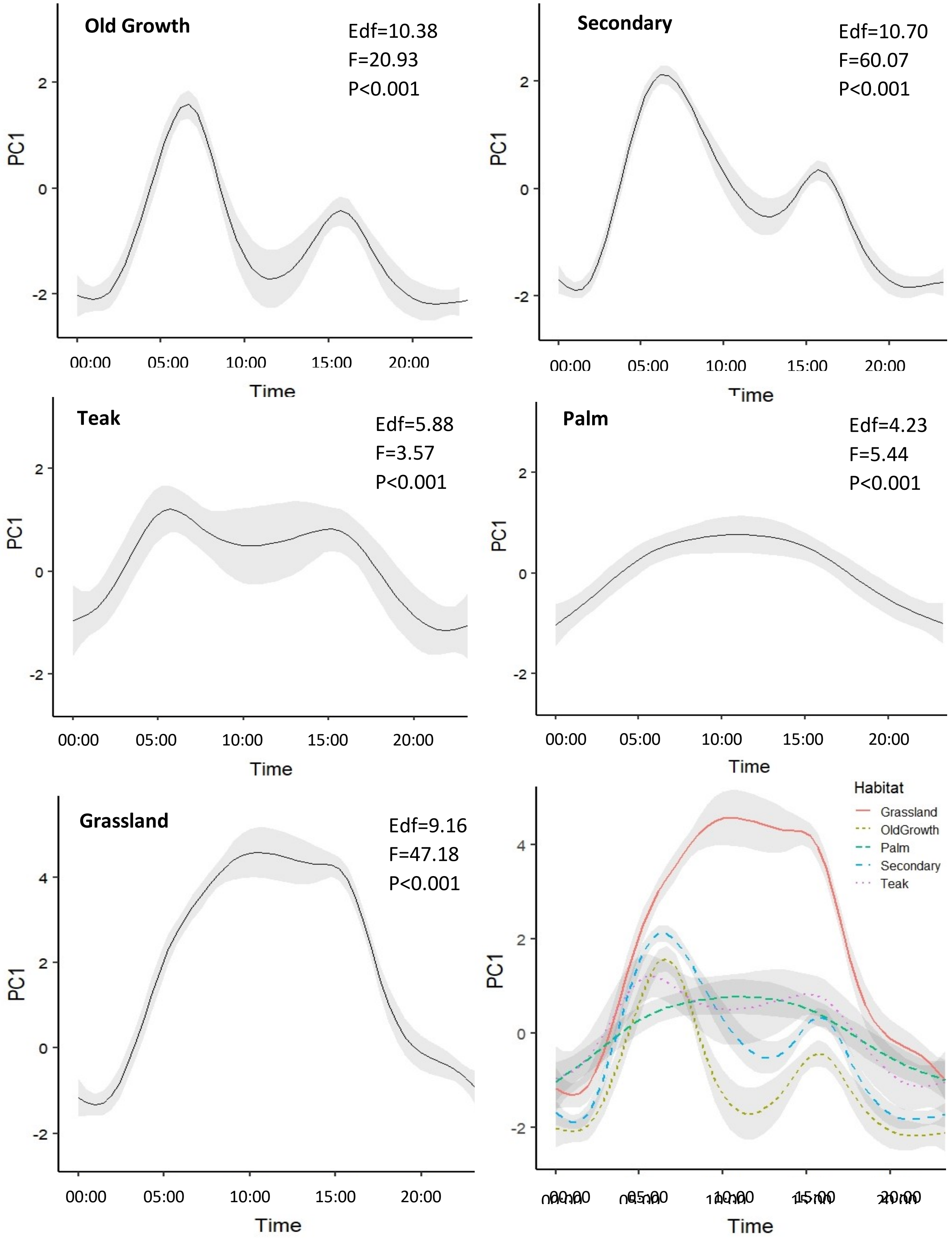


Figure 2.3 Smooth Curves for PC1. Estimated smoothing curves showing the change in PC1 across the diel cycle in different land uses. Shaded area represents 95% confidence bands. Edf, F and p values for each land use are marked on the plots. Final plot shows all land use types together.

2.2.2.2 Index of Anthropogenic Sound: PC2

Edf values were highest in grassland and secondary forest, indicating that anthropogenic sound (PC2) varied across the day more in these land use types (Figure 2.4 & Supplementary Information 1.3- Table 1.7). On visual inspection, in secondary forest, the changes in PC2 do not show any large increase in anthropogenic sound, as in grassland, the large edf values are due to the values oscillating around zero (Figure 2.4). The relationship between anthropogenic sound and time is significant in all land use types (p=<0.05), showing that anthropogenic sound varied non-linearly throughout the day. The F-value is lower in native forest habitats, suggesting a weaker association between time and anthropogenic sound in these land use types (Figure 2.4).

GAMM plots of PC2 across the diel cycle in different land use types show a large drop in PC2 during the day in palm and teak plantations and grassland, indicating increased anthropogenic sounds in these habitats. We can see a small drop in PC2 in old growth and secondary forests later in the day and although in secondary forest PC2 oscillates across the cycle, there is little meaningful biological change (Figure 2.4).

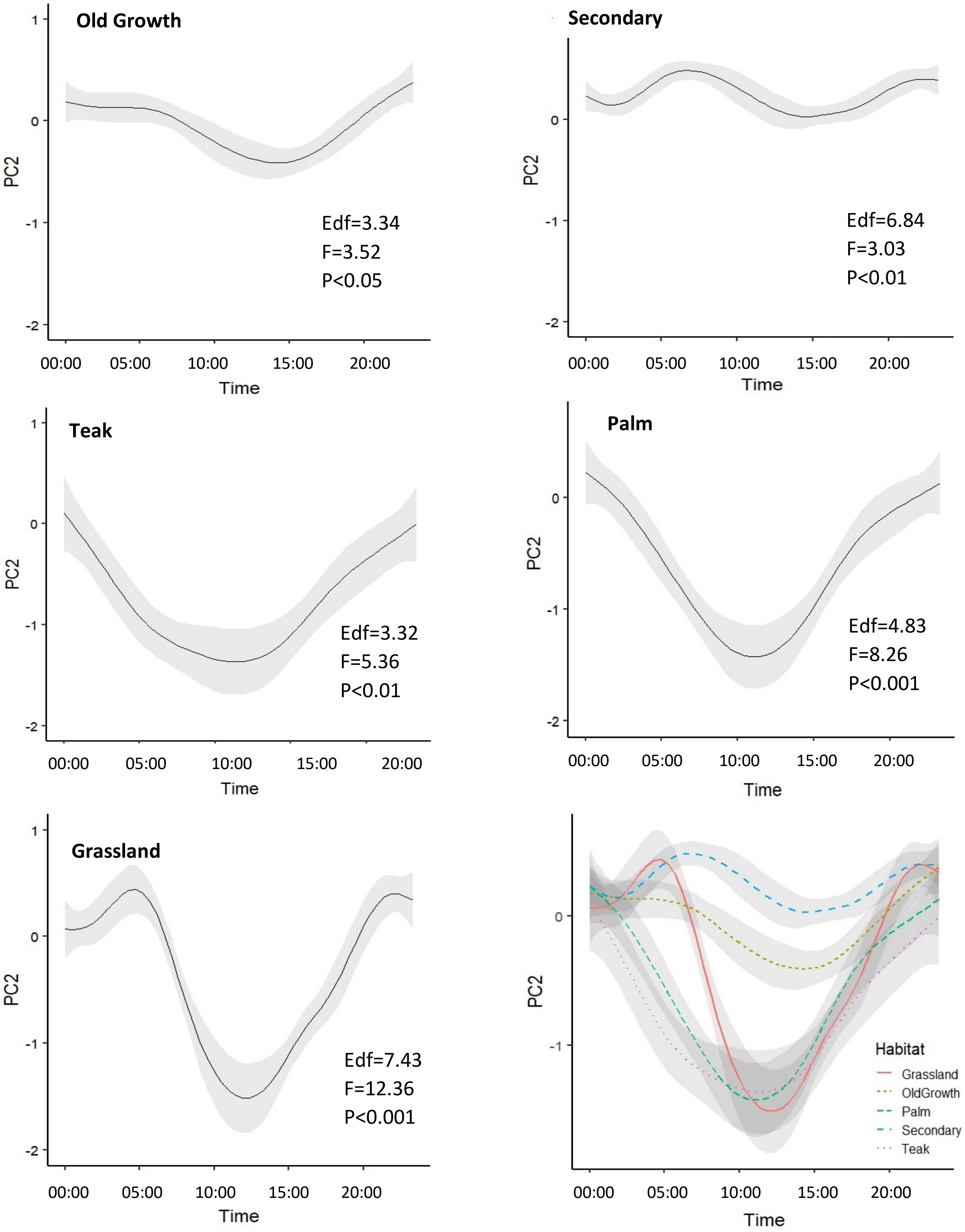


Figure 2.4 Smooth Curves for PC2. Estimated smooth curves showing the change in PC2 across the diel cycle in different land uses. Shaded area represents 95% confidence bands. Edf, F and p values for each land use are marked on the plots. Final plot shows all land use types together.

2.3.3. Changes in Acoustic Diversity at Key Times in the Diel Cycle

We then quantified the differences in biotic sound (PC1) and anthropogenic sound (PC2) between land use types at key times in the diel cycle (i.e., dawn:06:30-07:00, mid-afternoon:14:00-13:30, dusk:16:30-17:00 and night:00:00-00:30).

Acoustic biotic diversity (PC1) was significantly higher in old growth and secondary forests and grasslands at dawn, when compared to palm and teak plantations (Figure 2.5 a). During the day and at dusk, only grassland showed any significant differences, with native forests and plantations showing little difference (Figure 2.5 b & c). At night acoustic biotic diversity was significantly lower in native forests when compared to plantation forestry (Figure 2.5 d).

At dawn and during the day anthropogenic sound was higher (lower values of PC2) in disturbed land use types than native forests, however this difference was only significant between secondary forests and disturbed land use (Figure 2.5 e & f). At dusk and during the night anthropogenic sound remained constant across habitats (Figure 2.5 g & h).

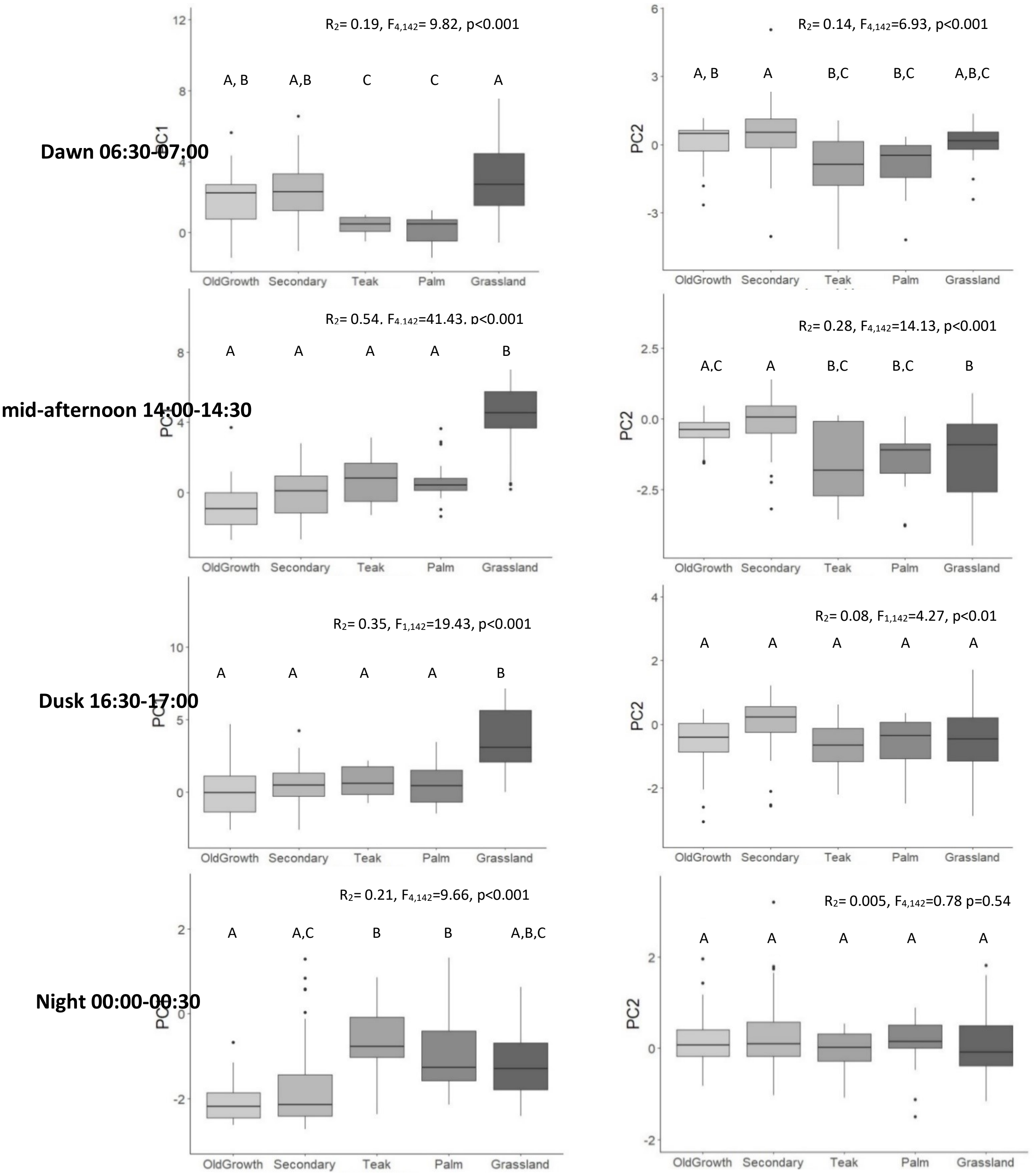


Figure 2.5. Boxplots for PC1 and PC2 at Key Points in the Diel Cycle. Boxplots showing the differences in PC1 and PC2 between land use types at key times in the diel cycle (dawn: 06:30-07:00, mid-afternoon: 14:00-13:30, dusk: 16:30-17:00 and night: 00:00 00:30). R^2, F and p values for each model are marked on the graphs. Pairwise differences between land use are indicated with letters A, B and C, where different letters represent a significant difference between land use.

2.4. Discussion

By using a soundscape approach across 170 sites, we found a loss of the characteristic dawn and dusk peaks and associated chorus in disturbed land use types. This suggests that there are changes in the biological community and species behaviour in disturbed areas, which is likely due to three main factors: loss of species diversity, changes in species composition and/or changes in acoustic behaviour; all which have important conservation and management implications.

2.4.1. Loss of Species Diversity

If reduced species diversity is driving the lost dawn and dusk chorus, it is the species that call during these times that have likely been lost. Birds make up a large portion of sounds in both the dawn and dusk chorus (Stanley *et al.*, 2016; Ducrettet *et al.*, 2020; Gil and Llusia, 2020). Amphibians generally call at dusk and during the night (Bridges, Dorcas and Montgomery, 2000; Hilje and Aide, 2012; Guerra *et al.*, 2020), however, diurnal species have been found to call at dawn (Caldart *et al.*, 2016), and orthopterans and mammals call across the day and night (Greenfield, 2015; Stanley *et al.*, 2016).

Reduced acoustic biotic diversity has previously been found in disturbed habitats, resulting from reduced forest quality (Sueur *et al.*, 2008; Tucker *et al.*, 2014), in rice paddies and pasture (Dröge *et al.*, 2021), in forests with less complex vegetation structure (Hao *et al.*, 2021) and in logged forests (Burivalova *et al.*, 2021). Although they had a sample size of just two sites, Villanueva-Rivera *et al.*, (2011) sampled across the diel cycle and also found loss of dawn and dusk peaks in agricultural sites, when compared to temperate forests in the USA. Our research shows a similar pattern in plantation forestry and grasslands at a much larger scale in the tropics.

Soundscape studies, by their nature, cannot directly link loss of acoustic biotic diversity to loss of species, however, previous studies have found a strong correlation between acoustic biotic diversity and species richness, abundance and biomass (Sueur *et al.*, 2008; Joo, Gage and Kasten, 2011; Fairbrass *et al.*, 2017; Buxton, Agnihotri, *et al.*, 2018; Bradfer-Lawrence *et al.*, 2020; Smith *et al.*, 2020; Dröge *et al.*, 2021; Holgate, Maggini and Fuller, 2021). As a result, it is plausible that species contributing to the dawn and dusk chorus have been lost where we see little or no evidence of a dawn or dusk chorus.

A similar pattern has been found across other non-acoustic studies. Loss of native tree cover and its replacement with disturbed and structurally less complex habitats, has consistently been shown to reduce the diversity of birds (Bell, 1979; Edwards *et al.*, 2010; Villanueva-Rivera *et al.*, 2011; Lees *et al.*, 2015; Lee and Goodale, 2018; Ocampo-Ariza *et al.*, 2019; Dröge *et al.*, 2021), mammals (Gibbs, MacKey and Currie, 2009; Norris *et al.*, 2010; Harikrishnan *et al.*, 2012; Yue *et al.*, 2015; Oliveira *et al.*, 2019; Iezzi, De Angelo and Di Bitetti, 2020), anurans (Gibbs, MacKey and Currie, 2009; Cole *et al.*, 2014; Gallmetzer and Schulze, 2015; Paoletti *et al.*, 2018), and orthopterans (Hassall *et al.*, 2006; Tangmitcharoen *et al.*, 2006; Wong *et al.*, 2016; Méndez-Rojas, Cultid-Medina and Escobar, 2021).

2.4.2. Changes in Species Composition

Despite loss of dawn and dusk peaks in disturbed land use, our study found similar or higher levels of acoustic diversity at other times of the day in these areas, especially in grasslands. Consequently, loss of dawn and dusk peaks in disturbed land use may not necessarily be due to these areas containing fewer species, but different species. Generalist species can adapt to a wider range of land use, especially in disturbed habitats, and as a result are able to replace specialists in these habitats (Clavel, Julliard and Devictor, 2011). This has been shown in both agricultural grasslands and plantations, where species composition was significantly different to forested sites, with grasslands and plantations containing few unique species and mostly disturbance tolerant generalists (Bell, 1979; MacLean *et al.*, 2003; Hassall *et al.*, 2006; Tangmitcharoen *et al.*, 2006; Magura, Tóthmérész and Molnár, 2008; Harikrishnan *et al.*, 2012; Gallmetzer and Schulze, 2015; Grant and Samways, 2016; Paoletti *et al.*, 2018; Oliveira *et al.*, 2019). Hatfield *et al.*, (2020) compared species richness and composition across an interior-edge-matrix gradient of forest, plantation and pasture sites in the Atlantic Forest of Brazil using point counts. They found similar species richness in plantation and pasture sites and significantly higher species richness in forested sites, however, community composition was significantly different between all three land uses. This was driven by a significantly higher richness of disturbance tolerant species in pasture and forest specialists in forests, with plantations showing similar levels of both types of species and showing more similarity to forest than did pasture. This paper highlights the differences that exist in species composition between forests, plantations and grasslands, which are not clearly visible in broader studies that do not consider species level variables. This change in composition is concerning since habitat specialists are at a greater risk of extinction than generalists (Davies, Margules and Lawrence, 2004).

No published evidence has been found to suggest that generalists have different calling patterns to forest specialists, and do not produce a dawn and dusk chorus. However, our observation during data collection was that large flocks of social birds, such as parakeets that inhabited woody patches in grasslands, were seen to call intensely throughout the day and not necessarily at dawn and dusk. If acoustic indices are being driven by abundance or activity of biotic sound, as found in previous studies (Boelman *et al.*, 2007; Bradfer-Lawrence *et al.*, 2020; Holgate, Maggini and Fuller, 2021), as well as or instead of species richness, this may be one explanation for our finding of similar or higher acoustic index values in disturbed sites throughout the day.

2.4.3. Changes in Acoustic Behaviour

It is possible that the same species are still present but have changed their calling behaviour and are no longer calling at dawn and dusk. Higher anthropogenic sound was identified during the day in disturbed habitats. Previously, this has been found to reduce call activity (Lenske and La, 2014), change the type of call produced (Brumm, 2004), and cause some species to call at different times of the day or night (Fuller, Warren and Gaston, 2007). This may also explain why higher acoustic diversity was detected at night in disturbed habitats. Our results also showed peak dawn chorus activity was earlier in teak plantations, compared to native forests. Research suggests that both increased light (Berg, Brumfield and Apanius, 2006; Da Silva, Valcu and Kempenaers, 2016; Da Silva and Kempenaers, 2017) and anthropogenic sound (Arroyo-Solís *et al.*, 2013; Dorado-Correa, Rodríguez-Rocha and Brumm, 2016) can cause earlier onset of the chorus as birds try to maximise their signal transmission. If anthropogenic sound is affecting the acoustic space in these disturbed habitats, impairing or changing acoustic behaviour, it is possible that this will reduce population fitness, since communication ability is directly linked to species survival (Kleyn, da Cruz Kaizer and Passos, 2021), and has been found to interfere with mating, egg laying, provision of young and fledging success (Halfwerk *et al.*, 2011; Schroeder *et al.*, 2012).

In this study, teak plantations retained some of the characteristic dawn and dusk chorus found in native forest habitats. No published research was found showing a direct comparison between teak plantations and other disturbed land uses, however, it can be hypothesised from this result that teak plantations within this study site are more similar to forested sites than are grasslands or palm plantations. Secondary forest showed similar levels of acoustic diversity to old growth forests, however, the dawn and dusk peaks were also less prominent. Secondary forests are not thought to support the same level of biodiversity as old growth forests (Gibson *et al.*, 2011), and in a meta-analysis of 65 studies, species composition was found to differ by an average of 58% (Dent and Wright, 2009). It can, therefore, be hypothesised that secondary forests in this study may also be subject to changes in the biological community and/or species behaviour. Despite this we should not underestimate the value of secondary forests, which are considered highly important for sustaining biodiversity, especially when they complement existing old growth forests (Dent and Wright, 2009).

2.4.4. Acoustic indices: Changes in Species Diversity or Sound Abundance?

Despite loss of dawn and dusk peaks in disturbed land use, acoustic biotic diversity was similar at other points across the diel cycle in plantation forestry and much higher during the day in grassland. Although acoustic indices are found to be linked to measures of species richness and abundance, their ability to function correctly can often be masked by anthropogenic sounds and continuous biotic sounds such as stridulating insects and can vary between ecosystems and geographically (Fairbrass *et al.*, 2017; Bradfer-Lawrence *et al.*, 2019; Gibb *et al.*, 2019; Ross *et al.*, 2021). Field observations suggest that acoustic diversity indices, particularly in grassland sites, may be controlled by the continuous calling of flocks of social birds. This suggests that just a few species in an ecosystem could alter the behaviour of the acoustic indices and therefore caution should be taken when interpreting the outputs of indices.

2.4.5. Conservation and Management Implications

This study has shown that conversion of native old growth forests in the tropics into agricultural land, forestry plantations and even re-established secondary forests, disrupts the diel cycle, most notably causing a loss of the dawn and dusk chorus. These changes in the biological community and species behaviour can impact the resilience of ecosystem functionality, leading to a loss of key processes such as pollination and decomposition (Oliver *et al.*, 2015), reinforcing the importance of native old growth forests for biodiversity conservation (Gibson *et al.*, 2011). Despite some questions over the functionality of acoustic indices, they were able to reveal key differences in acoustic diversity across different ecosystems, however, our research highlights the importance of studies that cover the breadth of the diel cycle, since analysis at key points during the diel cycle did not reveal such dramatic changes between land use types and the loss of the dawn and dusk choruses.

Reforestation and afforestation has been recommended as a way to reverse forest loss, capture atmospheric carbon and mitigate climate change (Bastin *et al.*, 2019), yet if these schemes do not focus on planting native forests the benefits to biodiversity will be lost. Currently 45% of the land committed for afforestation or restoration under the Bonn Challenge are monoculture plantations of commercial trees, which cannot match the ability of native forests for carbon storage or supporting biodiversity (Lewis *et al.*, 2019). Our research highlights the importance of planting native trees, especially in the tropics, where forests regenerate quicker and biodiversity is at its highest (Lewis *et al.*, 2019).

Chapter Three: Effects of Land Use Change and Human Disturbance on the Geoffroy’s Spider Monkey

Abstract

Background: As more land is altered by human activity and more species become at risk of extinction, it is essential that we understand how to conserve rare and threatened species across human-modified landscapes. Owing to their rarity and often sparse distributions, threatened species can be difficult to study and efficient methods to sample them across wide temporal and spatial scales have been lacking. Passive acoustic monitoring (PAM) is increasingly recognised as an efficient method for collecting data on rare species; however, the development of automated species detectors required to analyse such large amounts of data is not keeping pace.

Methods: Here, we collected over 60,000 hours of acoustic data across 341 sites in a region over 1000 km^2 to show that PAM, together with a newly developed automated detector, can be successfully used to detect the endangered Geoffroy’s spider monkey (*Ateles geoffroyi*) and assess how this species responds to anthropogenic disturbance.

Results: We found that the Geoffroy’s spider monkey was absent below a threshold of 80% forest cover and within 1 km of primary paved roads. In contrast to what was expected, we found equal occurrence in old growth and secondary forests.

Implications: We have shown that this methodology is successful in the study of a vocal rare and threatened species, suggesting that similar species could be studied in the same way. We provide threshold values for percentage forest cover and paved roads, which highlights the sensitivity of this species to anthropogenic change will be valuable in setting targets and developing conservation strategies for the protection of this species.

3.1. Introduction

The number of species threatened with extinction is increasing drastically. A recent report by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) found that over 1 million species are now under threat, which impacts the ecosystems and processes they support (IPBES, 2019). Monitoring and evaluating the response of threatened species and communities to anthropogenic change is essential for effective management and improved decision making (Stem *et al.*, 2005; Bennett *et al.*, 2018; Dixon *et al.*, 2019; Gibb *et al.*, 2019). Yet despite decades of research, we still lack rapid and efficient methods to assess how species respond to habitat changes across human-modified landscapes and the knowledge to implement conservation strategies to protect them (Estrada, 2006; Arroyo-Rodríguez and Fahrig, 2014; Wrege *et al.*, 2017; Legge *et al.*, 2018; Bezanson and McNamara, 2019; Junker *et al.*, 2020).

Threatened species can be difficult to study owning to their reduced population sizes, sparse distributions and often elusive nature (Bissonette, 1999; Campos-Cerqueira and Aide, 2016). Thus, collecting data on species ecology or conservation requirements often involves wide spatial and temporal scales (Bissonette, 1999; Campos-Cerqueira and Aide, 2016; Williams, O'Donnell and Armstrong, 2018), which can be constrained by practical and economic challenges (Arroyo-Rodríguez and Fahrig, 2014; Williams, O'Donnell and Armstrong, 2018). Traditional survey methods for primates, such as line transects, often hinder the ability to carry out large scale studies, since they are expensive, time consuming, practically challenging and require the researcher to be present at all times (Gibb *et al.*, 2019; Campos *et al.*, 2021). Ecological studies using traditional methods that include capturing individuals, involve the close proximity of researchers and can be invasive, cause stress and suffering to wildlife, impact animal welfare and even bias results (Iossa *et al.*, 2007; Zemanova, 2020). When attempting to study species that react to human presence, we can alter the exact response that we are trying to measure simply by our presence, especially in areas where hunting occurs (Wrege *et al.*, 2017; Penar, Magiera and Klocek, 2020).

The emerging field of passive acoustic monitoring (PAM) can overcome these constraints. Acoustic sensors can be deployed in the field for long periods of time and monitor continuously, without the need for the researcher to be present. This allows for the potential to increase the temporal extent of the study, reduces disturbance on the individuals, and increases the chance of detecting rarer species (Blumstein *et al.*, 2011; Mennill *et al.*, 2012; Kalan *et al.*, 2015; Sueur and Farina, 2015; Browning *et al.*, 2017; Penar, Magiera and Klocek, 2020). PAM has been shown to be effective in the study of rare species of birds (Celis-Murillo, Deppe and Ward, 2012; Williams, O'Donnell and Armstrong, 2018), mammals (Kalan *et al.*, 2015; Wrege *et al.*, 2017) and anurans (Willacy, Mahony and Newell, 2015). The reduction of person-power required in the field, increased feasibility in challenging terrain and the increasing affordability of sensors also offers the ability to study across greater spatial scales, allowing researchers to understand the impacts of anthropogenic disturbance across much larger areas (Gibb *et al.*, 2019; Sugai *et al.*, 2019) Crucially, using PAM would also allow for designing landscape-scale studies, which arguably provide a better approach to collecting biodiversity data than patch-scale studies, currently the norm in the field (Arroyo-Rodríguez and Fahrig, 2014). Camera trapping offers many of the same benefits as PAM, however in a recent comparative study on chimpanzees (*Pan troglodytes)* PAM was five times more effective at detecting individuals (Crunchant *et al.*, 2020).

While PAM dramatically reduces the burden to collect field data, the methods for extracting information from the recordings poses significant challenges. Large acoustic data sets are time consuming to analyse manually, requiring automated detection and classification systems to extract sounds (Kalan *et al.*, 2015; Browning *et al.*, 2017). The development of these tools requires specialist skills and large labelled training datasets, which are difficult to collate, especially for rare species (Browning *et al.*, 2017), hence the creation of automated models for detecting species is recognised as a major bottleneck in the field, especially in the tropics, since most models have been created for temperate regions (Browning *et al.*, 2017). Several automated analysis tools for primates have been developed across African and Asian species (Pozzi, Gamba and Giacoma, 2010; Mielke and

Zuberbühler, 2013; Heinicke *et al.*, 2015; Kalan *et al.*, 2015, 2016; Spillmann *et al.*, 2015; Clink *et al.*, 2017; Dufourq *et al.*, 2021), but models for Neotropical species are lacking, with only one model created based on calls from a small group of captive marmosets, designed for use in the medical field (Turesson *et al.*, 2016).

Of the 504 species of primate, 60% are threatened with extinction and 75% are declining as a result of human disturbance (Estrada *et al.*, 2017). The Geoffroy's spider monkey (*Ateles geoffroyi*) is classified by the IUCN as Endangered and its population is predicted to decline by 50% over a 45 year period (Cortes-Ortíz *et al.*, 2021).

There have been several studies investigating how the Geoffroy's spider monkey responds to anthropogenic change, revealing inconsistent results. Most studies have found this species to prefer continuous tracts of mature old growth forests, where there are larger sleeper trees and higher fruit biomass and human disturbance is restricted (van Roosmalen, 1980; Chapman, 1989; Sorensen and Fedigan, 2000; Ramos-Fernández and Ayala-Orozco, 2003; Urquiza-Haas, Peres and Dolman, 2009). Studies have also shown that this species will use secondary forest, but to a lesser degree (Ramos-Fernández and Ayala-Orozco, 2003; Ramos-Fernandez *et al.*, 2013; Arroyo-Rodríguez *et al.*, 2017a; Whitworth *et al.*, 2019), with only one study finding equal use of both old growth and secondary forests (Weghorst, 2007). In contrast to this, some studies have shown this species to occur in more disturbed forest fragments (Chaves, Stoner and Arroyo-Rodríguez, 2012; Galán-Acedo, Arroyo-Rodríguez and Chapman, 2021) and have even found them to occur in agroforestry plantations and vegetation corridors used for travelling and feeding (Estrada *et al.*, 2006; Estrada, Raboy and Oliveira, 2012; Arroyo-Rodríguez *et al.*, 2017a). There is very little information available on the effects of human development, however avoidance of roads and population centres has been found (Van Hulle and Vaughan, 2008; Asensio *et al.*, 2017).

Owing to its endangered and declining status, general sensitivity to human disturbance, sparse distributions and large home ranges, combined with the requirement for rapid and efficient methods to assess how primates respond to habitat changes across human-modified landscapes, the Geoffroy's spider monkey is an excellent study species for testing the use of PAM as a tool to study rare and threatened species.

The aim of this study is to determine if a new method, using PAM and a newly developed automated detection and classification system for the spider monkey call, is effective at retrieving information on the Geoffroy's spider monkey in over 340 sites across a region spanning 1093 km^2 in the Osa Peninsula, Costa Rica. To the best of my knowledge this is the first study of the Geoffroy's spider monkey with such a broad scale and coverage. We use presence and absence, as well as number of calls, to assess how this endangered and rare primate responds to habitat loss and human influence across a gradient of disturbance. Specifically, we answer the following questions: 1. Is PAM effective in studying the Geoffroy's spider monkey across large spatial scales. 2. How does land use change, forest cover and density of roads and human settlements affect the presence and call rate of the spider monkey.

3.2. Methods

3.2.1. Study Site

Our study area covers approximately 1,000 km^2 in the South-Pacific coast of Costa Rica. The terrain is generally low altitude, with a maximum elevation of 792 meters. Mean annual rainfall ranges from 3,000-6,500 mm and mean yearly temperature is 27°C, with high levels of humidity throughout the year. There are two distinct seasons, wet and dry season, with the highest rainfall occurring September through December (Gilbert *et al.*, 2016). The peninsula contains the last remnants of tropical broadleaf evergreen lowland rainforest on the Central American Pacific (Gilbert *et al.*, 2016), embedded within a mosaic of pasture, plantations and urban centres (Figure 3.1). Due to the geology and geography of the area, the peninsula contains high levels of biodiversity and endemism (Sánchez-Azofeifa *et al.*, 2002). Managed under the Area de Conservación Osa (ACOSA), the Osa

Peninsula contains three core protected areas, Piedras Blancas and Corcovado National Parks and a Ramsar wetland site, the Terreba-Sierpe Wetlands. There are also nine smaller private and public wildlife refuges and the Golfo Dulce Forest Reserve (Sánchez-Azofeifa *et al.*, 2002; Gutierrez *et al.*, 2019).

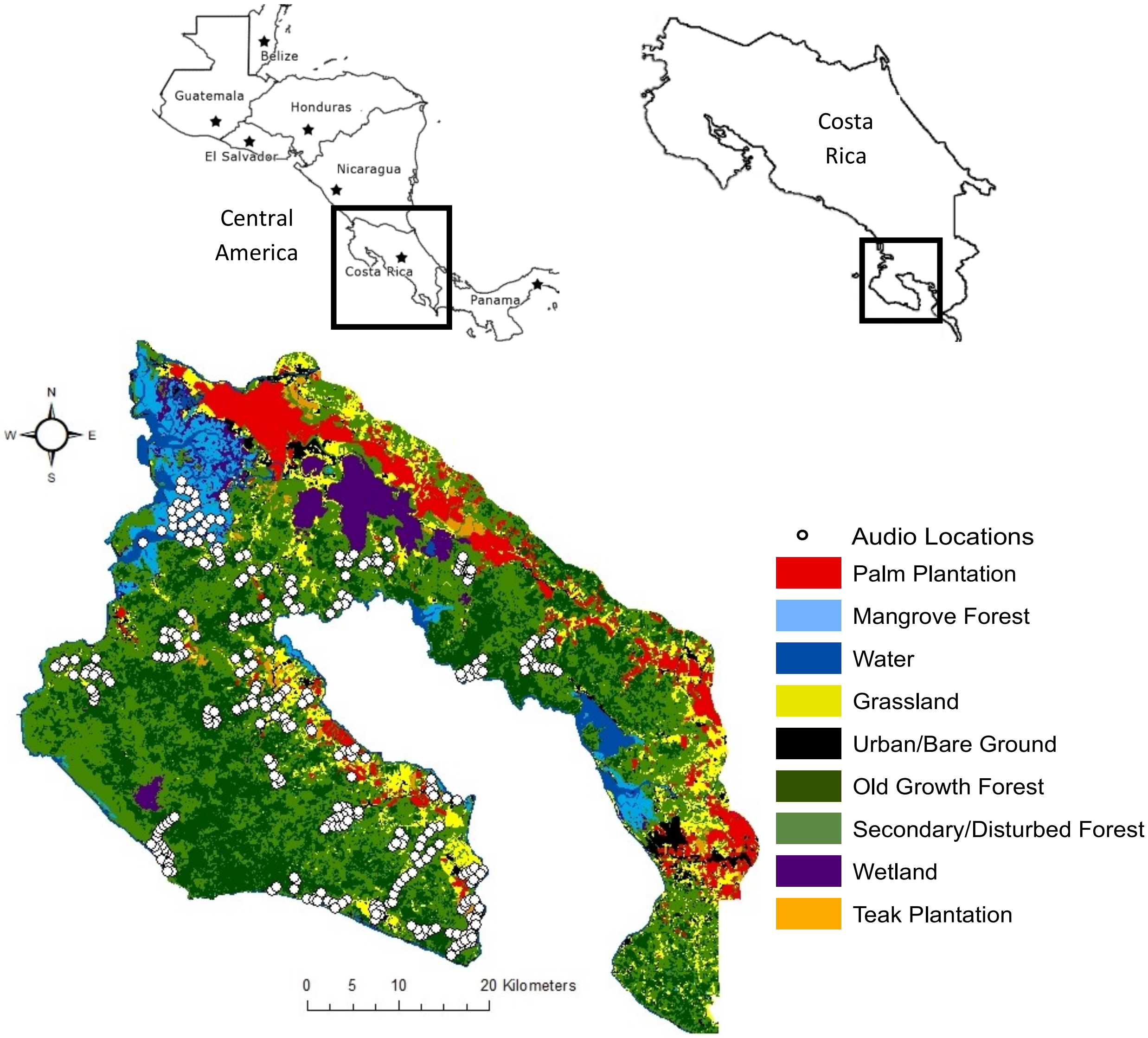


Figure 3.1. Land Use Map of the Osa Peninsula. Map showing the nine land use categories in the region, created at a scale of 5 x 5 m using Landsat 5 Thematic Mapper (TM) and Landsat 8 Operational Land Imager (OLI) (Shrestha *et al.*, 2018). White circles represent the sample sites where each audio recorder was placed.

3.2.2. Study Species

The Geoffroy's spider monkey, is currently classified by the IUCN as Endangered and globally its population is expected to decline by 50% within a 45 year period (Cortes-Ortíz *et al.*, 2021). They are found from south-eastern Mexico to north-western Colombia (Di Fiore, Link and Campbell, 2011). The Geoffroy's spider monkey is a large-bodied primate with a home range of up to 4 km^2, a frugivorous diet and requirement for large mature trees as sleeping sites (van Roosmalen, 1980; Chapman, 1989; Sorensen and Fedigan, 2000; Zaldívar *et al.*, 2004; Weghorst, 2007; Wallace, 2008a, 2008b; Arroyo-Rodríguez *et al.*, 2017a). Due to this, they require large areas of undisturbed mature forest and are therefore particularly sensitive to forest loss and fragmentation (Boyle and Smith, 2010; Ramos-Fernández and Wallace, 2010), making them a forest specialist (Arroyo-Rodríguez et al., 2017a).

3.2.3. Sampling Design

Land use at each site was calculated using land use maps provided by NASA, created at a scale of 5 x 5 m using Landsat 5 Thematic Mapper (TM) and Landsat 8 Operational Land Imager (OLI) (Shrestha *et al.*, 2018) (Figure 3.1). The map was classified into nine land use categories, with recordings for this study taken in old growth and secondary forests, palm and teak plantations, mangroves and grassland sites (Figure 3.1). Wetlands, water and urban areas were excluded from the analysis due to inaccessibility. Wetlands also consist mainly of a single species of fern and contain no fruiting trees, which due to body mass and dietary requirements, it is unlikely that the spider monkey would use.

To ensure a representative number of sampling sites were chosen across each land use category, we used a stratified sampling approach. We calculated the percentage cover of each land use category across the region and placed a representative number of recorders in each category. To ensure even coverage of the study region we selected sampling locations in a uniform distribution across the Osa Peninsula. Due to access issues it was not possible to randomly choose sampling locations in all areas, therefore, to ensure independence among sampling locations, the first recorder in each area was placed by walking 500 m in a random direction and the remaining placed at a minimum of 500 m apart. Where possible, trails were not used to avoid bias, however, where this was not possible, devices were placed a minimum distance of 200 m perpendicular to a trail; as indicated by GPS. Non-audio data were collected for each point including GPS location, elevation and land use, to verify data from NASA land use maps. For more information on sampling design please see Chapter One.

Given that biotic sounds generally travel a maximum distance of 200 m (Figueira *et al.*, 2015), we used a minimum distance of 500 m between recorders, ensuring independence in the samples and avoiding pseudo-replication. Recording devices were also placed at a minimum distance of 200 m from habitat boundaries, to be confident that calls were from within the classified habitat.

Data were collected at 341 sites totalling 60,000 hours of recordings. Recordings were obtained using Audio Moth devices (Open Acoustics Devices, UK). Recorders were set up for seven consecutive days to increase the chances of detecting the spider monkey if they were present. The devices were set to record on a schedule of 05.00-09 30, 14:00-18:30 and 21:00- 03:00, to ensure data were collected at key periods of spider monkey activity (Wallace, 2001) including the periods of night activity (Whitworth *et al.*, 2019). We recorded constantly over the recording schedule at a sample rate of 48000 kHz, 2.5 times higher than the maximum call of the Geoffroy's spider monkey. Sampling was conducted within dry season (December-August) due to restricted access to many areas of the study site during wet season.

3.2.4. Development of an Automated System for Signal Classification

Animals often use several different calls for communication, however it was beyond the scope of this study to develop a classification algorithm for each of the 13 calls of the spider monkey (Eisenberg, 1976). In a pilot study, we developed and tested the suitability of passive acoustic monitoring as a method for studying the Geoffroy's spider monkey, where we found that over 80% of recorded calls were the “whinny” and every calling period contained several of this call type (see Chapter One for more details). The whinny represents general communication related to feeding and movement (Ramos-Fernández, 2008). This call was therefore chosen for creating a classification algorithm to study this species.

3.2.5.1. Labelled Call Database

The creation of automated detection and classification algorithms in acoustics requires a large database, ideally 500+ labelled samples of the target sound, which is difficult to collate for rare species. Using pilot data collected at 12 different sites across the study area and one region in the north of Costa Rica, we manually listened to 600 hours of acoustic data and isolated 580 examples of the target sound. Both good and bad quality calls were used and those in both quiet and noisy environments, to best represent the natural environment. Audio files containing calls were then annotated in programme praat, which produces .txt files of exact call location, duration and frequency, suitable for use in machine learning software (Boersma and Weenink, 2018).

3.2.5.2. Convolutional Neural Network

The algorithm was developed together with the Department of Computing, Imperial College London, published as part of the Interspeech Challenge 2021 (Rizos *et al.*, 2021), however the methodology is briefly explained here. A convolutional neural network (CNN) was used to train the classifier to detect the whinny. A CNN is a deep learning algorithm, where a multi-layered artificial neural network learns from large amounts of sample data without the need for prior feature extraction (Lecun, Bengio and Hinton, 2015). CNN’s can only learn from images, not sound, so data is first transformed into a pictorial representation of the sound through a process called short-time Fourier transformation (Mac Aodha *et al.*, 2018). Data are fed though each layer in the network, where more complex features are extracted as it progresses though the layers. The final process of classification provides a set of confidence scores about how likely the sound is to belong to a particular class (Lecun, Bengio and Hinton, 2015).

3.2.5.3. Model Validation

Model results showed that recall was 75%, which means that the model returned 75% of the true positives when a confidence threshold of 50% was set. As we were using a semi-automated approach, we manually checked all returned positives, and then used these results to build up a database of calls. Precision was a little lower at 53%, indicating that the model was making some incorrect classifications, i.e. false positives. The F1 score was 62%, which takes into account precision and recall, providing an overall estimate of model accuracy. As we were using a semi-automated approach and validating all returned positives, the number of true positives returned, the recall, was more important for the purposes of this study.

To further validate these results, we tested the model on two sets of acoustic data where we knew how many positive calls were contained in the files. One folder contained very little background noise and the second contained many other biotic and abiotic sounds, making it more difficult for the model to classify. The first set of files, with little background noise, contained 76 calls. The model returned 67 positives, all of which were correct with zero false positives, only 9 calls were missed. The second folder, with lots of background noise, contained 35 calls. The model returned 220 positives, 29 which were correct and 191 false positives, only 6 calls were missed. Under both scenarios very few calls were missed, however it was clear that a semi-automated approach was required, where all returned positives are validated, to avoid overestimating occupancy or call rate. Lower precision and a semi-automated approach is common, especially in tropical ecosystems where there is a lot of background noise and other species calling (Heinicke *et al.*, 2015).

Using the best model above, we then ran data from all 341 sites through the model algorithm using a confidence threshold of 50%. The model outputs all positives into .csv files and an associated folder with clipped audio files. We listened to all returned audio files and marked the number of true positive detections per day per site. All analysis was carried out in Python v.3.6 (Van Rossum and Drake, 2009).

3.2.5. Statistical Analysis

3.2.6.1. Explanatory Variables

We installed acoustic recorders in six of the nine land use categories: Old growth and secondary forest, mangrove forest, grassland, palm and teak plantations. We did not place recorders in urban areas due to restrictions on recording in public spaces or in wetlands due to inaccessibility. To correctly assess species responses to habitat changes, it is crucial that predictors are measured at the scale at which the species responses are strongest, known as scale of effect (Jackson and Fahrig, 2015; Galán-Acedo *et al.*, 2019). To assess the scale of effect of forest cover, primary (paved) and secondary (unpaved) roads and buildings, we calculated percentage forest cover (%), the density of roads (km) and the area of buildings (km^2) in a buffer around each site at intervals between 100-5,000 m radius for forest cover and 100-1,000 m for roads and buildings (see Supplementary Information 2.1. Table 2.6). We then tested at which spatial scale the variables had the strongest effect on the spider monkey. We created GIS layers for roads and buildings across the study site using satellite images.

The data showed complete separation across land use and primary road variables, which happens when a combination of the explanatory variables produces a perfect prediction of the response variable (Albert and Anderson, 1984). This led to high standard errors, confidence intervals and p-values. To account for this, a model containing these variables was fitted separately in package *brglm2* (Kosmidis, 2020) that can model complete separation. We fitted all other models in the *nlme* (Pinheiro, Bates and DebRoy, 2020) and *lme4* package (Bates *et al.*, 2015).

3.2.6.2. Occupancy

A detection period constituted one 24-hour period of recording, providing a 7-day detection history. A detection was registered if the audio device recorded the call of the Geoffroy's spider monkey each day. Detections were coded as 1 and non-detections as 0. We used a single-species, single-season occupancy model assuming a closed system for the 7-day sampling period, where there are no changes to occupancy between survey days. It should be noted that it is difficult to guarantee a closed system and therefore occupancy model results should be viewed with caution, since violations of closure can lead to overestimates of the probability of occurrence (Rota *et al.*, 2009). We first created a model where we assumed that detection probability and site occupancy were constant across time and space, to provide a comparison against naïve estimates. We also constructed a set of candidate models where the occupancy was modelled as a function of forest cover, area cover of buildings and density of secondary roads, and detection probability as a function of forest cover. Occupancy analyses were conducted in package *unmarked* (Fiske and Chandler, 2011). We used Akaike's information criterion, corrected for small sample size (AICc), Delta AIC (QAICc) and Akaike's weights (*w*) to select the best model that compromised between precision and complexity, from a biologically relevant candidate set of models (Burnham and Anderson, 2002). We considered all models where QAICc<2.

3.2.6.3. Generalised Linear Models

To determine the naïve probability of occurrence of the spider monkey across our study site, we used logistic regression with a logit link function. Site occurrence was calculated by combining the detection histories from occupancy analysis into one parameter, coded as 1 or 0 for presence or absence per site. To measure site call abundance, we calculated the total number of vocalisations recorded across all sampling days, to provide one measure per site. Although there was some correlation between variables, it was generally low (R^2= 0.15-0.27) with the exception of buildings and primary road variables (R^2= 0.58) (Supplementary Information 2.1- Figure 2.1), however these were run separately due to complete separation in the primary road data. Primary road and land use were significantly correlated (p <0.01) and hence, within package *brglm2,* these variables were run separately. For the model where call rate was the response variable, we first tested for overdispersion and zero-inflation in the data using package *DHARMa* (Hartig, 2020) and found significant overdispersion but did not find any evidence for zero-inflation (Supplementary Information 2.1- Figure 2.2). To account for overdispersion, we used a GLM with negative binomial distribution, diagnostic plots indicated no significant overdispersion when using this distribution (Supplementary Information 2.1- Figure 2.3 a). R package *brglm2* does not yet have an option for quasipoisson or negative binomial analysis and therefore the models for call rate containing land use and primary road variables were run using a Poisson distribution. Although overdispersion was found in these models (Supplementary Information 2.1- Figures 2.3 b & c), since the data exhibits complete separation, we do not need to be too concerned. Finally, we used the Likelihood-ratio test and model AIC to assess model fit between Poisson and negative binomial models. The negative binomial model significantly outperformed the Poisson model (Supplementary Information 2.1- Table 2.1). Bonferroni's correction for multiple pairwise comparisons was applied to adjust p-values and reduce the risk of type I errors.

In order to reliably compare the contribution of variables across models and understand how much of the variance explained by each explanatory variable is individual, or shared and cannot be ascribed separately to any one variable, we ran variance partitioning analysis in package *hier.part* (Mac Nally and Walsh, 2004). We used residual plots to assess violations in model assumptions for binomial, Poisson and negative binomial models. All plots showed no deviation from the expected distribution or heteroscedasticity in the residuals, with the exception of the Poisson models as expected (Supplementary Information 2.1- Figures 2.4 & 2.5).

3.2.6.4. Spatial Autocorrelation

Due to the nested structure in the data, we tested for spatial autocorrelation across all generalised linear models. We created a distanced based weight matrix using model residuals and sampling site coordinates. Using *gstat* package (Pebesma, 2004) we then produced a variogram plot to visually determine the presence of autocorrelation. Finally, we calculated the Moran's I statistic in *ape* package (Paradis and Schliep, 2019). If no autocorrelation is present, then the observed autocorrelation should be close to 0 and to the expected value.

Spatial autocorrelation was found across all models, violating the spatial independence assumption of regression analysis. To account for this, we constructed a spatial auto-covariate that was included as an additional predictor variable. For each site we calculated a distance-weighted average of neighbouring response values, using a minimum neighbour's distance of 210 m, with sites further away receiving lower weightings (Dormann *et al.*, 2007). To test whether the auto-covariate function reduced autocorrelation in the residuals we used Moran's I statistic. No autocorrelation was present across the models when the auto-covariate function was added (Supplementary Information 2.1- Tables 2.2 & 2.3). We also used the Likelihood-ratio test and AIC to determine if the addition of an auto-covariate function improved model fit. In cases where the auto-covariate function reduced autocorrelation but model fit remained equal, it was still included in the model (Supplementary Information 2.1- Tables 2.4 & 2.5).

3.3. Results

The automated detection and classification algorithm for the spider monkey whinny returned a total of 2977 true positives across 273 days in 64 out of 341 sites and 52,248 false positives. To listen to this data manually it would take 20 years, listening on a schedule of 8 hours per day, 365 days of the year. It took eight weeks to pass all 341 sites through the algorithm and a further four weeks to identify all true positives using a semi-automated approach. Had we been able to use the HPC service, which was not possible due to coronavirus, the eight weeks would have been considerably reduced.

3.3.1. Scale of Effect

For forest cover, the strongest response was at 200 m radius for presence ($R^2 = 0.77$) and call rate ($R^2= 0.97$), although the response remained strong until we reached a radius of 2000-3000 m. Forest cover appears to have a non-linear relationship with response the variables, therefore a polynomial term was added to the models. For secondary roads, the strongest response was at 200 m radius for presence ($R^2= 0.09$) and for call abundance ($R^2= 0.3$), however all spatial scales showed a similar response (mean $R^2= 0.07$, SD= 0.01). For primary roads, the strongest response was at 1000 m radius for presence ($R^2= 0.6$) and for call abundance ($R^2= 0.95$). For buildings, the strongest response was also at 1000 m radius for presence ($R^2= 0.22$) and for call abundance ($R^2= 0.85$) (Supplementary Information 2.1- Tables 2.6). Thus, from here on, all results are presented where each explanatory variable was measured at these scales.

3.3.2. Occupancy Models

Presence of the Geoffroy's spider monkey in 64/341 sites yielded a naïve occupancy estimate of 0.187. Our single-site, single-species occupancy model, in which we assumed constant occupancy and detection probabilities, estimated spider monkey site occupancy at 0.192 (se= 0.02) and detection frequency at 0.675 (se= 0.02). A 0.5% difference between our naïve and model estimates, and relatively high detection frequency, suggests that the species was detected at almost all sites where they were present. Due to similar naïve and model estimates of occupancy, the failure of the occupancy model to converge with our variables that exhibit complete separation, and the fact that we would have not been able to account for spatial auto-correlation in occupancy models, we present here only the results of logistic regression analysis. Results from occupancy analysis can be found in the supplementary material, yielding similar results to logistic regression analysis (Supplementary Information 2.2)

3.3.3. Presence and Call rate

Land use has a significant effect on the presence of the spider monkey (Figure 3.2.a), with spider monkeys only found in old growth and secondary forests. The probability of occurrence was significantly lower in grassland, palm and mangrove when compared to old growth and secondary forests (Figure 3.2.a. Supplementary Information 2.3. Table 2.9). We registered no records of the spider monkey in teak plantations, however, this difference was not significant due to high standard errors and confidence intervals from model fitting. Probability of occurrence was not significantly different between old growth and secondary forests (Figure 3.2.a. Supplementary Information 2.3. Table 2.9). Spider monkey calls were only found in old growth and secondary forests. Call rate varied significantly between habitats, being higher in old growth and secondary forest when compared to other land use types (Figure 3.2.b. Supplementary Information 2.3. Table 2.10).

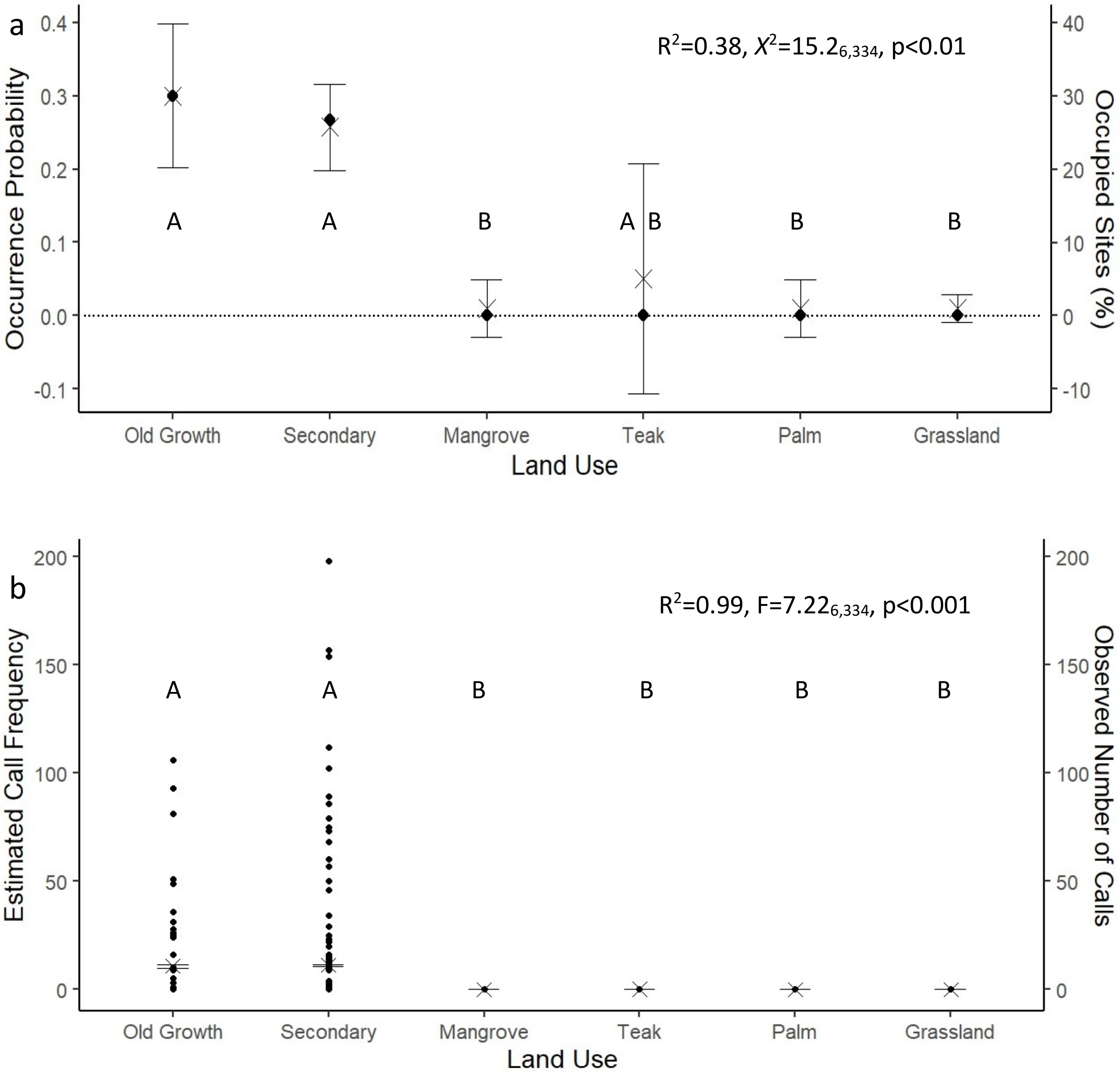


Figure 3.2. Land Use Model Results. a. Probability of species occurrence in each land use type on the y-axis (X), error bars represent 95% confidence intervals and percentage of occupied sites in each land use type on the z-axis (●) b. Results from model predictions showing estimated call rate in each land use type on the y-axis (X), error bars represent 95% confidence intervals and observed number of calls per site in each land use type on the z-axis (●). Pairwise differences between land use are indicated with letters A and B, where different letters represent a significant difference between land use. R^2, X^2, F and p values are annotated on each plot.

Spider monkeys were strongly associated with higher levels of forest cover, only being found above 80% cover. Call rate was significantly higher at higher levels of forest cover, with an average of 13.5 calls per site across the 7-day recording period at 100% forest cover, dropping to almost zero below 80% forest cover (Figure 3.3 a & e. Supplementary Information 2.3. Table 2.11 & 2.12). Primary road had a significant effect on spider monkey occurrence and call rate (Figure 3.3 b & f. Supplementary Information 2.3. Table 2.11 & 2.12). Crucially the spider monkey was not found at any site with primary road within a 1 km radius (Figure 3.3 b & f). Occurrence and call rate were not significantly affected by total area of buildings (Figure 3.3 c & g. Supplementary Information 2.3. Table 2.11 & 2.12), however the spider monkey was not found where cover of houses exceeded 18 km^2 within a 1 km radius of the site (Figure 3.3 c & g. Supplementary Information 2.3. Table 2.11 & 2.12). The effect of secondary road on spider monkey occurrence and call rate showed a non-significant decrease (Figure 3.3 d & h. Supplementary Information 2.3. Table 2.11 & 2.12). Despite this, the spider monkey was only found where density of secondary roads were below 0.6 km within 200 m radius of the site (Figure 3.3 d & h).

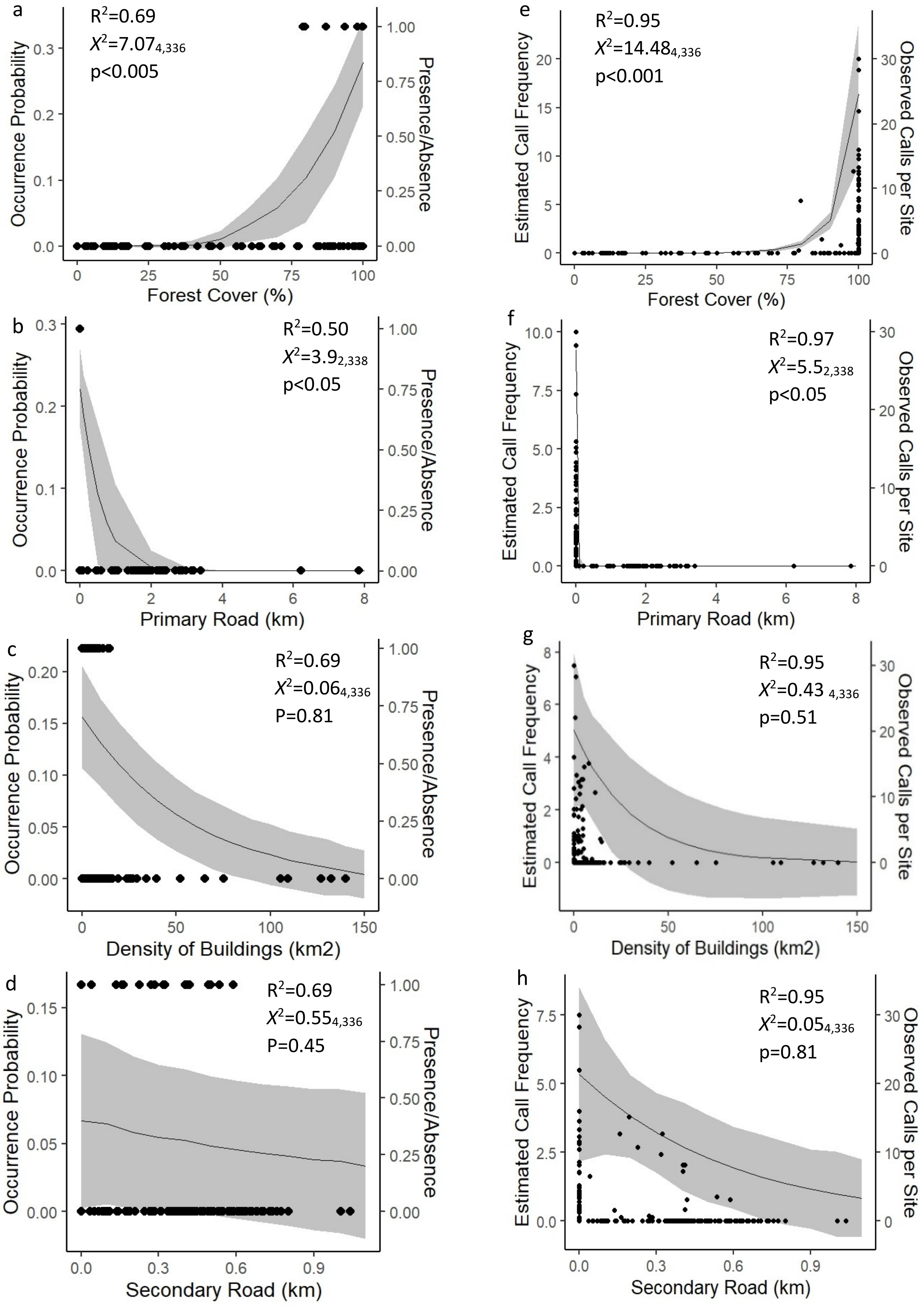

a
$R^2=0.69$
$X^2=7.07_{4,336}$
$p<0.005$
Occurrence Probability
Presence/Absence
Forest Cover (%)
0.0
0.1
0.2
0.3
0.00
0.25
0.50
0.75
1.00
0
25
50
75
100
b
$R^2=0.50$
$X^2=3.9_{2,338}$
$p<0.05$
Occurrence Probability
Presence/Absence
Primary Road (km)
0.0
0.1
0.2
0.3
0
2
4
6
8
c
$R^2=0.69$
$X^2=0.06_{4,336}$
P=0.81
Occurrence Probability
Presence/Absence
Density of Buildings (km2)
0.00
0.05
0.10
0.15
0.20
0
50
100
150
d
$R^2=0.69$
$X^2=0.55_{4,336}$
P=0.45
Occurrence Probability
Presence/Absence
Secondary Road (km)
0.00
0.05
0.10
0.15
0.0
0.3
0.6
0.9
e
$R^2=0.95$
$X^2=14.48_{4,336}$
$p<0.001$
Estimated Call Frequency
Observed Calls per Site
Forest Cover (%)
0
5
10
15
20
30
f
$R^2=0.97$
$X^2=5.5_{2,338}$
$p<0.05$
Estimated Call Frequency
Observed Calls per Site
Primary Road (km)
0.0
2.5
5.0
7.5
10.0
g
$R^2=0.95$
$X^2=0.43\ _{4,336}$
p=0.51
Estimated Call Frequency
Observed Calls per Site
Density of Buildings (km2)
0
2
4
6
8
h
$R^2=0.95$
$X^2=0.05_{4,336}$
p=0.81
Estimated Call Frequency
Observed Calls per Site
Secondary Road (km)
0.0
2.5
5.0
7.5

Figure 3.3. Continuous Variables Model Results. **a-d**. Probability of occurrence on the y-axis and observed presence/absence on the z-axis (●) in relation to a. Forest Cover (%) measured within 200 m. b. Density of primary roads measured within a 1 km radius of the site. c. Cover of buildings measured within a 1 km radius of the site. d. Density of secondary roads measured within a 200 m radius of the site and **e-h.** Results from model predictions showing model estimated call rate per site on the y-axis and observed average number of calls per site on the z-axis (●) in relation to a. Forest Cover (%) measured within 200 m. b. Density of primary roads within a 1 km radius of the site c. Cover of buildings within a 1 km radius of the site and d. Density of secondary roads within a 200 m radius of the site. Shaded area represents 95% confidence intervals. R^2, X^2 and p values are annotated on each plot.

3.3.4. Variance Partitioning

Variance partitioning for models containing both occupancy and call rate as the response variable showed that there was a portion of the variation within most variables that were shared and could not be attributed to one single variable. The variance contained within secondary road density and for area cover of buildings were mostly attributed to other variables for both occurrence and call rate. As expected from the model results above, forest cover, land use and primary road density are the main drivers of changes in occurrence and call rate, even when accounting for shared variance (Table 3.1). Models containing call rate as the response variable showed a similar pattern and can be found in the supplementary material (Supplementary Information 2.3. Table 2.13).

Table 3.1. Variance Partitioning Results: Occurrence. Variance partitioning analysis for occurrence models showing individual and shared variance and % individual variance for each explanatory variable. Larger values indicate more variance attributed to that variable.

Variable	Individual Variance	Shared variance	Individual variance (%)
Land Use	0.19	0.18	28.4
Forest Cover	0.22	0.19	34.1
Primary Road Density	0.2	0.04	31.4
Secondary Road Density	0.03	0.06	4
Area of Buildings	0.01	0.01	2

3.4. Discussion

In this study we have shown that passive acoustic monitoring (PAM), combined with an automated detection and classification system for extracting calls, can be successfully used to assess how a rare and threatened species, the Geoffroy's spider monkey (*Ateles geoffroyi*), responds to changes across the landscape at a wide spatial scale. We were able to analyse 60,000 hours of data across 341 sites over a large region in the tropics. Our results show that this species does not occur below a threshold of 80% forest cover and is absent from areas within 1 km of primary paved roads. In contrast to what was expected, we found equal occurrence in old growth and secondary forests and a limited tolerance of human development. Despite large amounts of seemingly suitable habitat in the region, the spider monkey remains absent from many forested areas, suggesting a lack of connectivity in the region.

3.4.1. Application of Passive Acoustic Monitoring for the Geoffroy's Spider Monkey

The automated detector used in this study was able to analyse over 60,000 hours of data in just 8 weeks, which would not have been possible otherwise. We returned a total of 2977 calls across 64 out of 341 sites. Despite a low naïve site occupancy estimate of only 18.7%, using occupancy modelling to account for imperfect detection provided an estimate of 19.2%, suggesting that our estimate of occupied sites using calls extracted by the automated detector are very accurate. This is likely because there were no instances when we only detected a single call, generally, in sites where we detected the spider monkey, we detected dozens of calls over a few days. Detection probability from occupancy modelling was 68% and recall from the automated detector was 75%, which means we potentially may have missed approximately 25% of calls and therefore may be underestimating call rate, however we set call confidence at 50% to increase the number of calls returned and avoid missing true positives. Because model precision was only 53%, we used a semi-automated approach, where we manually confirmed all positives returned by the model, reducing the chance of false positives. Site occupancy would have been artificially inflated if we had not taken this approach, with all sites showing false positives, severely biasing the results and affecting conservation and management recommendations.

In this study we used call rate as an index of relative abundance. This relationship has been shown to hold true in many other species such as elephants (Thompson *et al.*, 2010), marine mammals (Van Parijs, Smith and Corkeron, 2002), amphibians (Graves and Nelson, 2004; Crump *et al.*, 2017) and birds (Buxton *et al.*, 2013; Pérez-Granados *et al.*, 2019). Although no study has directly quantified this relationship in spider monkeys, Chapman and Lefebvre (1990) observed there to be more calls when there were more individuals present. In spider monkeys the whinny is known to be a general communication call between individuals about location, movement and food sources between or within groups or sub groups (Chapman and Lefebvre, 1990; Ramos-Fernández, 2008). Unlike the repetitive nature of alarm calls, whinnies are single calls that are emitted from one individual to another, thought to contain information about caller identify (Chapman and Lefebvre, 1990; Chapman and Weary, 1990; Teixidor and Byrne, 1999). This suggests that more calls should be indicative of more individuals. However, since spider monkeys operate in a fission-fusion society, more individuals in a group doesn't necessarily translate to a larger total group size and could indicate that that the sub-groups formed are larger, which usually occurs when food abundance is greater in the area (van Roosmalen, 1980; Chapman, 1990). It is also possible that since spider monkeys are known to reduce calling in the presence of observers (Teixidor and Byrne, 1999), that the same number of individuals are present, but that they are living in a more disturbed environment, where they do not feel safe to call as frequently. Validating this link would be beneficial for future acoustic studies with the spider monkey. This can be done by using acoustic recorders to determine the number of calls emitted from a group, whilst simultaneously counting the number of individuals in a group. However, since observer presence is known to reduce calling in the spider monkey (Teixidor and Byrne, 1999), data on group numbers would need to be collected thorough remote sensing, perhaps using camera traps.

3.4.2. Geoffroy's Spider Monkey: Response to Land Use Change

3.4.2.1. Highly Suitable Habitat

Geoffroy's spider monkey occurrence and call rate were at their highest in areas with over 80% native forest cover. Identifying thresholds, or "tipping points" below which biodiversity may decline, is essential in the design of conservation strategies to prevent local extinction of species (Ficetola and Denoël, 2009; de Oliveira Roque *et al.*, 2018). Previous research on this species in Mexico shows that they were present in areas where forest cover was above 50%, being locally extinct below this threshold (Galán-Acedo, Arroyo-Rodríguez and Chapman, 2021). Previous work to identify thresholds of forest cover for communities in the Amazon and Atlantic rainforests in Brazil highlighted a 30-40% forest cover threshold to preserve the integrity of vertebrate communities (Banks-Leite *et al.*, 2014; Ochoa-Quintero *et al.*, 2015), and a recent review suggested that a global threshold of 40% forest cover could be used (Arroyo-Rodríguez *et al.*, 2020). The reason that the requirements are so much higher for the Geoffroy's spider monkey is likely due to their specialised diet of mature fruits and requirement for mature sleeper trees (van Roosmalen, 1980; Sorensen and Fedigan, 2000; Ramos-Fernández and Ayala-Orozco, 2003; Urquiza-Haas, Peres and Dolman, 2009).. In a study of African bird species, declines in overall richness were seen below 42% forest cover, however for species with more specialised diets, diversity started to decline once forest cover was below 74%, suggesting more specialist species require higher thresholds of forest cover (Kupsch *et al.*, 2019). Although reported community based thresholds are lower, it is recognised that higher thresholds may be needed in the tropics (Arroyo-Rodríguez *et al.*, 2020), and blanket thresholds such as this do not take into account local differences in species thresholds or for more sensitive species (Banks-Leite *et al.*, 2021).

In this study, occurrence probability was similar across old growth and secondary forests, as found previously in the same region (Weghorst, 2007). However, studies conducted in other regions have found that spider monkeys generally prefer continuous tracts of old growth forests (van Roosmalen, 1980; Sorensen and Fedigan, 2000; Ramos-Fernández and Ayala-Orozco, 2003; Parry, Barlow and Peres, 2007; Urquiza-Haas, Peres and Dolman, 2009), and occur in secondary forests at significantly lower levels (Ramos-Fernández and Ayala-Orozco, 2003; Ramos-Fernandez *et al.*, 2013).The reason for the disparity in these results is likely due to the definition and characteristics of secondary forests, which may vary across studies since the term secondary forest can be used to describe forests of varying age. Owing to the protected status of forests in Costa Rica, secondary forests are generally 30 years+ (Whitworth *et al.*, 2019), and the land use maps used in this study defined secondary forests as 40 years+ (Shrestha *et al.*, 2018), therefore secondary forests, as defined here, may be considerably more mature than forests in other studies. It is also possible that high levels of hunting in more accessible secondary and fragmented forests in other study regions, which reduce population densities of the Geoffroy's spider monkey (Peres, 2001; Aquino *et al.*, 2013), do not exist to the same levels here since the spider monkey is not the main target species in our study region.

3.4.2.2. Unsuitable Habitat

Previous studies have found use of shaded coffee (*Coffea spp*.) and cacao (*Theobroma cacao*) plantations by the Geoffroy's spider monkey, however this was only where plantations had a structure and spacing suitable for locomotion and when shaded with native forest, providing a diversity of mid and upper canopy structures and species for feeding, shelter, protection and resting (Estrada *et al.*, 2006). They have been also found to use live fences of mature trees (Estrada *et al.*, 2006; Arroyo-Rodríguez *et al.*, 2017a), however these studies suggest that they are only used as stepping stones to other, more favourable habitats. Studies of the Geoffroy's spider monkey rarely sample non-native forests, likely due to time and economic constraints of previous sampling methods, therefore there is limited evidence for their use. In our study we did not find use of non-native forest habitats, of grasslands or forestry plantations, suggesting that these habitats are not suitable for permanent or temporary use. This is likely due to the palm and teak plantations in the region having a much lower floral diversity than coffee and cacao plantations, highlighting the importance of planting native species in forest plantations to improve human-disturbed environments for wildlife. Studies of this species in mangrove ecosystems are also rare, however use of mangroves have previously been found (Eisenberg and Kuehn, 1966; Navarro-Fernández, Carmen and Escobedo-Cabrera, 2003). In our study we did not find them in this habitat, it is therefore possible that mangroves are not suitable.

A strong effect of paved roads has been previously found for species of mammal, owing to increased gap width and heavier traffic volume (Asensio, Schaffner and Aureli, 2012; Cibot *et al.*, 2015; Chen and Koprowski, 2016; Mulero-Pázmány, D'Amico and González-Suárez, 2016; Asensio *et al.*, 2021), alteration of roadside vegetation structure (Zhou *et al.*, 2020), secondary road development and increased human presence (Laurance, Goosem and Laurance, 2009). The Geoffroy's spider monkey has previously been found to cross both paved and unpaved roads to a similar degree in the north of Costa Rica, however only where canopy opening was small enough to facilitate locomotion (Asensio *et al.*, 2017). In our study we find that they responded very differently to paved roads, not being found at any site with primary (paved) road within a 1 km radius. Our results from variance partitioning show that very little of the variance attributed to this variable is shared, further highlighting the importance of primary roads on this species. This is the first time such an effect has been shown and provides further evidence as to the sensitivity of this species to human disturbance. The use of PAM in this study allowed us to cover a large enough area with enough sampling locations to reveal such an effect.

3.4.2.3. Limited Suitability

Density of secondary roads and human settlements were not found to significantly affect probability of occurrence or call rate. Despite these results the Geoffroy's spider monkey was only found in areas with limited levels of unpaved roads and buildings, suggesting that that cannot tolerate areas with high human development. Previous research in this area related to *Ateles* is lacking, with only one study on the effects of roads, where avoidance of unpaved roads was also found (Asensio *et al.*, 2017) and two studies related to human population size or buildings, where no separate effects were found (Van Hulle and Vaughan, 2008; Urquiza-Haas, Peres and Dolman, 2009).

3.4.3. Study Limitations, Wider Context and Conclusions

Whilst this study was successful in using PAM to study at a wide spatial scale and with high coverage, due to logistical constraints we were not able to cover the region uniformly. Sampling over a large spatial scale also meant that temporal analysis was restricted, missing seasonal variation in movement patterns that may exist due to the timing of fruiting trees. It is therefore possible that the spider monkey exists in other areas across the study region, however, the high number of sampling locations minimises any bias. The use of PAM as a methodology improves our ability to study across wide temporal scales, however as with other methods weather can limit accessibility and data collection. Heavy rain prevented our ability to hear most calling species in the recordings and likewise may limit the ability of the detector to classify calls. This limitation does however exist for other methodologies, since it is very difficult to visually detect or hear spider monkeys in the field during periods of heavy rain. Due to accessibility of sites we were also not able to complete fieldwork during a three-month period of the rainy season, however again, this is a limitation for not just PAM but all methodologies where access to field sites with challenging conditions are required.

Using PAM combined with an automated detector for the spider monkey call has allowed us to effectively determine the dispersal limitations and threats for a rare and endangered species over a large scale, whilst limiting the impact of our presence on the results. Our results corroborate previous research showing that the Geoffroy's spider monkey is highly sensitive to anthropogenic changes, requiring over 80% of forest cover and avoiding any paved roads within 1 km. We also highlight the dangers of paving roads through important habitat.

The automated detector developed for this study was costly in terms of time and expertise to develop, however, it can now be used in future studies of this species in the area, and potentially across its range. Developing automated detectors for noisy tropical regions is challenging and whilst we have missed some calls and potentially underestimated call rate, the results suggest that we have not underestimated occupancy, highlighting the value in this methodology. Future work should first focus on improving this detector by combining the original call database that we have for the region, of 580 calls, with the additional 3000 detected in this study. This detector can then be tested on the calls of *Ateles geoffroyi* across its range from Mexico to Colombia, to see if the calls are similar enough to be detected and background noise isn't substantially different to interfere in the classification process. As with human speech it is also possible in the future that this work could be expanded to train the algorithm to recognise individuals, paving the way for density-based studies. This work could be further expanded to the seven other species of spider monkey, all of which their main call is the whinny (Ramos-Fernández, 2008). All but one of these species are endangered, and one, the brown spider monkey, is critically endangered (IUCN, 2021), it is therefore essential to understand how they respond to changes across the landscape in human-modified environments, and this methodology could provide a means to effectively achieve this goal.

Chapter Four: The Functionality of a Protected Area to Provide Connectivity for the Geoffroy's Spider Monkey (*Ateles geoffroyi*)

Abstract

Background: Globally, protected areas (PAs) are one of the main approaches for biodiversity conservation, covering 17% of the terrestrial earth surface, yet only 20-50% of PAs are successful in protecting biodiversity. Connectivity between protected areas, and indeed between all patches of native habitat, is an essential aspect for the effective protection of biodiversity, however, recent estimates suggest that less than 10% of PAs are structurally connected via undisturbed habitats and most monitoring and planning even fails to take connectivity into account. In this study, we investigate whether a sustainable-use PA is effective in facilitating connectivity for an endangered forest specialist between two strictly protected national parks.

Methods: We used passive acoustic monitoring to collect data at 341 sites across the Osa Peninsula, Costa Rica and assess occurrence of the Geoffroy's spider monkey across the PA network in the region. We used habitat suitability modelling to predict suitable habitat for the spider monkey and identify potential barriers to connectivity. Finally, we use least-cost analysis to determine an ideal biological corridor and predict potential bottlenecks.

Results: Our results show that the Golfo Dulce Forest Reserve, a large sustainable-use PA, is acting as a buffer to Corcovado National Park and is able to support populations of the Geoffroy's spider monkey. However, as the Geoffroy's spider monkey was undetected in Piedras Blancas National Park and occurrence was limited to the area surrounding Corcovado, it is possible that this Reserve is not facilitating connectivity as intended. Primary roads and low forest cover were the most important

predictors of poor habitat suitability, both acting as barriers to connectivity and potentially impeding the conservation of an endangered species.

Implications: As the global community commits to protect at least 30% of the Earth's surface, it is essential to consider connectivity to ensure the effective protection of biodiversity, especially under predicted climate change scenarios. We show that paved roads and areas of low forest cover are major barriers to connectivity across the network of PAs, findings which can help future restoration efforts in the region to improve conservation outcomes.

4.1. Introduction

The world is in a period of rapid biodiversity loss (Ceballos *et al.*, 2015) and PAs are becoming ever more important for conserving biodiversity (Laurance, Useche, *et al.*, 2012; Watson *et al.*, 2014). Connectivity between protected areas is one of the essential aspects for sustaining viable populations of species, especially with the threat of climate change (Laurance, Carolina Useche, *et al.*, 2012; Stewart *et al.*, 2019). When assessing the effectiveness of PAs in preserving biodiversity, it is therefore essential to evaluate if they are connected. However, currently, connectivity across the PA network is generally absent from reporting procedures (Ward *et al.*, 2020).

PAs are considered a key tool in tackling biodiversity loss (Watson *et al.*, 2014; Gray *et al.*, 2016). They are implemented to conserve ecosystems and wildlife, whilst having a wider role in contributing to local livelihoods, tourism and in the mitigation of and adaptation to climate change (UNEP-WCMC and IUCN, 2016). The 2020 Strategic Plan for Biodiversity called for the protection of 17% of terrestrial areas by 2020 (CBD, 2010) and it is expected that targets for 2030 will be set at 30% (Waldron *et al.*, 2020). Whilst more land is being protected, the quality of protection is falling short (UNEP-WCMC and IUCN, 2016), sparking a debate over whether we should be focusing on improving the effectiveness of current PAs instead of protecting more land (Lacerda, 2004; Laurance, Useche, *et al.*, 2012; UNEP-WCMC and IUCN, 2016; Geldmann *et al.*, 2019).

Connectivity across a PA network is essential for the effective protection of biodiversity (UNEP-WCMC and IUCN, 2016; Ward *et al.*, 2020). The 2020 Strategic Plan for Biodiversity states that PAs should be well connected to each other (CBD, 2010) and studies have recommended that PAs should be integrated into wider planning, with the connecting habitat receiving equal attention to the PA itself to facilitate the movement of wildlife (Laurance, Useche, *et al.*, 2012; Stewart *et al.*, 2019). Yet globally, over 90% of PAs are currently not connected via undisturbed land (Ward *et al.*, 2020). For example, structural connectivity within Borneo's current system of PAs was measured at less than 20% (Proctor, McClean and Hill, 2011). Owing to their transient nature and often threatened status, mammals are consistently found to survive as isolated populations in PAs and be threatened by lack of connectivity across Asia and Europe (Bleyhl *et al.*, 2017), Australia (Ottewell *et al.*, 2019), Africa (Brennan *et al.*, 2020) and Latin America (Mendoza *et al.*, 2013). Studies have identified several common barriers to connectivity, including lack of native vegetation, roads, infrastructure and human settlements, artificial water sources and fences (Mendoza *et al.*, 2013; Pardo Vargas *et al.*, 2016; Bleyhl *et al.*, 2017; Tucker *et al.*, 2018; Ottewell *et al.*, 2019; Brennan *et al.*, 2020).

Both structural and functional connectivity between landscapes allows for access to suitable food sources, shelter, facilitation of gene flow and the dispersal and migration of species, thereby allowing populations to colonise and access new habitats and respond to shifts in habitat and climate (Crooks and Sanjayan, 2006; Barrows, Fleming and Allen, 2011; Rudnick *et al.*, 2012). In addition to species-specific benefits, connected landscapes increase ecosystem functionality and resilience (Beller *et al.*, 2019). Urbanisation and person-made infrastructures, farming, unsustainable forestry and mining has led to loss and fragmentation of forests and is known to breakdown natural connectivity (Tucker *et al.*, 2018; Watson *et al.*, 2018), reducing the resilience of species and ecosystems and ultimately reducing species population viability (UNEP, UNEP-WCMC and IUCN, 2020). As species are increasingly being forced to survive in human modified landscapes (Gardner *et al.*, 2009) the connectivity between PAs will be essential for the preservation of biodiversity (UNEP-WCMC and IUCN, 2016).

Areas with a lower category of protection are generally not as effective at protecting wildlife (Carrillo, Wong and Cuarón, 2000; Lacerda, 2004). There are seven categories of IUCN PAs. National parks (Category II) are large areas set aside to conserve ecological processes, species and ecosystems, with visitor use being limited (IUCN, 2014). Category VI (PA with sustainable use of natural resources), the least restrictive in terms of its conservation requirements, is designed to conserve ecosystems, habitats and species, whilst permitting sustainable use of the area in a way that protects nature (IUCN, 2014). Whilst PAs in lower categories may not be as effective in protecting biodiversity, their wide-spread use and use as areas to facilitate connectivity, makes it essential to ensure these areas are effectively protected and are both structurally and functionally connected for the free movement of wildlife.

By the 1970s Costa Rica had lost over half of its forests. Over the last 50 years, a system of almost 200 PAs covering 26% of its land, together with strong national policies, restoration programmes and subsidies for landowners, has turned this small country into a global leader in conservation (González-Maya *et al.*, 2015; Kappelle, 2016). The system appears to be effective in reducing forest loss, with national parks under strict protection (IUCN category l and ll) almost completely halting deforestation (Sánchez-Azofeifa *et al.*, 2002; González-Maya *et al.*, 2015). Despite these successes, the country's PA network has grown far beyond current human and financial resources required to maintain it and high human pressure in the surrounding areas is reducing connectivity across the PA network (Sánchez-Azofeifa *et al.*, 2002; Bovarnick, 2007). In a global study of connectivity, Costa Rica was found to have just 2.5% of its PA network connected (Ward *et al.*, 2020).

Of top priority for the Osa region in Costa Rica, is the maintenance of connectivity between core PAs on the peninsula and connectivity with the rest of Costa Rica and Central America (Ankersen, Regan and Mack, 2006). The Osa Peninsula contains three core PAs, Piedras Blancas and Corcovado National Parks (IUCN Category II) and a Ramsar wetland site, the Terreba-Sierpe Wetlands, the Golfo Dulce Forest Reserve (IUCN Category VI) and several smaller privately managed wildlife refuges

(Figure 1). These PAs, together with a growing ecotourism industry and foreign investment, have helped to preserve large areas of forest on the peninsula (Ankersen, Regan and Mack, 2006). Despite a large portion of the area being under some level of protection and ongoing conservation efforts over the last 40 years, there are still numerous challenges across the Osa region resulting from loss and isolation of forests and limited resources leading to lack of enforcement against illegal logging, hunting and mining (Ankersen, Regan and Mack, 2006). The main purpose of the Golfo Dulce Forest Reserve is to provide connectivity between core PAs; in this study we investigate whether this PA is effective in facilitating connectivity across the PA network as intended.

We chose to use the Geoffroy's spider monkey to model connectivity, firstly due to its historic occurrence across the region. This species was hunted to extinction in the region in the early-mid 20th century, with only a small remnant population surviving in Corcovado National Park (pers comms, J.Espinoza, July 2018). A study in 2000, after the designation of the Golfo Dulce Forest Reserve, found very low numbers of the Geoffroy's spider monkey in the Reserve, suggesting that there has been some recovery of the species (Carrillo, Wong and Cuarón, 2000), but we do not know the extent of this recovery and if the reserve is facilitating connectivity for this species between Corcovado and Piedras Blancas National Parks as intended. Secondly, the Geoffroy's spider monkey has a critical function in the ecosystem; the productivity of their latrine sites and seed dispersal of hardwood species alters the structure of the forest, owing to this they have been cited as ecosystem engineers (van Roosmalen, 1980; Whitworth et al., 2019) and are an important species to protect. Finally, they require large areas of undisturbed mature forest and are therefore particularly sensitive to forest loss and fragmentation (Boyle and Smith, 2010; Ramos-Fernández and Wallace, 2010), making them a forest specialist (Arroyo-Rodríguez et al., 2017a) and an ideal case to study the connectivity of native habitat.

To do this we ask the following questions: 1. Where does the Geoffroy's spider monkey occur across the PA network? 2. Where does suitable habitat exist for the Geoffroy's spider monkey? 3. Is the

Golfo Dulce Forest Reserve facilitating connectivity across the PA network? 4. What and where are the barriers to connectivity? 5. How can we mitigate against any lack of connectivity?

4.2. Methods

4.2.1. Study Site

Our study area covers 1093 km^2 in the South Pacific coast of Costa Rica. The terrain is generally low altitude, with a maximum elevation of 792 meters. Mean annual rainfall ranges from 3,000-6,500 mm and mean yearly temperature is 27 ^{o}C, with high levels of humidity throughout the year. There are two distinct seasons, wet and dry season, with the highest rainfall occurring September through December (Gilbert *et al.*, 2016). The peninsula contains the last remnants of tropical broadleaf evergreen lowland rainforest on the Central American Pacific (Gilbert *et al.*, 2016), imbedded within a mosaic of pasture, plantations and urban centres (Figure 4.1.a). Due to the geology and geography of the area, the peninsula contains high levels of biodiversity and endemism (Sánchez-Azofeifa *et al.*, 2002).

Managed under the Area de Conservacion Osa (ACOSA), the Osa Peninsula contains three core PAs, Piedras Blancas and Corcovado National Parks (IUCN Category II) and a Ramsar wetland site, the Terreba-Sierpe Wetlands, all under strict protection. There is also the Golfo Dulce Forest Reserve (IUCN Category VI) and nine smaller private and public wildlife refuges, with no designated level of protection (Figure 4.1 b). The Terreba-Sierpe wetlands (30,654 ha) were declared a national park in 1997, Corcovado (42, 560ha) in 1975, Piedras Blancas (14,019ha) in 1992 and the Golfo Dulce Forest Reserve (60,000ha) in 1979 (Sánchez-Azofeifa *et al.*, 2002; Osa Conservation, 2016; Gutierrez *et al.*, 2019). The Golfo Dulce Forest Reserve (IUCN Category VI) is a mixed-use reserve, where sustainable use of natural resources is permitted, but restrictions on owning land and both construction and extraction of resources, including timber and wildlife, are in place (Carrillo, Wong and Cuarón, 2000;

Ankersen, Regan and Mack, 2006). This area was initially designated with the aim to protect a buffer around Corcovado National Park and for managed forestry activities. After the creation of Piedras Blancas National Park in 1992, its role was prioritised to provide connectivity with Corcovado National Park. The Osa Biological Corridor was later created to protect forests between and around all PAs on the peninsula, with the additional objective to link these areas with the rest of Costa Rica and the Mesoamerica Biological Corridor (Ankersen, Regan and Mack, 2006). This area will not be considered for the purposes of this study since its boundaries are under review, the committee for its designation and protection is no longer functional and it is yet to be inscribed into the national system or receive any formal protections (pers comms, W. Barrantes, July 2021).

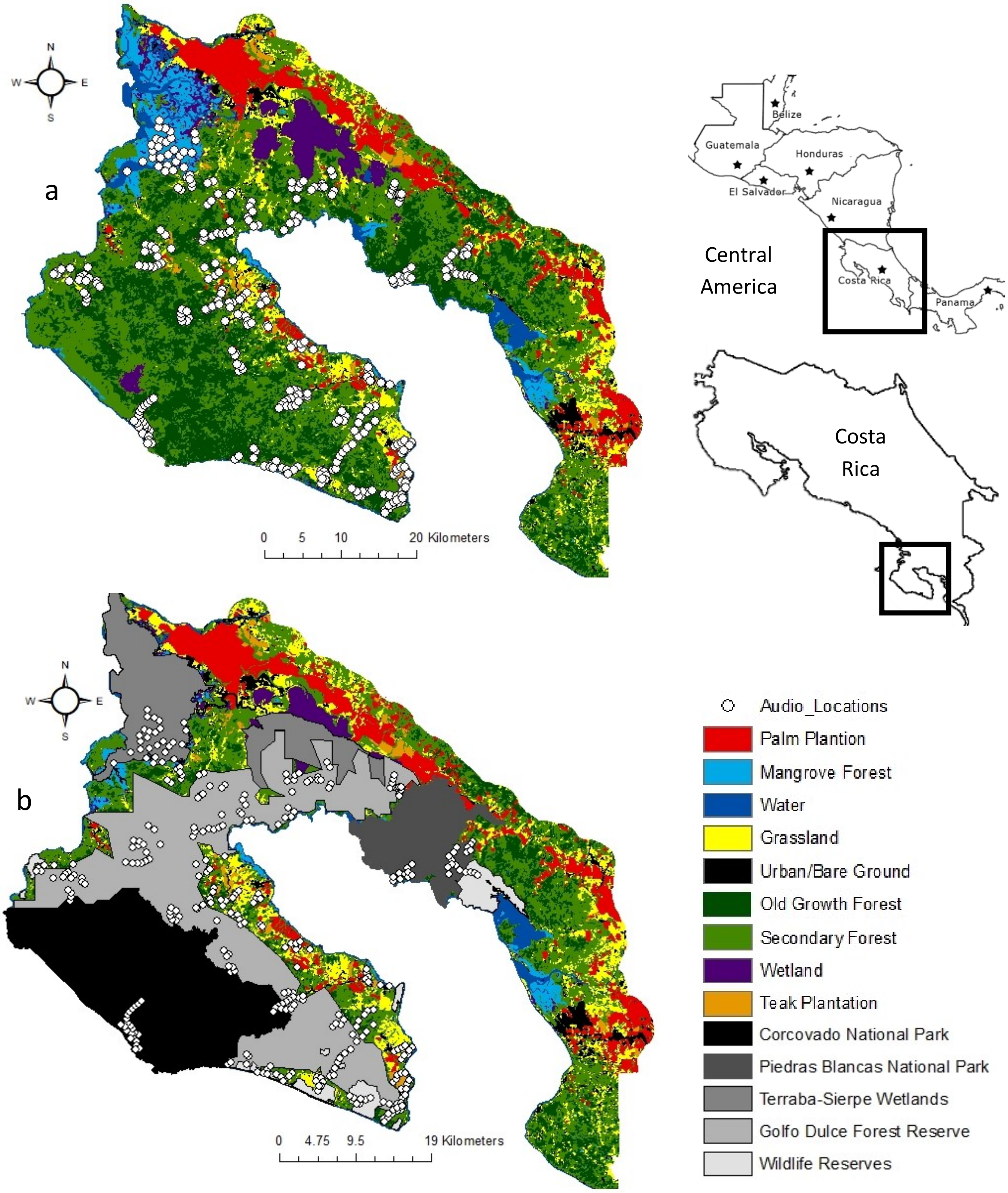


Figure 4.1 a. Land Use Map of the Osa Peninsula Land use map of the Osa peninsula containing nine land use categories, created at a scale of 5 x 5 m using Landsat 5 Thematic Mapper (TM) and Landsat 8 Operational Land Imager (OLI) (Shrestha *et al.*, 2018). **b. Protected Area Map of the Osa Peninsula**. White circles represent the sample sites where each audio recorder was placed.

4.2.2. Study Species

The Geoffroy's spider monkey is currently classified by the IUCN as Endangered and globally its population is expected to decline by 50% within a 45 year period (Cortes-Ortíz *et al.*, 2021). They are found from south-eastern Mexico to north-western Colombia (Di Fiore, Link and Campbell, 2011). The Geoffroy's spider monkey is a large-bodied primate with home ranges of up to 4 km^2, a frugivorous diet and requirement for large mature trees as sleeping sites (van Roosmalen, 1980; Chapman, 1989; Sorensen and Fedigan, 2000; Zaldívar et al., 2004; Weghorst, 2007; Wallace, 2008a, 2008b; Arroyo-Rodríguez et al., 2017a)**.** Due to this, they require large areas of undisturbed mature forest and are therefore particularly sensitive to forest loss and fragmentation (Boyle and Smith, 2010; Ramos-Fernández and Wallace, 2010).

4.2.3. Sampling Design

Land use at each site was calculated using land use maps provided by NASA, created at a scale of 5 x 5 m using Landsat 5 Thematic Mapper (TM) and Landsat 8 Operational Land Imager (OLI) (Shrestha *et al.*, 2018) (Figure 4.1.a). The map was classified into nine land use categories, with recordings for this study taken in old growth and secondary forests, palm and teak plantations, mangroves and grassland sites Figure 4.1.a). Protection level for each site was calculated using GIS layers of national park, reserve and wildlife refuge borders (Figure 4.1.b). All points located outside a PA were classified as unprotected. Wetlands, water and urban areas were excluded from the analysis due to inaccessibility. Wetlands also consist mainly of a single species of fern and contain no fruiting trees, which due to body mass and dietary requirements, it is unlikely that the spider monkey would use.

To ensure a representative number of sampling sites were chosen across each land use and protection category, we used a stratified sampling approach. We calculated the percentage cover of each land use and protection category across the region and placed a representative number of recorders in each area. To ensure even coverage of the study region we selected sampling locations in a uniform distribution across the Osa Peninsula. Due to access issues it was not possible to randomly choose sampling locations, therefore, to ensure independence among sampling locations, the first recorder in each accessible area was placed by walking 500 m in a random direction and the remaining placed at a minimum of 500 m apart. Where possible, trails were not used to avoid bias, however, where this was not possible, devices were placed a minimum distance of 200 m perpendicular to a trail; as indicated by GPS. Non-audio data were collected for each point including GPS location, elevation and land use, to verify data from NASA land use maps. For more information on sampling design please see Chapter One.

Given that biotic sounds generally travel a maximum distance of 200 m (Figueira *et al.*, 2015), we used a minimum distance of 500 m between recorders, ensuring independence in the samples and avoiding pseudo-replication. Recording devices were also placed at a minimum distance of 200 m from habitat boundaries, to ensure sounds were solely from the classified habitat.

Data were collected at 341 sites totalling 60,000 hours of recordings. Recordings were obtained using Audio Moth devices (Open Acoustics Devices, UK). Recorders were set to operate for seven consecutive days to increase the chances of detecting the spider monkey if they were present. The devices were set to record on a schedule of 05:00-09:30, 14:00-18:30 and 21:00- 03:00, to ensure data were collected at key periods of spider monkey activity (Wallace, 2001) including the periods of night activity (Whitworth *et al.*, 2019). We recorded constantly over the recording schedule at a sample rate of 48000 kHz, 2.5 times higher than the maximum call of the Geoffroy's spider monkey. Sampling was conducted within dry season (December-August) due to restricted access to many areas of the study site during wet season.

4.2.4. Statistical Analysis

4.2.4.1. Explanatory Variables

We installed audios in six of the nine land use categories: Old growth and secondary forest, mangrove forests, grassland, palm and teak plantations. We did not place recorders in urban areas due to restrictions on recording in public spaces or in wetlands or water due to inaccessibility. Protection level for each site was calculated using GIS layers of national park, reserve and refuge borders (Figure 4.1 b). If points were located outside of the PAs, they were classified as unprotected. Distance to Corcovado National Park was measured as a way to quantify how far the spider monkey has dispersed from the park and was calculated using distance across land mass between each point and the park. All GIS work was carried out in ArcGIS software v.10.6 (ESRI, 2011).

The data showed complete separation across protection, which happens when a combination of the explanatory variables produces a perfect prediction of the response variable (Albert and Anderson, 1984). This led to high standard errors, confidence intervals and p-values. To account for this, protection was fitted separately in package *brglm2* (Kosmidis, 2020) that can model complete separation. We fitted other models in the *nlme* (Pinheiro, Bates and DebRoy, 2020) and *lme4* package (Bates *et al.*, 2015).

4.2.4.2. Development of an Automated System for Signal Classification

To extract the spider monkey calls from the audio recordings an algorithm was developed together with the Department of Computing, Imperial College London. We ran data from all 341 sites through the model algorithm, listened to all positive outputs and marked the number of true positive detections per day per site. All analysis was carried out in Python v.3.6 (Van Rossum and Drake, 2009). For more information on the development and validation of this model see Chapter Three.

4.2.4.3. Generalised Linear Models

To determine the naïve probability of occurrence of the spider monkey across our study site, we used logistic regression with a logit link function. Site occurrence was calculated by combining daily detection histories into one parameter, coded as 1 or 0 for presence or absence per site. We used residual plots from logistic regression models to assess violations in model assumptions. Plots showed no significant overdispersion, deviation from the expected distribution or heteroscedasticity in the residuals (Supplementary Information 3.1- Figure 3.1 & 3.2). Bonferroni's correction for multiple pairwise comparisons was applied to adjust p-values and reduce the risk of type I errors.

4.2.4.4. Spatial Autocorrelation

Due to the nested structure in the data, we tested for spatial autocorrelation across all generalised linear models. We created a distanced based weight matrix using model residuals and sampling site coordinates. Using *gstat* package (Pebesma, 2004) we then produced a variogram plot to visually determine the presence of autocorrelation. Points should roughly run in a horizontal line from the y-axis if no autocorrelation is present. Finally, we calculated the Moran's I statistic in *ape* package (Paradis and Schliep, 2019). If no autocorrelation is present, then the observed autocorrelation should be close to 0 and to the expected value.

Spatial autocorrelation was found across all models, violating the spatial independence assumption of regression analysis. To account for this, we constructed a spatial auto-covariate that was included as an additional predictor variable. For each site we calculated a distance-weighted average of neighbouring response values, using a minimum neighbour's distance of 210 m, with sites further away receiving lower weightings (Dormann *et al.*, 2007). To test whether the auto-covariate function reduced autocorrelation in the residuals we used Moran's I statistic. No autocorrelation was present across the models when the auto-covariate function was added (Supplementary Information 3.1- Table 3.1). We then used the Likelihood-ratio test and AIC to determine if the addition of an auto-covariate function improved model fit. In cases where the auto covariate function reduced autocorrelation but model fit remained equal, it was still included in the model (Supplementary Information 3.1- Table 3.2)

4.2.5. Habitat Suitability Modelling

Presence-absence data used to calculate habitat suitability for the spider monkey were based on acoustic data collected and analysed from the above 341 sites. An automated detection and classification algorithm for the spider monkey call, the whinny, used to determine presence in the recordings, returned a total of 64 occupied and 271 unoccupied sites (see Chapter Three for more details) (Figure 4.2).

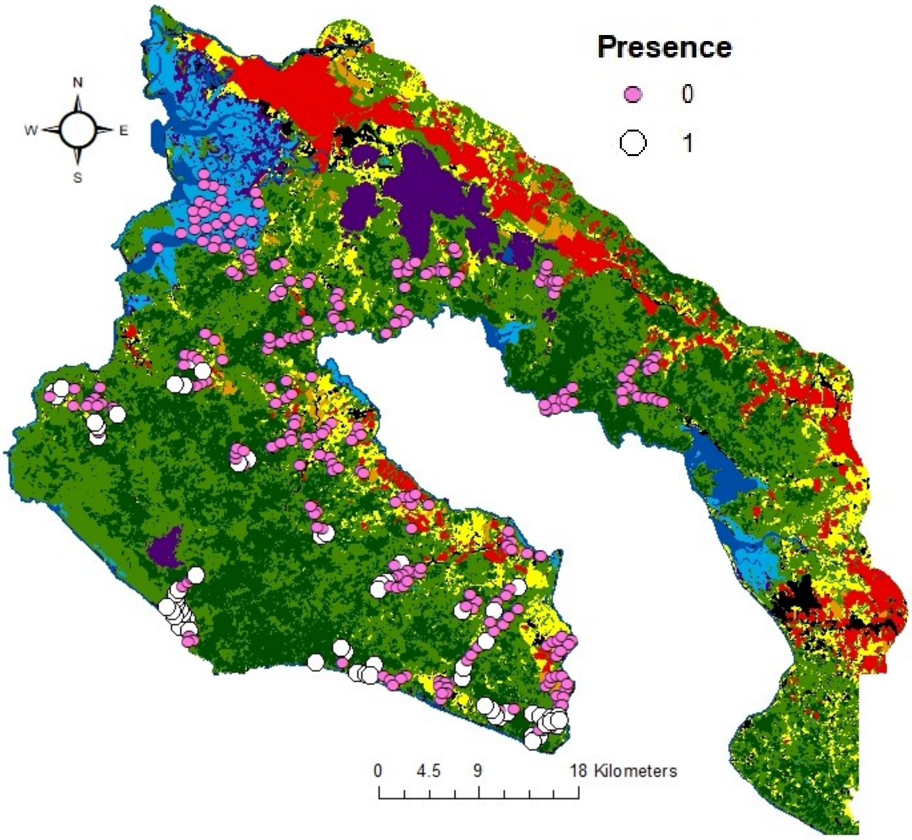


Figure 4.2. Presence and Absence Map for the Geoffroy's Spider Monkey. Land use map of the Osa peninsula containing nine land use categories, created at a scale of 5 x 5 m using Landsat 5 Thematic Mapper (TM) and Landsat 8 Operational Land Imager (OLI) (Shrestha *et al.*, 2018). White circles

represent the locations where the study species was recorded as present and pink circles where it was recorded as absent.

4.2.5.1. Selection of Explanatory Variables

In Chapter Three, land use, forest cover and primary road density were all found to significantly affect occurrence probability of the spider monkey. Area of buildings and density of secondary roads had a non-significant negative effect (For further information see Chapter Three). Forest cover, primary and secondary road density and area cover of buildings were considered for inclusion in the habitat suitability model. Land use was excluded as it represented the same measure as forest cover.

It is recommended that to correctly assess a species response to predictor variables, the variables should be measured at the scale at which the species-landscape relationship is the strongest (Jackson and Fahrig, 2015; Galán-Acedo *et al.*, 2019). To assess the scale of effect of forest cover, primary (paved) and secondary (unpaved) roads and buildings, we calculated percentage forest cover (%), the density of roads (km) and the area of buildings (km^2) in a buffer around each site at intervals between 100-5,000 m radius for forest cover and 100-1,000 m for roads and buildings (see Supplementary Information 2.1. Table 2.6). We then tested at which scale the variables had the strongest effect on the spider monkey. We created GIS layers for roads and buildings across the study site using satellite images. Roads were separated into primary for paved roads and secondary for smaller non-paved roads.

Using spider monkey presence as the response variable, the strongest response to forest cover was at a radius of 200 m (R^2=0.77), although the response remained strong until we reached a radius of 2000 m. For secondary roads, the strongest response was at a radius of 200 m (R^2=0.09) however all spatial distances showed a similar response (mean R^2= 0.07, SD=0.01). For primary roads and buildings, the strongest response was at a radius of 1000 m (R^2=0.6 and R^2=0.22). Each explanatory variable was therefore measured at these scales.

Using NASA land use maps and feature layers of roads and buildings, we constructed raster layers for each explanatory variable in ArcGIS software v.10.6 (ESRI, 2011). We calculated percentage forest cover by reclassifying land use maps into native forest cover or other land use, since native forest cover was a key driver for spider monkey occupancy (see Chapter Three). We then calculated forest cover for each pixel at radius of 200 m around the sampling point (Figure 4.3). Mangrove forests of the Terreba-Sierpe wetlands were classified as 'other land use' and not native forest cover. This decision was taken as the study species was absent from this land use (see Chapter Three) and classification as native forest cover would have likely deemed these areas as suitable in the absence of land use as an explanatory variable in the habitat suitability model. Wetland areas were not surveyed due to the area being inaccessible, however flora in this area is predominantly a species of fern and so was also classified as zero forest cover. The same was done for density of secondary roads at a radius of 200 m and 1000 m for primary roads and area cover of buildings. All maps were created with the same projection system, resolution and extent (Figure 4.3).

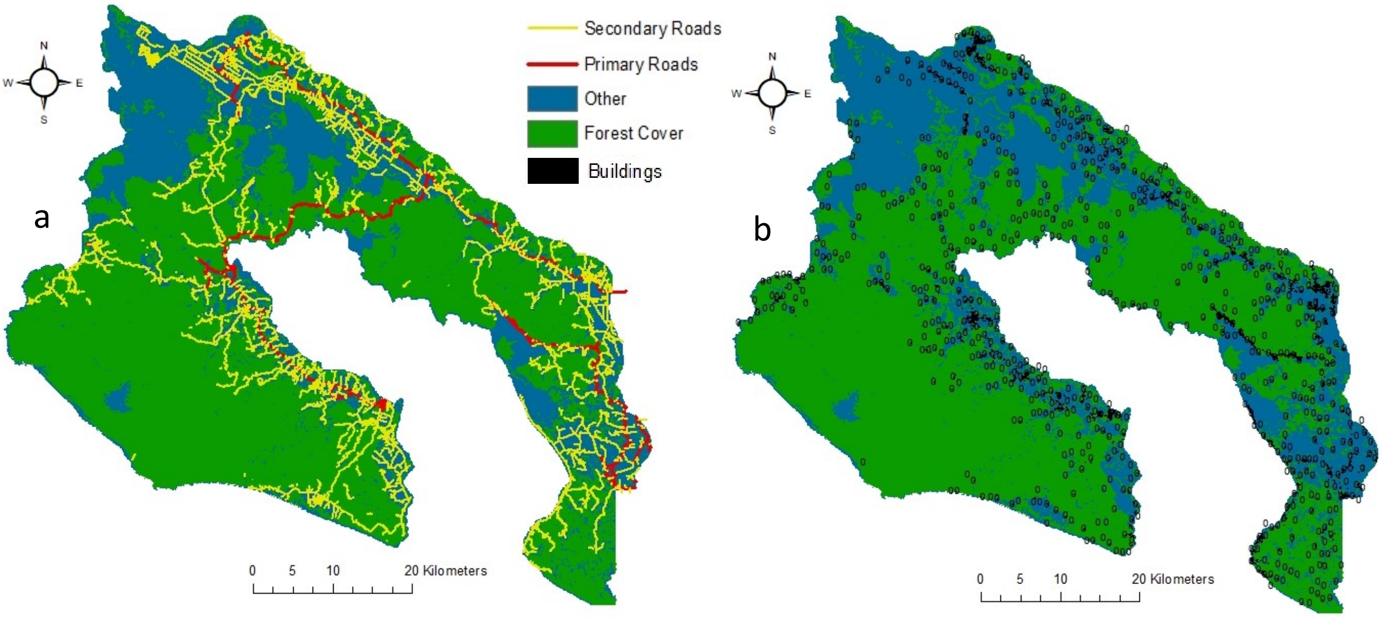


Figure 4.3.a. Forest Cover and Roads Map. Forest cover map of the Osa peninsula showing native forest cover in green and non-forested areas (including mangrove forests) in blue with primary (paved) roads in red and secondary (non-paved) roads in yellow and **b. Forest Cover and Buildings**

Map. Forest cover map of the Osa peninsula showing native forested areas in green and non-forested areas in blue and buildings in black.

Collinearity between explanatory variables decreases the efficiency and increases the uncertainty in species distribution modelling (De Marco and Nóbrega, 2018). Correlation plots between explanatory variables revealed primary road and buildings to be highly correlated (R^2=0.73) (Supplementary Information 3.1- Table 3.2). Previous results suggest that primary road is more important for predicting occupancy probability for the spider monkey than buildings (see Chapter Three), and variable importance for the best performing model was higher for primary road (25.8) than for buildings (18) when all variables were included in the habitat suitability model. We therefore excluded buildings as an explanatory variable from the model.

4.2.5.2. Model Algorithms

Choice of modelling method in habitat suitability models can lead to highly different results, making model choice particularly important (Elith *et al.*, 2006; Marmion *et al.*, 2009; Thuiller *et al.*, 2009; Naimi and Araújo, 2016). It has recently been recommended to use an ensemble approach, where the outputs and predictions of several different models are considered (Araújo and New, 2007; Naimi and Araújo, 2016). We therefore tested eight different regression and machine learning models, all employing both presence and absence data, to test which was better at predicting habitat suitability: Generalized Linear Models (GLM), Generalized Additive Models (GAM), Boosted Regression Trees (BRT), Multivariate Adaptive Regression Spline (MARS), Classification and Regression Trees (CART), Multivariate Adaptive Regression Spline (MARS), Random Forests (RF), Support Vector Machine (SVM), and Flexible Discriminant Analysis (FDA).

4.2.5.3. Model Performance

Models were verified using a five-fold cross-validation procedure where data were randomly partitioned into training (70%) and testing datasets (30%) for five model runs to reduce any potential effects of spatial autocorrelation (Naimi and Araújo, 2016). TSS true statistic score (TSS) and Area Under the ROC (Receiver Operating Characteristic) Curve (AUC) were calculated and used to test the predictability of the model (Elith *et al.*, 2006; Naimi and Araújo, 2016). A TSS of > 0.5 indicates good predictability. The AUC value is calculated by summing the area under the ROC curve and provides a measure of how well the model can correctly classify presences and absences. An AUC of 0.5 indicates that the model is no better at predicting than by random chance, > 0.7 is considered adequate and, > 0.8 shows excellent model fit (Elith *et al.*, 2006; Naimi and Araújo, 2016). The ROC curve is used as a visual of measure model performance, with curves closer to the top-left corner indicating better performance (Supplementary Information 3.2- Figure 3.4). Fitted response curves and measures of variable importance, which show the strength and directionality of response and percentage of variation explained by that variable, were used to assess the relationship between explanatory variables and habitat suitability (Supplementary Information 3.2- Table 3.5).

4.2.5.4. Model Outputs

Habitat suitability scores were calculated across the study area ranging from 0-1; higher values indicate a more suitable habitat. To incorporate the predictions and assumptions of different models in predicting habitat suitability across the study region, we combined the best performing and biologically realistic models to improve the robustness of forecasting (Araújo and New, 2007; Naimi and Araújo, 2016). All statistical analysis were carried out in *sdm* package (Naimi and Araújo, 2016), in R 3.6.0 (R Core Team, 2020).

4.2.6. Corridor Design

Least-cost corridor and Circuitscape analysis were used to design a biological corridor between Corcovado and Piedras Blancas National Parks. Least-cost corridor analysis was performed using the Linkage Pathways tool 2.0 in ArcGIS (McRae and Kavanagh, 2011). This analysis maps least-cost pathways by assigning a value to each cell that reflects the energetic cost to a species moving through that area, using characteristics defined in the resistance map, such as forest cover and road density. Cost-weighted distance analysis between the core areas gives higher resistance scores to areas that are less suitable and low resistance scores to those that are considered suitable (McRae and Kavanagh, 2011).

For the model inputs, we created two vector layers in ArcGIS to represent the core areas that connectivity was to be mapped between, using the boundaries of Corcovado and Piedras Blancas National Parks. We then created a raster layer of resistance values by inverting the values of the habitat suitability map, so that cells with high suitability scores became areas of low resistance and visa-versa. The corridor was truncated at a threshold of 2 km to limit the corridor design to only those areas between and immediately surrounding the core areas (McRae and Kavanagh, 2011).

The linkage pathways tool outputs two corridor designs, a vector layer representing the single path of least resistance and a raster layer that assigns a resistance value to every cell, allowing alternative paths to be considered in the surrounding area if sections of the absolute least cost path are unsuitable. Higher values are given for cells that represent higher resistance values, and are therefore less suitable for inclusion within the corridor (McRae and Kavanagh, 2011). We chose to add a 2 km buffer width around the path of least resistance. This was chosen because previous research has shown that riparian corridors of up to 800 m wide may be suitable for many species of bird and mammals with smaller home ranges, however larger bodied, wider-ranging species, such as the spider monkey, white-lipped peccary and jaguar were found to be rare or absent at these widths (Lees and Peres, 2008). 2 km is the minimum recommended width of a biological corridor, to enable long-term genetic flow and recolonisation for corridor dwellers: those species that cannot pass through the corridor in a single event of hours or days (Beier, 2019). This width is suggested to be suitable for 96% of terrestrial mammals, any less than this and potential edge effects would severely reduce its viability (Beier, 2019).

To determine areas that are critical for connectivity, we used the Pinchpoint Mapper tool 2.0, part of the Linkage Mapper toolbox (McRae, 2012). Pinchpoint Mapper utilizes circuit theory to identify and map areas in the corridor where there are current constrictions to movement, such as bottlenecks. These areas represent sections where movement is already funnelled and where loss of suitable habitat could impede connectivity (McRae, 2012). We used the above corridor design and resistance maps as inputs and a 2 km cut-off for pinch points (McRae, 2012). The final maps were visualized in ArcGIS 10.8.

4.3. Results

4.3.1. Generalised Linear Models

The automated detection and classification algorithm for the spider monkey whinny returned a total of 2977 true positives across 64 out of 341 sites and 52,248 false positives.

4.3.1.1. Distance to Corcovado National Park

Occurrence decreased significantly with increasing distance from Corcovado National Park, with the Geoffroy's spider monkey only being found within 20 km of the national park (Figure 4.4. Supplementary Information 3.2- Table 3.3)

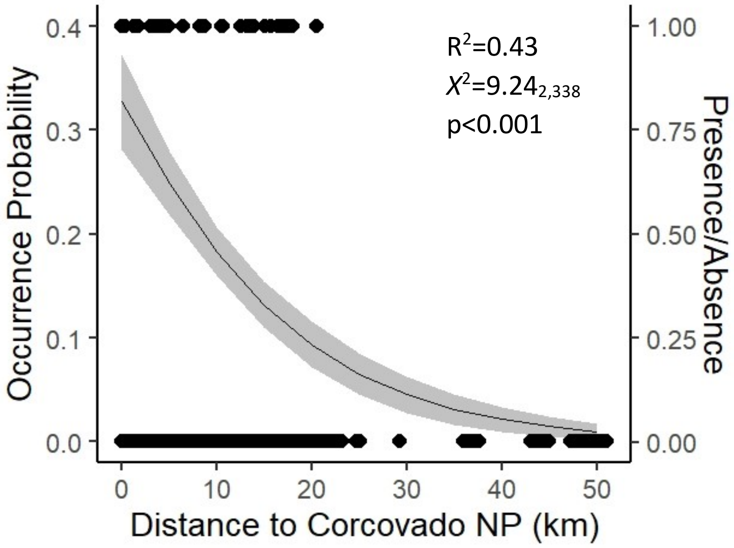


Figure 4.4. Model Results: Distance to Corcovado. Probability of occurrence on the y-axis and observed presence/absence on the z-axis (●) in relation to distance to Corcovado National Park. Shaded area represents 95% confidence intervals. R^2, X^2 and p values are annotated.

4.3.1.2. Protection

Results showed that 93% of the Golfo Dulce Forest Reserve is forested, compared to 92-96% within national parks (Piedras Blancas and Corcovado National Park respectively), 94% within the private wildlife refuges, and only 36% in unprotected areas, showing that forest cover is comparable in the reserve to levels in strictly PAs. Protection has a significant effect on the occurrence of the spider monkey (Figure 4.5). Private wildlife refuges and Corcovado National Park showed the highest probability of occurrence and were significantly different to all other areas, but not from each other (Figure 4.5. Supplementary Information 3.2- Table 3.4). The Golfo Dulce Forest Reserve showed significantly higher occurrence, when compared to unprotected areas and both Piedras Blancas National Park and the Terreba-Sierpe Wetlands. No significant differences were found between unprotected areas, Piedras Blancas National Park and the Terreba-Sierpe Wetlands, where few or no records of the spider monkey were found (Figure 4.5. Supplementary Information 3.2- Table 3.4)

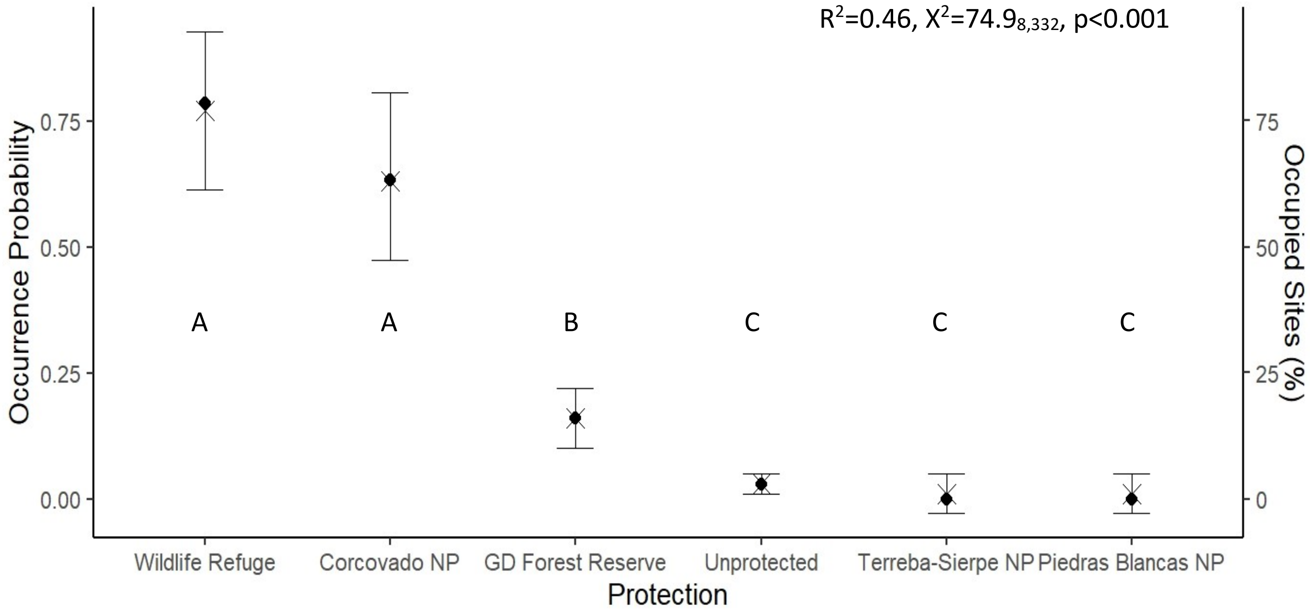


Figure 4.5. Model Results: Protection. Probability of species occurrence in each protection level on the y-axis (X), error bars represent 95% confidence intervals and percentage of occupied sites in each protection level on the z-axis (●). Pairwise differences between land use are indicated with letters A, B and C, where different letters represent a significant difference between land use. R^2, X^2 and p values are annotated.

4.3.2. Habitat Suitability Models

4.3.2.1. Model Performance

All models, with the exception of SVM, showed good performance, with AUC scores above 0.7 and TSS scores above 0.5. Random Forest (RF) was the best performing model with an AUC score of 0.8 and TSS score of 0.57. SVM was the worst performing model with an AUC score of 0.64 and a TSS score of 0.38 (Table 4.1. Supplementary Information 3.2- Figure 3.4).

Table 4.1. Habitat Suitability Model Performance Metrics. Performance metrics (AUC and TSS) for all eight modelling methods. Larger AUC and TSS values indicate better model performance.

Method	**AUC**	**TSS**
Generalized linear models (GLM)	0.76	0.55
Generalized additive models (GAM)	0.78	0.56
Boosted regression trees (BRT)	0.76	0.5
Random forests (RF)	0.8	0.57
Classification and regression trees (CART)	0.77	0.52
Flexible Discriminant Analysis (FDA)	0.76	0.52
Multivariate adaptive regression spline (MARS)	0.75	0.53
Support vector machine (SVM)	0.64	0.38

4.3.2.2. Variable Contribution

Forest cover was consistently the most important variable in predicting habitat suitability, with variable importance scores ranging from 40.4 - 54.4 %. Except for GAM and CART, primary road was the second most important variable in predicting habitat suitability (15.1 - 27.6 %), followed by secondary roads (3.1 - 24.6%) (Table 4.2). On visual inspection of the fitted response curves, only RF, FDA and SVM revealed biologically realistic patterns as expected from previous results where spider monkey occurrence showed a strong positive correlation with forest cover and negative correlation with both primary and secondary roads, with the effect being weaker in secondary roads (see

Chapter Three). Across other methods, one or more of the variables resulted in a flat line, indicating that the model is not correctly modelling the effect from the variable (Supplementary Information 3.2- Figure 3.5), these models were therefore not considered for use in the final ensemble model. SVM was also excluded from the final model due to poor performance scores (Table 4.1).

Table 4.2. Habitat Suitability Model Variance Explained. Results showing the percentage of variance explained in each model from the three different environmental variables: forest cover, primary and secondary road.

Method	**Forest Cover (%)**	**Primary Road (%)**	**Secondary Road (%)**
Generalized linear models (GLM)	41.9	27.6	3.1
Generalized additive models (GAM)	51.7	20.1	22.8
Boosted regression trees (BRT)	54.4	16.5	6.8
Random forests (RF)	44.1	24.9	13.2
Classification and regression trees (CART)	41.7	22.2	24.6
Flexible Discriminant Analysis (FDA)	33.8	15.1	5.4
Multivariate adaptive regression spline (MARS)	48.3	25	23
Support vector machine (SVM)	40.4	16.9	14.4

4.3.2.3. Ensemble Model

An ensemble model was constructed using a weighted average of RF and FDA models. AUC and TSS values were similar or higher for the ensemble model (Supplementary Information 3.2. Table 3.3).

Using this model, habitat suitability was predicted for the study area (Figure 4.6). The habitat suitability map showed, as expected from the variable contribution results above, that the most suitable habitat for the spider monkey are areas with 100% forest cover, more than 1 km from primary roads and not within close proximity to secondary roads and disturbed land use types (0.3-0.36). Areas with high forest cover but closer to secondary roads and disturbed land use types also appear to be quite suitable (0.25-0.30), however higher densities of secondary roads lead to a drop in habitat suitability. (0.15-0.25). Areas with no native forest cover, such as palm and teak plantations and grasslands or within close proximity primary roads had very low habitat suitability scores (0.05-0.15), and the lowest habitat suitability scores (<0.05) were found in areas where both primary roads and/or a high density of secondary roads occurred in the same area as low forest cover.

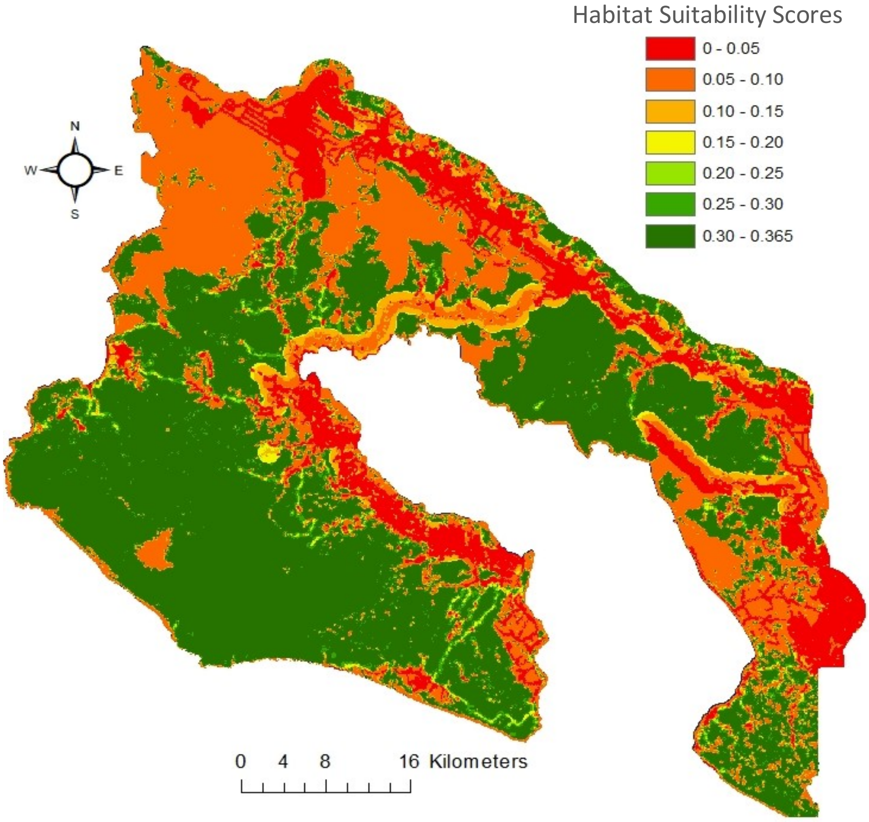


Figure 4.6. Habitat Suitability Model Map. Predicted habitat suitability map of the Osa Peninsula using an ensemble approach for the Geoffroy's spider monkey. Higher values and greener colours indicate more suitable habitat, warmer, redder colours and lower numbers indicate less suitable habitat.

4.3.3. Corridor Design

Least-cost corridor analysis highlighted the least-cost path of movement for the Geoffroy's spider monkey, shown as a single-celled black line and a heatmap of resistance values for all land cover pixels in between Corcovado and Piedras Blancas National Parks. Greener colours (lower values) represent areas with the least resistance and warmer colours (higher values) highlight areas with higher resistance to movement. A 2 km buffer zone around the absolute least-cost path shows the area to be included in the corridor if the corridor is designed in-line with the minimum recommended guidelines for corridor width (Beier, 2019) (Figure 4.7).

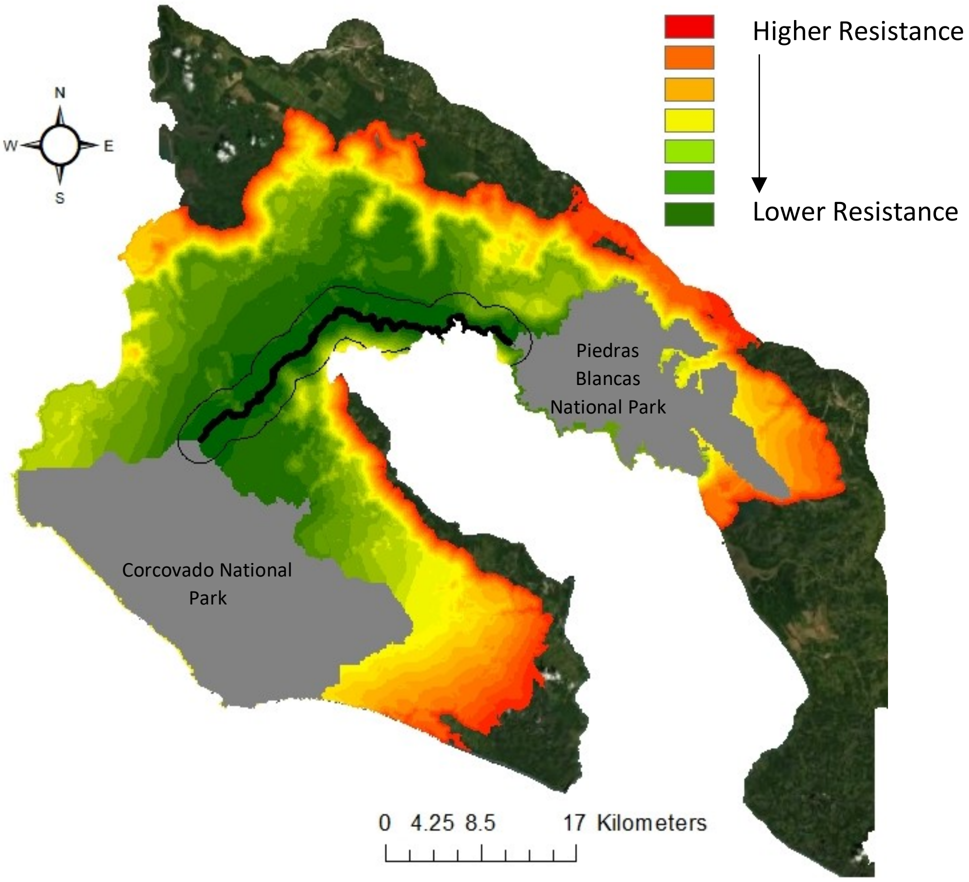


Figure 4.7. Least-cost Corridor Map. Least-cost Corridor Map showing the absolute least-cost path represented as a thick black line. Greener colours show areas with the least resistance to movement and warmer colours represent areas with higher resistance to movement. The buffer around the absolute least cost path represents the minimum corridor width of 2 km. Grey features represent core protected areas: Corcovado and Piedras Blancas National Parks.

Pinchpoint analysis highlights specific areas in the corridor where there are potential bottlenecks. Darker green colours represent areas where movement is less constricted and warmer colours represent areas where there are critical impediments to movement (Figure 4.8). One area within the 2 km buffer zone stands out as a potential bottleneck that could impede connectivity (Figure 4.8). This area represents a section of forest in between the primary road and Piedras Blancas National Park. Other potential bottlenecks exist in the middle of the corridor, representing areas where there are patches of grassland, palm and teak together with secondary roads.

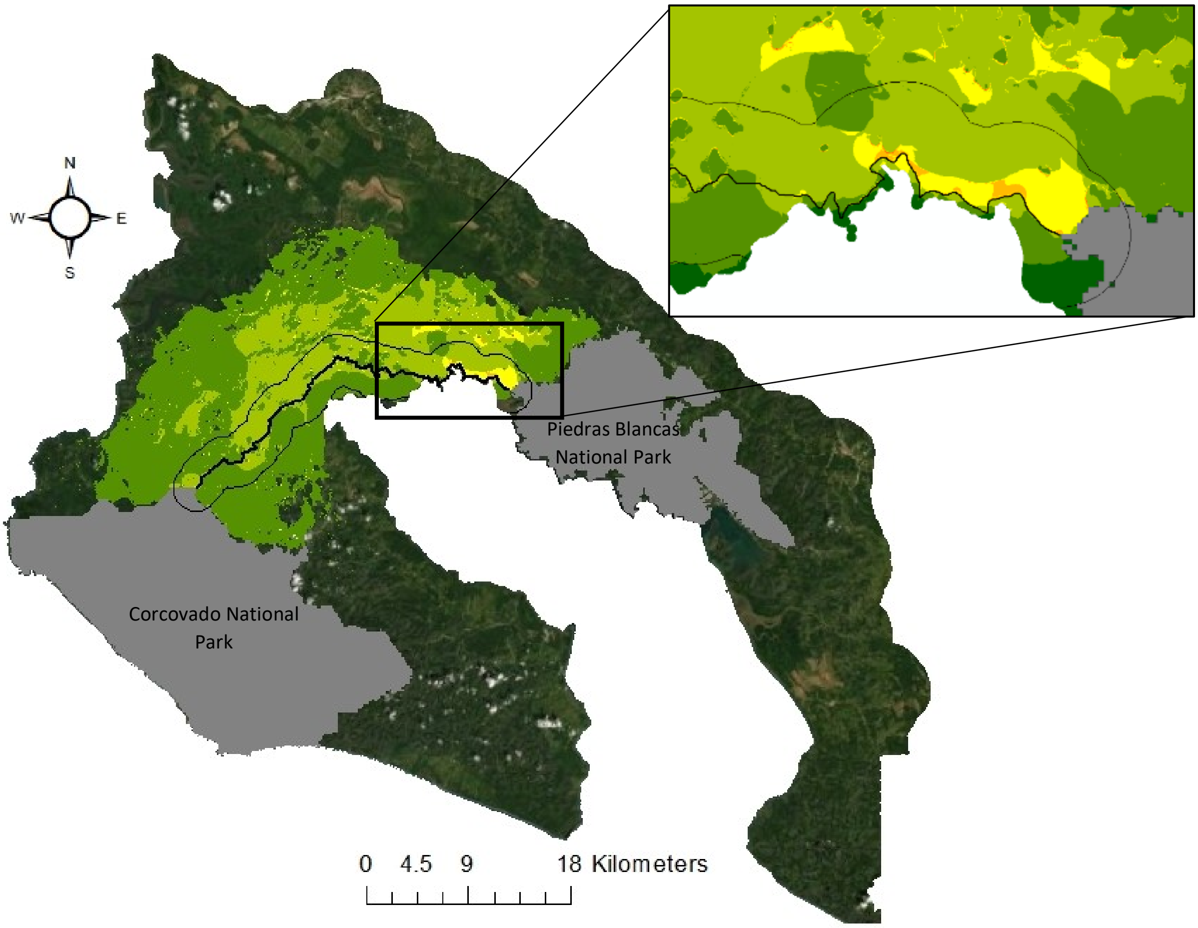


Figure 4.8. Pinchpoint Analysis Map. Darker green colours represent areas where movement is less constricted and warmer colours represent areas where there are potential bottlenecks. The zoomed-in portion of the map highlights the main bottleneck next to Piedras Blancas National Park

4.4. Discussion

In this study we investigated the effectiveness of a PA in facilitating connectivity between two core PAs for an endangered forest specialist. Results suggest that the Golfo Dulce Forest Reserve is providing habitat for the Geoffroy's spider monkey but does not seem to be facilitating connectivity across the PA network for this species . The Geoffroy's spider monkey was undetected in Piedras Blancas National Park and despite large areas of suitable habitat in the Golfo Dulce Forest Reserve, they were not found more than 20 km from Corcovado National Park. The main barrier to connectivity is an area where a primary road intersects Piedras Blancas National Park. We also found sections in the middle of the Golfo Dulce Reserve where a mix of pasture, plantations and secondary roads are reducing landscape permeability. If the Golfo Dulce Forest Reserve is to facilitate connectivity for sensitive species between Corcovado and Piedras Blancas National Parks as intended, then mitigation strategies are needed. We indicate the exact location of the bottleneck, where investment to improvement to connectivity would likely produce the most significant conservation outcomes.

4.4.1. Functionality of the Golfo Dulce Forest Reserve

The absence of the Geoffroy's spider monkey from the Golfo Dulce Forest Reserve immediately before its designation (pers comms, J.Espinoza, July 2018) and subsequent detection here, shows that this species is now able to survive in the reserve area, albeit at lower occupancy than Corcovado National Park. Studies have revealed a similar pattern for other large-bodied mammals in the region. In 2000, jaguar (*Panthera onca*), puma (*Puma concolor*), Baird's tapir (*Tapirus bairdii*), and peccary (*Pecari spp*) were found in Corcovado, but were absent from the Golfo Dulce Forest Reserve (Carrillo, Wong and Cuarón, 2000), yet 20 years later, all of these species are now found in the reserve (Soto *et al.*, 2021). This shows that the Reserve is providing additional habitat for native fauna and is likely mitigating edge effects for Corcovado National Park.

4.4.2. Connectivity within the Golfo Dulce Forest Reserve

The Golfo Dulce Forest Reserve was intended to facilitate connectivity between Corcovado and Piedras Blancas National Park, however, the fact that spider monkeys remain undetected more than 20 km from Corcovado and within Piedras Blancas, suggests that they cannot utilise the entire reserve area. Our results, corroborated by previous studies (Sorensen and Fedigan, 2000; Ramos-Fernández and Ayala-Orozco, 2003; Urquiza-Haas, Peres and Dolman, 2009; Asensio *et al.*, 2017), imply that this is due to a lack of connectivity, impeded by a paved road and areas of low forest cover, mainly owing to pasture and palm plantations. Similar to our findings for the Geoffroy's spider monkey, occurrence of jaguar, Baird's tapir and white-lipped peccary (*Tayassu pecari*), are also limited to areas around Corcovado and these species remain undetected in Piedras Blancas (Soto *et al.*, 2021).

Although our results suggest a lack of connectivity in the reserve, which was intended to facilitate connectivity across the PA network, it could be possible that they are dispersing and that there is another threat driving local extinction. Although we did not collect information on hunting in the region, past studies have found a significant reduction of hunted species in the Golfo Dulce Forest Reserve when compared to Corcovado (Carrillo, Wong and Cuarón, 2000) and hunting remains a serious problem, most of which is not subsistence hunting, but undertaken for sport by hunters from other areas of Costa Rica (Ankersen, Regan and Mack, 2006). Spider monkeys are known to avoid areas where hunting occurs (van Roosmalen, 1980; Aquino et al., 2013)**,** which could therefore impact landscape permeability, highlighting the need to address these issues in the region. Whether the absence of the Geoffroy's spider monkey and other threatened species from large parts of the reserve and Piedras Blancas is due to a lack of connectivity in the reserve or another threat, the situation is problematic, since Piedras Blancas National Park serves as a connection between the Osa Peninsula and populations on the mainland of Costa Rica.

4.4.3. Connectivity and Protected Area Management

It is suggested that effective management of PAs is the key to their ability to provide connectivity. Lack of connectivity is often found to be linked to the absence of complete management plans, management of the PA in isolation of the wider area or PA network (Saura *et al.*, 2018), and lack of adequate resources, governmental support or formal assessments of PA effectiveness (Saura *et al.*, 2017). Many of these challenges exist in the Osa region, including limited resources and subsequent lack of enforcement against illegal logging, hunting, mining and lack of a formal management plan (Ankersen, Regan and Mack, 2006). The Golfo Dulce Forest Reserve has also been subject to years of conflict between farmers and the government, which lead to unpermitted agricultural activities in the area (Ankersen, Regan and Mack, 2006). We now focus on mitigation strategies to improve functional connectivity, specifically for large-bodied specialist mammals.

4.4.4. Mitigation: Biological Corridor

Given the constraints above, we designed a 2 km wide corridor through the reserve using the path of least resistance. It has been suggested that this width is most suitable to maximise permeability across the PA network for the greatest number of species and avoids any potential edge effects that would severely reduce its viability (Beier, 2019). Smaller corridors may end up being a wasted investment as they are unlikely to function for a large number of species and anything too wide can become too expensive to manage (Beier, 2019). The width of the Golfo Dulce Forest Reserve, which was designed to facilitate connectivity, is on average 10 km wide. Providing land managers with a smaller 2 km wide area to focus mitigation strategies may facilitate monitoring and improve the feasibility of mitigation efforts. Providing a smaller focal area for conservation efforts could also have a negative effect, and lead to increased deforestation and other anthropogenic activities in the surrounding area where large areas of forest and species already exist. This corridor will also not solve the issue of the paved road, although the corridor does highlight the section where mitigation strategies may incur the least costs and resistance.

4.4.5. Mitigation: Roads

Paved roads were the second most important driver of habitat suitability for the spider monkey in this study, and previous results indicate that this primate does not occur within 1 km of a paved road (see Chapter Three). Since paved roads surround Piedras Blancas National Park, wildlife must cross the road to disperse between the national parks, and the section next to Piedras Blancas represents the most significant bottleneck in the corridor. A strong effect of paved roads has also been found in previous studies on mammals due to increased gap width and heavier traffic volume (Weston *et al.*, 2011; Asensio, Schaffner and Aureli, 2012; Cibot *et al.*, 2015; Chen and Koprowski, 2016; Mulero-Pázmány, D'Amico and González-Suárez, 2016; Asensio *et al.*, 2021) alteration of vegetation structure (Zhou *et al.*, 2020), secondary road development and increased human presence (Laurance, Goosem and Laurance, 2009). These effects have subsequently been found to increase road kill and hunting pressure due to increased access to undisturbed areas (Trombulak and Frissell, 2000).

For arboreal species, mitigation strategies to reduce the threats posed by roads include ensuring the gap in the forest canopy is small enough that natural crossings remain, or the creation of artificial canopy bridges (Gregory *et al.*, 2017; Asensio *et al.*, 2021). However, if the spider monkey does not occur within 1 km of paved roads due to additional disturbance in the surrounding area, then these bridges alone will have little effect and consideration should also be given to the wider effects of roads. There is very little research into the effectiveness of bridges for the Geoffroy's spider monkey, however, in a study on the Caribbean coast in Costa Rica, this species did not use artificial rope bridges that were installed on a paved road (Lindshield, 2016). Studies of other arboreal mammals and primates have found use of artificial bridges (Teixeira et al., 2013; Donaldson and Cunneyworth, 2015) and ground dwelling species of mammal have been found to use culverts and underpasses to pass through roads (Taylor et al., 2010). If roads are to be created or paved within PAs, they should consider key factors that may impact wildlife, such as gap width, traffic volume and speed and the secondary effects from increased development and resource extraction.

4.4.6. Mitigation: Private Protected Areas

One additional observation that we found within our results, was the high forest cover and occurrence of the Geoffroy's spider monkey in privately protected wildlife refuges, which was comparable to strictly protected national parks. This result is likely due to successful reforestation programmes (Zambrano, Broadbent and Durham, 2010; Lopez Gutierrez *et al.*, 2020) and the presence of hotels, land owners and other staff in these areas, subsequently deterring illegal logging and hunting (Lopez Gutierrez *et al.*, 2020). There is very little research surrounding the contribution of privately protected areas to biodiversity protection, however, they are increasingly becoming recognised as essential components of a PA network (Stolton *et al.*, 2014) and have previously been found to play a substantial role in the protection of medium-large bodied mammals (Clements *et al.*, 2019). There are many privately owned lands within the Golfo Dulce Forest Reserve that have the potential to facilitate connectivity.

4.4.7. Piedras Blancas National Park

Although no official records exist, hotels and tourists have reported sightings of spider monkeys in Piedras Blancas National Park, and it is known that an animal sanctuary on the border of the park has unofficially released a number of spider monkeys into the wild. Lack of detection suggests that their numbers remain very low and that they may be restricted to small areas. Future research should confirm the presence, status and health of this population, as their ability to successfully breed and disperse through the region will affect management decisions on how to protect this species.

4.4.8. Conclusion

The Golfo Dulce Forest Reserve, a large sustainable-use PA, is acting as a buffer to Corcovado National Park and is able to support populations of the Geoffroy's spider monkey, a rare and endangered forest specialist. However, our results suggest that it may not be facilitating connectivity across the PA network and the main bottleneck is driven by a single primary road and areas of palm plantation, pasture and secondary road. It is possible there are other stressors that we have not measured limiting dispersal, such as hunting, which is known to be problematic in the region, and these should be taken into consideration in any management plans for the area. The lack of connectivity is problematic since Piedras Blancas National Park serves as a connection between the Osa Peninsula and populations on the mainland. We have identified the key barriers to connectivity in the reserve and designed a small corridor which can serve as the focus for management efforts. The Osa Peninsula is one of the most biodiverse regions of the world, we show that with little investment it is possible to maintain and even improve the natural capital for generations to come.

Chapter Five: General Discussion

5.1. Advantages of Passive Acoustic Monitoring

Using Passive acoustic monitoring I was able to collect 60,000 hours of data, across 341 sites, over a large region encompassing over 1000 km^2. Without PAM I would not have been able to achieve this level of coverage in terms of number of sites or spatial scale. The alternative approach, line transects, would have been too time consuming and costly in terms of person-power to achieve the desired number of replicates or scale, resulting in a smaller study with potentially different objectives. Whilst in the field we encountered groups of our target species, the Geoffroy's spider monkey. They consistently displayed aggressive behaviour towards me and altered their behaviour and activity, which would certainly have biased data collection. Using PAM, my presence in the area was limited, reducing the negative implications on wildlife and bias on the data collected. During the pilot study, I attempted to walk line transects in the same area where I placed an audio recorder. When walking the transect, I only encountered the Geoffroy's spider monkey twice, however manual analysis of the recordings revealed the species to be present on all seven days. This highlights the functionality of this method for detecting rare species, which is likely owing to the use of a less invasive method and the increased temporal extent of the study. I have used the dataset for a broad assessment of biotic diversity and to target one call of the Geoffroy's spider monkey. This dataset has huge potential for further study and can be used in the future for additional assessments of acoustic biotic diversity, to analyse more calls of the Geoffroy's spider monkey and to analyse the calls of additional species. If I had collected data using line transects, this would not be possible since I would have had data only for our target species to answer specific questions.

5.2. Soundscape Ecology

5.2.1. The Importance of the Diel Cycle

The emergence of new technology, such as passive acoustic monitoring (PAM), has improved our ability to monitor landscapes continuously, allowing the study of temporal variability at a fine scale (Pijanowski *et al.*, 2011; Ducrettet *et al.*, 2020). The use of PAM combined with acoustic indices for rapid extraction of information, allowed me to monitor acoustic diversity across the diel cycle, revealing important changes in acoustic biotic diversity at dawn and dusk. By studying at this temporal scale, I was able to detect disruption to the dawn and dusk chorus in disturbed land use. Comparative analysis at key times of the day (dawn, dusk, midday, midnight) did not fully uncover these changes, revealing only a reduction in biotic diversity at dawn in disturbed land use. If I had not included the diel cycle in my analysis I would have missed important changes that have occurred in the acoustic space as a result of land use change. Previous studies have mainly focused on studying acoustic diversity at key points during the diel cycle, revealing inconsistent results (Bradfer-Lawrence *et al.*, 2019). Here we highlight the importance of studies that cover the breadth of the diel cycle and the ability of acoustic indices to reveal key differences in acoustic diversity across different ecosystems.

5.2.2. Misuse of Acoustic Indices

As discussed in Chapters One and Two, previous studies have revealed inconsistencies with the use of acoustic indices and questions as to their correlation with measures of species diversity remain, which must be taken into consideration in any study. It has been suggested that this is due to lack of a standardised approach across the field (Bradfer-Lawrence *et al.*, 2019) and the inherent differences that exist geographically and between ecosystems (Gibb *et al.*, 2019). For example, Eldridge *et al.*, (2016) found that bird species richness were correlated to acoustic indicies in temperate zones but not in the tropics, and suggested this was due to the diversity of other taxa in the tropics. It is also possible that interference from other sound sources prevents indices from accurately representing species diversity. For example, indices were found to be biased by anthropogenic sound (Fairbrass *et al.*, 2017) and continuous biotic sounds from stridulating insects

(Ross *et al.*, 2021). The question also still remains about which component of diversity the acoustic indices are measuring, with some finding correlations with species richness (Eldridge *et al.*, 2018; Bradfer-Lawrence *et al.*, 2020; Dröge *et al.*, 2021) and others with abundance or activity (Boelman *et al.*, 2007; Bradfer-Lawrence *et al.*, 2020; Holgate, Maggini and Fuller, 2021). These results are also likely to differ between environments and indices. Therefore, although indices can reveal important patterns and changes in acoustic diversity, we must be cautious in our interpretation of the results, especially when not using comparative data sets.

The need for caution is highlighted in my results from Chapter Two. Here, although I found a loss of the dawn and dusk peaks in grasslands, indicating some divergence from a healthy functioning ecosystem, I found high acoustic biotic diversity throughout the day. Without questioning these outputs, I could have concluded that acoustic diversity was higher in grasslands than in native forests. However instead, using knowledge from the literature, which shows indices may represent acoustic activity and abundance and not necessarily richness and that they may be affected by continuous biotic sounds, I conclude that this result is potentially due to the indices being influenced by large flocks of social parakeets in the grasslands.

In this study I did not take comparative measurements of species diversity whilst in the field. This was due to comparative measurements emerging as a potential issue towards the end of the fieldwork period. I did consider validating the outputs of the acoustic indices by listening to the diversity of sounds in the recordings, however, due to the sheer number of sounds and species in some recordings and the spatial scale of the study, this would have been a complex and time consuming task and was outside the limits of the project. This could be considered for future publication, focusing on the functioning of the indices as well as the ecological outputs.

5.3. Machine Learning

5.3.1. The Advantages of Automated Approaches

Recently, the acoustic literature has discussed the significant reduction in analysis time owing to the use of automated species detectors (Browning *et al.*, 2017; Gibb *et al.*, 2019). The automated detector used in this study was able to analyse over 60,000 hours of data in just 8 weeks, with a further 4 weeks required for manually validating false positives. Without this, I estimate that manual listening, assuming 8 hours per day 7 days per week and not considering time to stop and record positives, would have taken 1092 weeks or 21 years. Here, I show the difference in analysis time between manual and automated approaches and hence the benefit of using automated species detectors for large datasets. It has been said that one of the major barriers to the future use of acoustics in ecology is the development of reliable automated classifiers (Browning *et al.*, 2017). Here I close this gap a little further by creating a detector for a rare endangered mammal in the neotropics.

5.3.2. Future Application

The large acoustic dataset that I collected has been used for my PhD to study the Geoffroy's spider monkey and to gain measures of overall species diversity using acoustic indices. However, the potential lines of study using this same dataset are vast, including the creation of more automated species detectors. The development of automated detectors are based on expertly labelled training datasets of species calls, which are difficult to collate, especially for rare species (Browning *et al.*, 2017; Gibb *et al.*, 2019). For a rare species such as the spider monkey, this required the collection of 12 weeks of pilot data and manually listening to over 1000 hours of recordings. This was a time-consuming activity and highlights the first barrier in the development these automated approaches, and why there is perhaps such a gap in the field. Over the last two years we have begun creating labelled training databases for other species using this dataset. In the 2020/2021 academic year we created an MSc project for a student from an Imperial College based course: Computational Methods in ~~Evolution and~~ Ecology and Evolution (CMEE). This student attempted to adapt the code used to train the spider monkey detector to train a detector for the mantled howler monkey. They were successful in adapting the code for both single and multi-call classification and achieved high accuracy. Not only does this show the adaptability of the original detector for other species, but also highlights the future work that could be done using this dataset to further close the gap in the field.

5.3.3. Barriers to Automated Approaches

The development of automated species detectors not only requires large labelled training datasets, but also specialised expertise and knowledge in the field of data science (Browning *et al.*, 2017; Gibb *et al.*, 2019). This can often present technical barriers for ecologists (Browning *et al.*, 2017; Gibb *et al.*, 2019) and has likely contributed to the gap in the field. In the absence of a collaboration with the Department of Computing, where a fellow PhD student, George Rizos, trained the detector for the Geoffroy's spider monkey, this project would not have been possible. Before Mr Rizos was successful in training the detector, there were two previous MSc students, Duncan Butler and Zhuoda Han from the CMEE course, who attempted the task, neither was able to develop a well-trained model. This highlights the level of expertise required for the development of these detectors. This is further exemplified by attempts at training a gunshot detector. Originally, the final chapter of this PhD was intended to be based around the effects of hunting on spider monkeys. A team of researchers had been successful in developing a model for gunshots in Belize using ~~this~~ a dataset of gunshots created from shooting firearms in Belize, however, discussions revealed that their model was unlikely to be transferable to other regions. A CMEE student attempted to create a model for our region using a mix of gunshot data from online sources and the region, however this proved unsuccessful. Both Google and the Lab of Ornithology at Cornell University have also created gunshot detectors, however, in a separate MSc project that I co-supervised, neither proved highly successful in extracting gunshots from an acoustic dataset in Africa (Huang *et al.*, 2021). This highlights both the difficulty in creating accurate detectors and a potential problem with their transferability, which should be tested.

Accurate automated species detectors are invaluable for the use of acoustics in ecology and enable rapid analysis of large acoustic datasets (Browning *et al.*, 2017; Gibb *et al.*, 2019) as I have demonstrated here in my study of the Geoffroy's spider monkey. However as discussed above, the barriers to their development, in terms of expertly labelled training databases and the technical skills and knowledge required, may be leading to a gap in the field (Browning *et al.*, 2017; Gibb *et al.*, 2019). Expertly labelled and publicly available call databases, together with collaborations between technically specialised data scientists and ecologists and a user-friendly tool for training species detectors are urgently required (Browning *et al.*, 2017; Gibb *et al.*, 2019).

5.4. The Use of Passive Acoustic Monitoring for Primate Studies

5.4.1. Current Application in the Field of Primatology

To date only 10 detectors have been developed for primate calls, these include the Bornean Gibbon (*Hylobates muelleri*) (Clink *et al.*, 2017), Hainan gibbon (*Nomascus hainanus*) (Dufourq *et al.*, 2021), chimpanzee (*Pan troglodytes*) (Kalan *et al.*, 2015), Diana monkey (*Cercopithecus diana*), king colobus (*Colobus polykomos*), western red colobus (*Procolobus badius*) (Heinicke *et al.*, 2015), blue monkeys (*Cercopithecus mitis stuhlmanni*) (Mielke and Zuberbühler, 2013), black lemurs (*Eulemur macaco macaco*),(Pozzi, Gamba and Giacoma, 2010) common marmoset (*Callithrix jacchus*) and Bornean orangutan (*Pongo pygmaeus wurmbii*) (Spillmann *et al.*, 2015)

(Pozzi, Gamba and Giacoma, 2010; Mielke and Zuberbühler, 2013; c *et al.*, 2015; Kalan *et al.*, 2015, 2016; Spillmann *et al.*, 2015; Clink *et al.*, 2017; Dufourq *et al.*, 2021).

Of these, only one species is from the neotropics and this detector was developed using calls from a single captive population, designed for use on captive populations in biomedical research (Turesson *et al.*, 2016). Training a detector on a single captive population would likely reduce its transferability to other datasets, since it does not capture intraspecies variability and captive bred individuals may have different call patterns. One further study took a different approach and isolated sounds within a selected frequency to look for calls of the Black and Gold Howler Monkey (*Alouatta caraya*) (Pérez-Granados and Schuchmann, 2021). This is an interesting approach as it will significantly reduce the time required to manually analyse the data, however, this would not function for many species of primate who call in the same frequency bands as birds, anurans and insects. At various points in this thesis I have highlighted the bias of passive acoustic monitoring to northern temperate species and to certain taxa, however, it appears within the primate literature there is a bias developing towards African and Asian species.

There are also questions as to their transferability. I have been unable to confirm if any detectors developed for primates have verified the functionality of the detector on other datasets. If they are not transferable then this will limit their use and a new detector would need to be developed for each region, which would limit the future use of acoustics in ecology and conservation.

5.4.2. Knowledge Gaps

Owing to their threatened status (Junker *et al.*, 2020), survival in human-modified landscapes (Arroyo-Rodríguez *et al.*, 2017a) and importance in the ecosystem (Estrada *et al.*, 2017), the conservation of primates is of primary importance. Despite the wealth of primate studies in the literature, knowledge gaps still exist, including the study of lesser-known and neotropical species (Estrada *et al.*, 2017), landscape scale studies (Arroyo-Rodríguez and Fahrig, 2014), long- term studies (Junker *et al.*, 2020) and species and habitat specific knowledge on threats (Estrada *et al.*, 2017). As a result of these knowledge gaps, we lack evidence-based strategies to effectively conserve primates (Estrada *et al.*, 2017; Junker *et al.*, 2020). In this study I have shown how using PAM combined with an automated species detector can facilitate a landscape scale study covering a region of over 1000 km^2. This scale and coverage allowed me to answer questions related to the effects of land use change, roads, buildings and protection status, providing habitat and species-specific knowledge on threats. Additionally, in Chapter Four, we used this information to develop evidence-based strategies to conserve an endangered neotropical primate, further contributing to gaps in the literature. The ability to record continuously facilitated the collection of sufficient replicates over a 7-day period, and combined with the non-invasive nature of the study, likely increased the detection probability for a rare species. This demonstrates how passive acoustic monitoring, combined with a computational approach, can help to fill important knowledge gaps related to the study of primates. Although more expensive, long term studies are also possible using this method, which is becoming even more feasible as battery life and storage capacity increase and with the development of real-time data transfer (Gibb *et al.*, 2019). This method is suitable for any primate that makes a recognisable call and is also likely to be feasible for some of the lesser studied species where knowledge gaps are even more severe.

5.4.3. Conservation Application

One of the main findings in Chapter Four was the absence of the Geoffroy's spider monkey within 1 km of primary roads. Paved roads across the study region are limited, however are still acting as a barrier to connectivity and causing a bottleneck in the corridor. There is a large system of secondary roads across the region, if these are paved through important native forest habitat it could have devastating consequences for this species and other sensitive species. This year on the Osa Peninsula, the government released plans to pave a 42 km stretch of secondary road that cuts through critical habitat for the Geoffroy's spider monkey and would have reduced connectivity in the region further. Using the evidence from this study I worked with local NGO's in the region to try and modify this development. Our work became part of a campaign that was able to temporarily halt the paving of this road and we will continue to work to ensure that roads passing through critical habitat in the region are either not paved, or that necessary measures are put into place to mitigate some of the negative consequences of road development on wildlife. This provides further evidence for how PAM can be used to provide species-specific knowledge on threats and evidence-based strategies for conservation.

5.5. The Use of Passive Acoustic Monitoring for Monitoring Protected Areas

PAs are considered a key tool in tackling biodiversity loss (Watson *et al.*, 2014; Gray *et al.*, 2016). They are implemented to conserve ecosystems and wildlife, whilst having a wider role in contributing to local livelihoods, tourism, and in the mitigation of and adaptation to climate change (UNEP-WCMC and IUCN, 2016). Despite their importance, globally, large portions of the protected area network are not effectively conserving habitats or species (Laurance, Useche, *et al.*, 2012; Watson *et al.*, 2014; Osipova *et al.*, 2020; Ward *et al.*, 2020) and few have even had any assessment of effectiveness or functionality (UNEP-WCMC and IUCN, 2016). The site-level data required to make these assessments is time consuming and expensive to obtain (Geldmann *et al.*, 2021) and researchers are continually searching for more efficient methods to evaluate conservation strategies (Wrege *et al.*, 2017). Here we have demonstrated how PAM can help to evaluate the effectiveness of a protected area for conserving rare and endangered species, be used for evidence-based conservation strategies and can serve as a baseline for future standardised assessments to monitor changes over time.

Monitoring the effectiveness of protected areas should not however be based on one species, even if that species does hold an important role in the ecosystem. Biological monitoring should encompass analysis of ecological communities at different trophic levels (Buxton, Lendrum, *et al.*, 2018). Pairing acoustic monitoring with other technology such as camera trapping, which is also a non-invasive method for studies at large spatial-temporal scales, offers one way to study community composition and species distribution across multiple anthropogenic stressors (Buxton, Lendrum, *et al.*, 2018).

5.6. Main Conclusions

Knowledge gaps across the acoustics, primatology and threatened species literature, are currently hindering our ability to conserve species and ecosystems. This is, in part, due to the challenges of efficient data collection and analysis at the spatial and temporal scales required to evaluate how species respond to habitat changes across human-modified landscapes. In this thesis I have shown that PAM, combined with computational approaches can be successful in evaluating and revealing changes in acoustic diversity across the diel cycle, for the study of rare and threatened species and to monitor aspects of protected area effectiveness. I believe this work has highlighted the potential of PAM for use in the field of ecology and conservation and has contributed to closing the knowledge gaps that currently exist across these fields.

5.7. Future Directions

Future work in the field of soundscape ecology should continue to validate the indices that have been developed across different geographical areas and ecosystems, to gain a better understanding of how they function in different areas and to understand what aspect of diversity they are measuring. As a follow on to the work undertaken here, we should firstly listen to a selection of recordings to validate the functionality of the indices and, secondly, it is possible to use the dataset to test new methods evaluating acoustic diversity and community composition (Furumo and Mitchell Aide, 2019). This work has highlighted the benefits of studying across the diel cycle to uncover potential changes in acoustic diversity and it is recommended that soundscape studies take this approach in the future.

Using PAM, combined with an automated detector for the spider monkey call, has allowed us to effectively determine the dispersal limitations and threats for an endangered species over a large spatial scale, whilst limiting the impact of our presence on the results. We have then used this information to develop a habitat suitability model, design a biological corridor, identify potential bottlenecks and we are now in discussions with community partners about management recommendations to improve conservation for this species across the region. Future work should focus on the continued development of these computational approaches through creating call libraries and both training and testing species call detectors, especially for data-deficient, rare species. Below I will present ideas of how the acoustic dataset that I have collated during this project could be used to fulfil some of these objectives.

5.7.1 Automated Classifier for the Genus *Ateles*

I have demonstrated the value of the Geoffroy's spider monkey model on the Osa Peninsula in increasing the knowledge of and improving the conservation for an endangered species. I now want to make this a transferable tool that can be used by researchers in other regions to implement similar projects. To do this I propose the following project to develop a range wide, broad model for the genus *Ateles*. Within this genus are seven species of spider monkey, six endangered and one critically endangered species (IUCN, 2021), all with the same call, the whinny.

Stages for the development are as follows:

1. **Model improvement *Ateles geoffroyi*:** This model was created with the support of the Department of Computing at Imperial College London. It was trained using a database of 580 calls, however, after extracting almost 3000 calls from the dataset, we can now use these for model improvement.
2. **Model testing *Ateles geoffroyi:*** Using the improved model we would test its functionality on acoustic datasets from other regions, where, although this species has the same call, the characteristics of this call and background noise may differ slightly. The aim is to determine how widely the Osa specific model can be applied. I already have partners in Northern Costa Rica and Mexico with acoustic datasets for testing.
3. **Model training and expansion *Ateles geoffroyi*:** Depending on the results of these tests, if model performance for other regions is lagging, then calls from these regions will be extracted and added to the labelled training dataset to improve model performance. The aim is to produce

a range-wide model for this species and to determine how much coverage or data is needed to obtain this and what might be the geographic variation in the calls.

4. **Model expansion genus *Ateles*:** Using the range-wide model for *Ateles geoffroyi* I would then test its performance on other species within the genus, repeating steps 2 and 3 as described above. We have partners at WWF Peru with an acoustic dataset that could be used for this purpose. If more data is needed this could be collected with a small amount of fieldwork by myself or through sending acoustic recorders to in-country partners.

5.7.2. Multiple Species Models

Using the large acoustic dataset, we have been working towards acoustic algorithms for additional species, which are in various stages of development. We have recently adapted the code developed for the spider monkey model and trained a multi-label classifier for two calls of the mantled howler monkey (*Alouatta palliata*). This multi-taxa approach could now be further developed in line with suggestions for project 1. We also have labelled training datasets for the Central American squirrel monkey (*Saimiri oerstedii*), great tinamou (*Tinamus major*), scarlet macaw (*Ara macao*) and yellow-throated toucan (*Ramphastos ambiguous)*. The conservation status of these species ranges from least concern to vulnerable, however, all populations are known to be declining. I would be particularly interested in developing the great tinamou model as this species, like the spider monkey, is a sensitive forest specialist subject to hunting pressure. Additionally, the genus *Tinamus* contains 47 species, many with a similar acoustic range and a combined geographic range covering Central and South America.

Bibliography

Albert, A. and Anderson, J. A. (1984) ‘On the existence of maximum likelihood estimates in logistic regression models’, *Biometrika*. Oxford Academic, 71(1), pp. 1–10. doi: 10.1093/biomet/71.1.1.

Ankersen, T. T., Regan, K. E. and Mack, S. A. (2006) ‘Towards a bioregional approach to tropical forest conservation: Costa Rica’s Greater Osa Bioregion’, *Futures*, 38(4), pp. 406–431. doi: 10.1016/j.futures.2005.07.017.

Mac Aodha, O. *et al.* (2018) ‘Bat detective—Deep learning tools for bat acoustic signal detection’, *PLoS Computational Biology*, 14(3), pp. 1–19. doi: 10.1371/journal.pcbi.1005995.

Aquino, R. *et al.* (2013) ‘Distribution and abundance of white-fronted spider monkeys, ateles belzebuth (atelidae), and threats to their survival in Peruvian Amazonia’, *Folia Primatologica*, 84(1), pp. 1–10. doi: 10.1159/000345549.

Araújo, M. B. and New, M. (2007) ‘Ensemble forecasting of species distributions’, *Trends in Ecology and Evolution*. Elsevier Current Trends, pp. 42–47. doi: 10.1016/j.tree.2006.09.010.

Arroyo-Rodríguez, V. *et al.* (2017a) ‘Spider Monkeys in Human-Modified Landscapes: The Importance of the Matrix’, *Tropical Conservation Science*, 10(July), p. 194008291771978. doi: 10.1177/1940082917719788.

Arroyo-Rodríguez, V. *et al.* (2017b) ‘Spider Monkeys in Human-Modified Landscapes’, *Tropical Conservation Science*, 10(July), p. 194008291771978. doi: 10.1177/1940082917719788.

Arroyo-Rodríguez, V. *et al.* (2020) ‘Designing optimal human-modified landscapes for forest biodiversity conservation’, *Ecology Letters*. John Wiley & Sons, Ltd, 23(9), pp. 1404–1420. doi: 10.1111/ELE.13535.

Arroyo-Rodríguez, V. and Fahrig, L. (2014) ‘Why is a landscape perspective important in studies of primates?’, *American Journal of Primatology*, 76(10), pp. 901–909. doi: 10.1002/ajp.22282.

Arroyo-Solís, A. *et al.* (2013) ‘Experimental evidence for an impact of anthropogenic noise on dawn chorus timing in urban birds’, *Journal of Avian Biology*, 44(3), pp. 288–296. doi: 10.1111/j.1600-048X.2012.05796.x.

Asensio, N. *et al.* (2017) ‘The effect of roads on spider monkeys’ home range and mobility in a heterogeneous regenerating forest’, *Biotropica*, 49(4), pp. 546–554. doi: 10.1111/btp.12441.

Asensio, N. *et al.* (2021) ‘The impact of roads on the movement of arboreal fauna in protected areas: The case of lar and pileated gibbons in Khao Yai National Park, Thailand’, *Journal of Tropical Ecology*. Cambridge University Press. doi: 10.1017/S0266467421000390.

Asensio, N., Schaffner, C. M. and Aureli, F. (2012) ‘Variability in core areas of spider monkeys (Ateles geoffroyi) in a tropical dry forest in Costa Rica’, *Primates*, 53(2), pp. 147–156. doi: 10.1007/s10329-011-0288-9.

Astaras, C. *et al.* (2020) ‘Boots on the ground: the role of passive acoustic monitoring in evaluating anti-poaching patrols’, *Environmental Conservation*, pp. 1–4. doi: 10.1017/S0376892920000193.

Banks-Leite, C. *et al.* (2014) 'Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot', *Science*. American Association for the Advancement of Science, 345(6200), pp. 1041–1045. doi: 10.1126/SCIENCE.1255768.

Banks-Leite, C. *et al.* (2021) 'The suggestion that landscapes should contain 40% of forest cover lacks evidence and is problematic', *Ecology Letters*. John Wiley & Sons, Ltd, 24(5), pp. 1112–1113. doi: 10.1111/ELE.13668.

Barnett, C. A. and Briskie, J. V. (2007) 'Energetic state and the performance of dawn chorus in silvereyes (Zosterops lateralis)', *Behavioral Ecology and Sociobiology*, 61(4), pp. 579–587. doi: 10.1007/s00265-006-0286-x.

Barrows, C. W., Fleming, K. D. and Allen, M. F. (2011) 'Identifying habitat linkages to maintain connectivity for corridor dwellers in a fragmented landscape', *Journal of Wildlife Management*, 75(3), pp. 682–691. doi: 10.1002/jwmg.138.

Bastin, J. F. *et al.* (2019) 'The global tree restoration potential', *Science*. American Association for the Advancement of Science, 364(6448), pp. 76–79. doi: 10.1126/science.aax0848.

Bates, B., Maechler, M. and Bolker, B. (2015) 'Fitting Linear Mixed-Effects Models Using lme4', *Journal of Statistical Software*, 67(1), p. 1:48. Available at: doi:10.18637/jss.v067.i01.

Bates, D. *et al.* (2015) 'Fitting Linear Mixed-Effects Models Using lme4', *Journal of Statistical Software*, 67(1), pp. 1–48. Available at: doi:10.18637/jss.v067.i01.

Beier, P. (2019) 'A rule of thumb for widths of conservation corridors', *Conservation Biology*. Blackwell Publishing Inc., 33(4), pp. 976–978. doi: 10.1111/cobi.13256.

Bell, H. L. (1979) 'The effects on rain-forest birds of plantings of teak, tectona grandis, in Papua New Guinea', *Wildlife Research*. CSIRO PUBLISHING, 6(3), pp. 305–318. doi: 10.1071/WR9790305.

Beller, E. E. *et al.* (2019) 'Building Ecological Resilience in Highly Modified Landscapes', *BioScience*. Oxford Academic, 69(1), pp. 80–92. doi: 10.1093/BIOSCI/BIY117.

Bennett, J. R. *et al.* (2018) 'When to monitor and when to act: Value of information theory for multiple management units and limited budgets', *J Appl Ecol*, 55, pp. 2102–2113. doi: 10.1111/1365-2664.13132.

Berg, K. S., Brumfield, R. T. and Apanius, V. (2006) 'Phylogenetic and ecological determinants of the neotropical dawn chorus', *Proceedings of the Royal Society B: Biological Sciences*. Royal Society, 273(1589), pp. 999–1005. doi: 10.1098/rspb.2005.3410.

Bezanson, M. and McNamara, A. (2019) 'The what and where of primate field research may be failing primate conservation', *Evolutionary Anthropology*. Wiley-Liss Inc., 28(4), pp. 166–178. doi: 10.1002/evan.21790.

Bissonette, J. A. (1999) 'Small sample size problems in wildlife ecology: A contingent analytical approach', *Wildlife Biology*. Nordic Board for Wildlife Research, 5(2), pp. 65–71. doi: 10.2981/wlb.1999.010.

Bleyhl, B. *et al.* (2017) 'Assessing landscape connectivity for large mammals in the Caucasus using Landsat 8 seasonal image composites', *Remote Sensing of Environment*. Elsevier, 193, pp. 193–203. doi: 10.1016/J.RSE.2017.03.001.

Blumstein, D. T. *et al.* (2011) ‘Acoustic monitoring in terrestrial environments using microphone arrays: Applications, technological considerations and prospectus’, *Journal of Applied Ecology*, 48(3), pp. 758–767. doi: 10.1111/j.1365-2664.2011.01993.x.

Boelman, N. T. *et al.* (2007) ‘Multi-trophic invasion resistance in Hawaii: Bioacoustics, field surveys, and airborne remote sensing’, *Ecological Applications*. Ecol Appl, 17(8), pp. 2137–2144. doi: 10.1890/07-0004.1.

Boersma, P. and Weenink, D. (2018) ‘Praat: doing phonetics by computer’. Available at: http://www.praat.org/.

Bovarnick, A. (2007) *Project executive summary: United Nations Development Programme*.

Boyle, S. A. and Smith, A. T. (2010) ‘Can landscape and species characteristics predict primate presence in forest fragments in the Brazilian Amazon?’, *Biological Conservation*. Elsevier Ltd, 143(5), pp. 1134–1143. doi: 10.1016/j.biocon.2010.02.008.

Bradfer-Lawrence, T. *et al.* (2020) ‘Rapid assessment of avian species richness and abundance using acoustic indices’, *Ecological Indicators*. Elsevier, 115, p. 106400. doi: 10.1016/J.ECOLIND.2020.106400.

Bradfer-Lawrence, T. *et al.* (2019) ‘Guidelines for the use of acoustic indices in environmental research’, *Methods in Ecology and Evolution*, 2019(March), pp. 1–12. doi: 10.1111/2041-210x.13254.

Brennan, A. *et al.* (2020) ‘Characterizing multispecies connectivity across a transfrontier conservation landscape’, *Journal of Applied Ecology*. John Wiley & Sons, Ltd, 57(9), pp. 1700–1710. doi: 10.1111/1365-2664.13716.

Bridges, A. S., Dorcas, M. E. and Montgomery, W. L. (2000) ‘Temporal Variation in Anuran Calling Behavior: Implications for Surveys and Monitoring Programs’, *Copeia*. Allen Press, 2000(2), pp. 587–592. doi: 10.1643/0045-8511(2000)000[0587:TVIACB]2.0.CO;2.

Browning, E. *et al.* (2017) ‘Passive acoustic monitoring in ecology and conservation’, *WWF Conservation Technology Series*, 1(2), pp. 1–75. Available at: https://www.wwf.org.uk/conservationtechnology/documents/Acousticmonitoring-WWF-guidelines.pdf.

Brumm, H. (2004) ‘The impact of environmental noise on song amplitude in a territorial bird’, *Journal of Animal Ecology*, 73(3), pp. 434–440. doi: 10.1111/j.0021-8790.2004.00814.x.

Bruner, A. *et al.* (2001) ‘Effectiveness of Parks in Protecting Tropical Biodiversity’, *Science*, 291(January), pp. 125–128. Available at: http://science.sciencemag.org/.

Buckland, S. T. *et al.* (2010) ‘Design and Analysis of Line Transect Surveys for Primates’, *International Journal of Primatology*, 31(5), pp. 833–847. doi: 10.1007/s10764-010-9431-5.

Burivalova, Z. *et al.* (2021) ‘The sound of logging: Tropical forest soundscape before, during, and after selective timber extraction’, *Biological Conservation*. Elsevier Ltd, 254, p. 108812. doi: 10.1016/j.biocon.2020.108812.

Burivalova, Z., Game, E. T. and Butler, R. A. (2019) ‘The sound of a tropical forest’, *Science*, 363(6422), pp. 28–29. doi: 10.1126/science.aav1902.

Burnham, K. and Anderson, D. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretical Approach*. Springer-Verlag.

Butchart, S. H. M. *et al.* (2012) 'Protecting Important Sites for Biodiversity Contributes to Meeting Global Conservation Targets', *PLOS ONE*. Public Library of Science, 7(3), p. e32529. doi: 10.1371/JOURNAL.PONE.0032529.

Buxton, R. T. *et al.* (2013) 'Examining patterns in nocturnal seabird activity and recovery across the western Aleutian Islands, Alaska, using automated acoustic recording', *Auk*. American Ornithological Society, 130(2), pp. 331–341. doi: 10.1525/auk.2013.12134.

Buxton, R. T., Agnihotri, S., *et al.* (2018) 'Acoustic indices as rapid indicators of avian diversity in different land-use types in an Indian biodiversity hotspot', *Journal of Ecoacoustics*, 2, p. GWPZVD. doi: 10.22261/jea.gwpzvd.

Buxton, R. T., McKenna, M. F., *et al.* (2018) 'Efficacy of extracting indices from large-scale acoustic recordings to monitor biodiversity', *Conservation Biology*, 32(5), pp. 1174–1184. doi: 10.1111/cobi.13119.

Buxton, R. T., Lendrum, P. E., *et al.* (2018) 'Pairing camera traps and acoustic recorders to monitor the ecological impact of human disturbance', *Global Ecology and Conservation*. Elsevier, 16, p. e00493. doi: 10.1016/J.GECCO.2018.E00493.

Caldart, V. M. *et al.* (2016) 'Calling Activity of a Stream-Breeding Frog from the Austral Neotropics: Temporal Patterns of Activity and the Role of Environmental Factors', *Herpetologica*. Herpetologist's League Inc., 72(2), pp. 90–97. doi: 10.1655/HERPETOLOGICA-D-15-00029.

Campos-Cerqueira, M. and Aide, T. M. (2016) 'Improving distribution data of threatened species by combining acoustic monitoring and occupancy modelling', *Methods in Ecology and Evolution*, 7(11), pp. 1340–1348. doi: 10.1111/2041-210X.12599.

Campos, I. B. *et al.* (2021) 'Assessing the potential of acoustic indices for protected area monitoring in the Serra do Cipó National Park, Brazil', *Ecological Indicators*. Elsevier, 120, p. 106953. doi: 10.1016/J.ECOLIND.2020.106953.

Carrillo, E., Wong, G. and Cuarón, A. D. (2000) 'Monitoring Mammal Populations in Costa Rican Protected Areas under Different Hunting Restrictions', *Conservation Biology*, 14(6), pp. 1580–1591. doi: 10.1111/j.1523-1739.2000.99103.x.

Ceballos, G. *et al.* (2015) 'Accelerated modern human-induced species losses: Entering the sixth mass extinction', *Science Advances*, 1(2). doi: 10.1126/sciadv.1400253.

Celis-Murillo, A., Deppe, J. L. and Ward, M. P. (2012) 'Effectiveness and utility of acoustic recordings for surveying tropical birds', *Journal of Field Ornithology*. Blackwell Publishing Inc., 83(2), pp. 166–179. doi: 10.1111/j.1557-9263.2012.00366.x.

Chapman, C. a. (1987) 'Flexibility in the Diet of Three Costa Rican Primates.Pdf', *Folia Primatologica*, pp. 90–105. doi: 10.1159/000156311.

Chapman, C. A. (1988) 'Patterns of foraging and range use by three species of neotropical primates', *Primates*, 29 (2)(April), pp. 177–194.

Chapman, C. A. (1989) 'Spider monkey sleeping sites: Use and availability', *American Journal of*

Primatology, 18(1), pp. 53–60. doi: 10.1002/ajp.1350180106.

Chapman, C. A. (1990) ‘Ecological Constraints on Group Size in Three Species of Neotropical Primates’, *Folia Primatologica*, 55(1), pp. 1–9. doi: 10.1159/000156492.

Chapman, C. A. *et al.* (2013) ‘Are Primates Ecosystem Engineers’, *Int J Primatol*, 34, pp. 1–14. doi: 10.1007/s10764-012-9645-9.

Chapman, C. A. and Lefebvre, L. (1990) ‘Manipulating foraging group size: spider monkey food calls at fruiting trees’, *Animal Behaviour*. Academic Press, 39(5), pp. 891–896. doi: 10.1016/S0003-3472(05)80953-4.

Chapman, C. A. and Weary, D. M. (1990) ‘Variability in spider monkeys’ vocalizations may provide basis for individual recognition’, *American Journal of Primatology*. Am J Primatol, 22(4), pp. 279–284. doi: 10.1002/ajp.1350220407.

Chaves, M. and Stoner, K. E. (2012) ‘Differences in Diet Between Spider Monkey Groups Living in Forest Fragments and Continuous Forest in Mexico’, 44(1), pp. 105–113.

Chaves, Ó. M., Stoner, K. E. and Arroyo-Rodríguez, V. (2012) ‘Differences in diet between spider monkey groups living in forest fragments and continuous forest in Mexico’, *Biotropica*. John Wiley & Sons, Ltd, 44(1), pp. 105–113. doi: 10.1111/j.1744-7429.2011.00766.x.

Chazdon, R. L. *et al.* (2009) ‘Beyond reserves: A research agenda for conserving biodiversity in human-modified tropical landscapes’, *Biotropica*, 41(2), pp. 142–153. doi: 10.1111/j.1744-7429.2008.00471.x.

Chen, H. L. and Koprowski, J. L. (2016) ‘Barrier effects of roads on an endangered forest obligate: Influences of traffic, road edges, and gaps’, *Biological Conservation*. Elsevier Ltd, 199, pp. 33–40. doi: 10.1016/j.biocon.2016.03.017.

Cibot, M. *et al.* (2015) ‘Chimpanzees facing a dangerous situation: A high-traffic asphalted road in the Sebitoli area of Kibale National Park, Uganda’, *American Journal of Primatology*. John Wiley and Sons Inc., 77(8), pp. 890–900. doi: 10.1002/ajp.22417.

Clavel, J., Julliard, R. and Devictor, V. (2011) ‘Worldwide decline of specialist species: Toward a global functional homogenization?’, *Frontiers in Ecology and the Environment*, 9(4), pp. 222–228. doi: 10.1890/080216.

Clements, H. S. *et al.* (2019) ‘Privately protected areas provide key opportunities for the regional persistence of large- and medium-sized mammals’, *Journal of Applied Ecology*. John Wiley & Sons, Ltd, 56(3), pp. 537–546. doi: 10.1111/1365-2664.13300.

Clink, D. J. *et al.* (2017) ‘Investigating Individual Vocal Signatures and Small-Scale Patterns of Geographic Variation in Female Bornean Gibbon (Hylobates muelleri) Great Calls’, *International Journal of Primatology*. International Journal of Primatology, 38(4), pp. 656–671. doi: 10.1007/s10764-017-9972-y.

Coffin, A. W. (2007) ‘From roadkill to road ecology: A review of the ecological effects of roads’, *Journal of Transport Geography*, 15(5), pp. 396–406. doi: 10.1016/j.jtrangeo.2006.11.006.

Cole, E. M. *et al.* (2014) ‘Spatial and temporal variation in population dynamics of Andean frogs: Effects of forest disturbance and evidence for declines’, *Global Ecology and Conservation*. Elsevier

B.V., 1, pp. 60–70. doi: 10.1016/j.gecco.2014.06.002.

COP (2010) *COP 10 Decision X/2. Strategic Plan for Biodiversity 2011-2020*, *Eleventh meeting of the Conference of the Parties (COP) to the Convention on Biological Diversity*. Available at: http://www.cbd.int/decision/cop/?id=12268 (Accessed: 16 August 2021).

Cortes-Ortíz, L. *et al.* (2021) *Ateles geoffroyi (Geoffroy's Spider Monkey) IUCN Red List Assessment*. Available at: https://www.iucnredlist.org/species/2279/191688782 (Accessed: 10 December 2021).

Cronin, D. T. *et al.* (2016) 'Impact of gun-hunting on monkey species and implications for primate conservation on Bioko Island, Equatorial Guinea', *Biological Conservation*. Elsevier Ltd, 197, pp. 180–189. doi: 10.1016/j.biocon.2016.03.001.

Crooks, K. R. and Sanjayan, M. (2006) 'Connectivity conservation: maintaining connections for nature', *Connectivity Conservation*, pp. 1–20. doi: 10.1017/CBO9780511754821.001.

Crump, P. *et al.* (2017) 'Predicting anuran abundance using an automated acoustics approach', *Journal of Herpetology*. Society for the Study of Amphibians and Reptiles, pp. 582–589. doi: 10.1670/16-174.

Crump, P. S. and Houlahan, J. (2017) 'Designing better frog call recognition models', *Ecology and Evolution*, 7(9), pp. 3087–3099. doi: 10.1002/ece3.2730.

Crunchant, A.-S. *et al.* (2020) 'Listening and watching: Do camera traps or acoustic sensors more efficiently detect wild chimpanzees in an open habitat?', *Methods in Ecology and Evolution*. John Wiley & Sons, Ltd, 11(4), pp. 542–552. doi: 10.1111/2041-210X.13362.

Davies, K. F., Margules, C. R. and Lawrence, J. F. (2004) *A SYNERGISTIC EFFECT PUTS RARE, SPECIALIZED SPECIES AT GREATER RISK OF EXTINCTION*, *Ecology*.

Defler, T. R. (1995) 'The time budget of a group of wild woolly monkeys (Lagothrix lagotricha)', *International Journal of Primatology*, 16(2), pp. 107–120. doi: 10.1007/BF02700155.

Deichmann, J. L. *et al.* (2018) 'It's time to listen: there is much to be learned from the sounds of tropical ecosystems', *Biotropica*, 50(5), pp. 713–718. doi: 10.1111/btp.12593.

Dent, D. H. and Joseph Wright, S. (2009) 'The future of tropical species in secondary forests: A quantitative review', *Biological Conservation*. Elsevier, pp. 2833–2843. doi: 10.1016/j.biocon.2009.05.035.

Desante, D. F. *et al.* (2005) 'MoSI (Monitoreo de Sobrevivencia Invernal): Assessing Habitat-Specific Overwintering Survival of Neotropical Migratory Landbirds', (January), pp. 926–936.

Dixon, K. M. *et al.* (2019) 'Features associated with effective biodiversity monitoring and evaluation', *Biological Conservation*. Elsevier, 238, p. 108221. doi: 10.1016/J.BIOCON.2019.108221.

Donaldson, A. and Cunneyworth, P. (2015) 'Case Study: Canopy Bridges for Primate Conservation', in *Handbook of Road Ecology*. wiley, pp. 341–343. doi: 10.1002/9781118568170.ch41.

Dorado-Correa, A. M., Rodríguez-Rocha, M. and Brumm, H. (2016) 'Anthropogenic noise, but not artificial light levels predicts song behaviour in an equatorial bird', *Royal Society Open Science*, 3(7). doi: 10.1098/rsos.160231.

Dormann, C. *et al.* (2007) ‘Methods to account for spatial autocorrelation in the analysis of species distributional data: A review’, *Ecography*, 30(5), pp. 609–628. doi: 10.1111/j.2007.0906-7590.05171.x.

Dröge, S. *et al.* (2021) ‘Listening to a changing landscape: Acoustic indices reflect bird species richness and plot-scale vegetation structure across different land-use types in north-eastern Madagascar’, *Ecological Indicators*. Elsevier, 120(April 2020), p. 106929. doi: 10.1016/j.ecolind.2020.106929.

Ducrettet, M. *et al.* (2020) ‘Monitoring canopy bird activity in disturbed landscapes with automatic recorders: A case study in the tropics’, *Biological Conservation*. Elsevier, 245(November 2019), p. 108574. doi: 10.1016/j.biocon.2020.108574.

Dufourq, E. *et al.* (2021) ‘Automated detection of Hainan gibbon calls for passive acoustic monitoring’, *Remote Sensing in Ecology and Conservation*. John Wiley & Sons, Ltd. doi: 10.1002/RSE2.201.

Edwards, D. P. *et al.* (2010) ‘Wildlife-friendly oil palm plantations fail to protect biodiversity effectively’, *Conservation Letters*, 3(4), pp. 236–242. doi: 10.1111/j.1755-263X.2010.00107.x.

Eisenberg, J. F. (1976) ‘Communication mechanisms and social integration in the black spider monkey, Ateles fusciceps robustus, and related species’, *Smithsonian Contributions to Zoology*, (213), pp. 1–108. doi: 10.5479/si.00810282.213.

Eisenberg, J. F. and Kuehn, R. . (1966) ‘The behaviour of Ateles geoffroyi and related species’, *Smithson. Misc. Coll*, 151, pp. 1–63.

Eldridge, A. *et al.* (2016) ‘A new method for ecoacoustics? Toward the extraction and evaluation of ecologically-meaningful soundscape components using sparse coding methods’, *PeerJ*, 4(2016), p. e2108. doi: 10.7717/peerj.2108.

Eldridge, A. *et al.* (2018) ‘Sounding out ecoacoustic metrics: Avian species richness is predicted by acoustic indices in temperate but not tropical habitats’, *Ecological Indicators*. Elsevier, 95(June), pp. 939–952. doi: 10.1016/j.ecolind.2018.06.012.

Elith, J. *et al.* (2006) ‘Novel methods improve prediction of species’ distributions from occurrence data’, *Ecography*, 29(2), pp. 129–151. doi: 10.1111/j.2006.0906-7590.04596.x.

ESRI (2011) ‘ArcGIS Desktop: Release 10’. Redlands, CA: Environmental Systems Research Institute.

Estrada, A. (2006) ‘Human and non-human primate co-existence in the Neotropics: a preliminary view of some agricultural practices as a complement for primate conservation’, *Ecological and Environmental Anthropology*, 2(November), pp. 17–29. Available at: http://digitalcommons.unl.edu/icwdmeea/3/.

Estrada, A. *et al.* (2006) ‘Primates in agroecosystems: conservation value of agricultural practices in Mesoamerican landscapes’, in Estrada, A. et al. (eds) *New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior and conservation*. New York: Springer Press, pp. 437–470.

Estrada, A., Garber, P., *et al.* (2017) ‘Impending extinction crisis of the world’s primates: Why primates matter’, *Science Advances*. American Association for the Advancement of Science, p. 26. doi: 10.1126/sciadv.1600946.

Estrada, A., Garber, P. A., *et al.* (2017) ‘Impending extinction crisis of the world ’ s primates : Why primates matter’, *Advance Science*, 3(229), pp. 1–16. doi: 10.1126/sciadv.1600946.

Estrada, A., Raboy, B. E. and Oliveira, L. C. (2012) ‘Agroecosystems and Primate Conservation in The Tropics: A Review’, *American Journal of Primatology*, 74(8), pp. 696–711. doi: 10.1002/ajp.22033.

Fahrig, L. (2003) ‘Effects of Habitat Fragmentation on Biodiversity’, *Annual Review of Ecology, Evolution, and Systematics*, 34(1), pp. 487–515. doi: 10.1146/annurev.ecolsys.34.011802.132419.

Fahrig, L. and Rytwinski, T. (2009) ‘Effects of roads on animal abundance: An empirical review and synthesis. Ecology and Society, 14(1), 21.’, 14(1). Available at: http://http//ecologyand society.org/vol14/jss1/art21.

Fairbrass, A. J. *et al.* (2017) ‘Biases of acoustic indices measuring biodiversity in urban areas’, *Ecological Indicators*. Elsevier, 83(August), pp. 169–177. doi: 10.1016/j.ecolind.2017.07.064.

Felton, A. M. *et al.* (2008) ‘Diet and feeding ecology of Ateles chamek in a Bolivian semihumid forest: The importance of Ficus as a staple food resource’, *International Journal of Primatology*, 29(2), pp. 379–403. doi: 10.1007/s10764-008-9241-1.

Ficetola, G. F. and Denoël, M. (2009) ‘Ecological thresholds: an assessment of methods to identify abrupt changes in species–habitat relationships’, *Ecography*. John Wiley & Sons, Ltd, 32(6), pp. 1075–1084. doi: 10.1111/J.1600-0587.2009.05571.X.

Figueira, L. *et al.* (2015) ‘Autonomous sound monitoring shows higher use of Amazon old growth than secondary forest by parrots’, *Biological Conservation*. Elsevier Ltd, 184, pp. 27–35. doi: 10.1016/j.biocon.2014.12.020.

Di Fiore, A., Link, A. and Campbell, C. J. (2011) ‘The Atelines: Behavioral and socioecological diversity in a New World radiation.’, in Campbell, C. et al. (eds) *Primates in perspective*. Oxford, England: Oxford University Press, pp. 155–188.

Fiske, I. and Chandler, R. (2011) ‘unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance’, *Journal of Statistical Software*, 43(10), pp. 1–23. Available at: http://www.jstatsoft.org/v43/i10/.

Francomano, D., Gottesman, B. L. and Pijanowski, B. C. (2021) ‘Biogeographical and analytical implications of temporal variability in geographically diverse soundscapes’, *Ecological Indicators*. Elsevier, 121(September 2020), p. 106794. doi: 10.1016/j.ecolind.2020.106794.

Fuller, R. A., Warren, P. H. and Gaston, K. J. (2007) ‘Daytime noise predicts nocturnal singing in urban robins’, *Biology Letters*, 3(4), pp. 368–370. doi: 10.1098/rsbl.2007.0134.

Furumo, P. R. and Mitchell Aide, T. (2019) ‘Using soundscapes to assess biodiversity in Neotropical oil palm landscapes’, *Landscape Ecology*. Springer Netherlands, 34(4), pp. 911–923. doi: 10.1007/s10980-019-00815-w.

Gage, S. H. *et al.* (2017) ‘Acoustic patterns at the Samford Ecological Research Facility in South East Queensland, Australia: The Peri-Urban SuperSite of the Terrestrial Ecosystem Research Network’, *Ecological Informatics*. Elsevier B.V., 38, pp. 62–75. doi: 10.1016/j.ecoinf.2017.01.002.

Galán-Acedo, C. *et al.* (2018) ‘Drivers of the spatial scale that best predict primate responses to landscape structure’, *Ecography*, (March). doi: 10.1111/ecog.03632.

Galán-Acedo, C. *et al.* (2019) ‘A global assessment of primate responses to landscape structure’, *Biological Reviews*. Blackwell Publishing Ltd, 94(5), pp. 1605–1618. doi: 10.1111/brv.12517.

Galán-Acedo, C., Arroyo-Rodríguez, V. and Chapman, C. A. (2021) ‘Beyond patch size: The impact of regional context and habitat quality on three endangered primates’, *Perspectives in Ecology and Conservation*. Associacao Brasileira de Ciencia Ecologica e Conservacao, 19(2), pp. 207–215. doi: 10.1016/j.pecon.2021.02.004.

Gallmetzer, N. and Schulze, C. H. (2015) ‘Impact of oil palm agriculture on understory amphibians and reptiles: A Mesoamerican perspective’, *Global Ecology and Conservation*. Elsevier B.V., 4, pp. 95–109. doi: 10.1016/j.gecco.2015.05.008.

Gardner, T. A. *et al.* (2009) ‘Prospects for tropical forest biodiversity in a human-modified world’, *Ecology Letters*, 12(6), pp. 561–582. doi: 10.1111/j.1461-0248.2009.01294.x.

Geldmann, J. *et al.* (2019) ‘A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures’, *Proceedings of the National Academy of Sciences*. National Academy of Sciences, 116(46), pp. 23209–23215. doi: 10.1073/PNAS.1908221116.

Geldmann, J. *et al.* (2021) ‘Essential indicators for measuring site-based conservation effectiveness in the post-2020 global biodiversity framework’, *Conservation Letters*. John Wiley & Sons, Ltd, 14(4), p. e12792. doi: 10.1111/CONL.12792.

Gibb, R. *et al.* (2019) ‘Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring’, *Methods in Ecology and Evolution*, 10(2), pp. 169–185. doi: 10.1111/2041-210X.13101.

Gibbs, K. E., MacKey, R. L. and Currie, D. J. (2009) ‘Human land use, agriculture, pesticides and losses of imperiled species’, *Diversity and Distributions*, 15(2), pp. 242–253. doi: 10.1111/j.1472-4642.2008.00543.x.

Gibson, L. *et al.* (2011) ‘Primary forests are irreplaceable for sustaining tropical biodiversity’, *Nature*. Nature Publishing Group, 478(7369), pp. 378–381. doi: 10.1038/nature10425.

Gil, D. and Llusia, D. (2020) ‘The Bird Dawn Chorus Revisited’, in *Coding Strategies in Vertebrate Acoustic Communication*, pp. 45–90. doi: 10.1007/978-3-030-39200-0_3.

Gilbert, L. E. *et al.* (2016) ‘The Southern Pacific Lowland Evergreen Moist Forest of the Osa Region’, *Costa Rican Ecosystems*, (April), pp. 360–411.

González-Maya, J. F. *et al.* (2015) ‘Effectiveness of protected areas for representing species and populations of terrestrial mammals in Costa Rica’, *PLoS ONE*. Public Library of Science, 10(5), p. e0124480. doi: 10.1371/journal.pone.0124480.

Gottesman, B. L. *et al.* (2020) ‘Acoustic monitoring reveals diversity and surprising dynamics in tropical freshwater soundscapes’, *Freshwater Biology*. John Wiley & Sons, Ltd, 65(1), pp. 117–132. doi: 10.1111/FWB.13096.

Grant, P. B. C. and Samways, M. J. (2016) ‘Use of ecoacoustics to determine biodiversity patterns across ecological gradients’, *Conservation Biology*, 30(6), pp. 1320–1329. doi: 10.1111/cobi.12748.

Graves, B. and Nelson, G. (2004) ‘Anuran population monitoring: comparison of the North American Amphibian Monitoring Program’s calling index with mark-recapture estimates for Rana clamitans’, *Journal of Herpetology*, 38. Available at: https://commons.nmu.edu/facwork_journalarticles/348 (Accessed: 4 June 2021).

Gray, C. L. *et al.* (2016) ‘Local biodiversity is higher inside than outside terrestrial protected areas worldwide’, *Nature Communications 2016 7:1*. Nature Publishing Group, 7(1), pp. 1–7. doi: 10.1038/ncomms12306.

Greenfield, M. D. (2015) ‘Signal interactions and interference in insect choruses: singing and listening in the social environment’, *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*. Springer Verlag, pp. 143–154. doi: 10.1007/s00359-014-0938-7.

Gregory, T. *et al.* (2017) ‘Natural canopy bridges effectively mitigate tropical forest fragmentation for arboreal mammals’, *Scientific Reports*. Nature Publishing Group, 7(1), pp. 1–11. doi: 10.1038/s41598-017-04112-x.

Guerra, V. *et al.* (2020) ‘Nightly patterns of calling activity in anuran assemblages of the Cerrado, Brazil’, *Community Ecology*. Akademiai Kiado, 21(1), pp. 33–42. doi: 10.1007/s42974-020-00013-8.

Gutierrez, B. L. *et al.* (2019) ‘An island of wildlife in a human-dominated landscape: The last fragment of primary forest on the Osa Peninsula’s Golfo Dulce coastline, Costa Rica’, *PLoS ONE*, 14(3), pp. 1–19. doi: 10.1371/journal.pone.0214390.

Halfwerk, W. *et al.* (2011) ‘Negative impact of traffic noise on avian reproductive success’, *Journal of Applied Ecology*, 48(1), pp. 210–219. doi: 10.1111/j.1365-2664.2010.01914.x.

Hao, Z. *et al.* (2021) ‘Vegetation structure and temporality influence the dominance, diversity, and composition of forest acoustic communities’, *Forest Ecology and Management*. Elsevier B.V., 482(September 2020), p. 118871. doi: 10.1016/j.foreco.2020.118871.

Harikrishnan, S. *et al.* (2012) ‘Biodiversity values of abandoned teak, Tectona grandis plantations in southern Western Ghats: Is there a need for management intervention?’, *Basic and Applied Ecology*, 13(2), pp. 139–148. doi: 10.1016/j.baae.2012.01.001.

Hartig, F. (2020) ‘DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models’. Available at: https://cran.r-project.org/package=DHARMa.

Hassall, M. *et al.* (2006) ‘Biodiversity and abundance of terrestrial isopods along a gradient of disturbance in Sabah, East Malaysia’, *European Journal of Soil Biology*, 42(SUPPL. 1), pp. 197–207. doi: 10.1016/j.ejsobi.2006.07.002.

Hatfield, J. H. *et al.* (2020) ‘Mediation of area and edge effects in forest fragments by adjacent land use’, *Conservation Biology*. Blackwell Publishing Inc., 34(2), pp. 395–404. doi: 10.1111/cobi.13390.

Heinicke, S. *et al.* (2015) ‘Assessing the performance of a semi-automated acoustic monitoring system for primates’, *Methods in Ecology and Evolution*, 6(7), pp. 753–763. doi: 10.1111/2041-210X.12384.

Hilje, B. and Aide, T. M. (2012) ‘Calling activity of the common tink frog (Diasporus diastema) (Eleutherodactylidae) in secondary forests of the Caribbean of Costa Rica’, *Tropical Conservation Science*, 5(1), pp. 25–37. doi: 10.1177/194008291200500104.

Hill, A. P. *et al.* (2018) ‘AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the environment’, *Methods in Ecology and Evolution*, 2018(December 2017), pp. 1–

13. doi: 10.1111/2041-210X.12955.

Holgate, B., Maggini, R. and Fuller, S. (2021) ‘Mapping ecoacoustic hot spots and moments of biodiversity to inform conservation and urban planning’, *Ecological Indicators*. Elsevier Ltd, 126, p. 107627. doi: 10.1016/j.ecolind.2021.107627.

Huang, M. *et al.* (2021) ‘Passive acoustic monitoring for investigating spatiotemporal variation of anthropogenic threats: a case study for Dja Faunal Reserve, Cameroon’, *Unpublished*.

Van Hulle, M. and Vaughan, C. (2008) *The Effect of Human Development on Mammal Populations of the Punta Leona Private Wildlife Refuge, Costa Rica*, *Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN*.

Iezzi, M. E., De Angelo, C. and Di Bitetti, M. S. (2020) ‘Tree plantations replacing natural grasslands in high biodiversity areas: How do they affect the mammal assemblage?’, *Forest Ecology and Management*. Elsevier, 473(December 2019), p. 118303. doi: 10.1016/j.foreco.2020.118303.

Ikeda, T. *et al.* (2016) ‘Seasonal and Diel Activity Patterns of Eight Sympatric Mammals in Northern Japan Revealed by an Intensive Camera-Trap Survey’, *PLOS ONE*. Edited by S. Yamazaki. Public Library of Science, 11(10), p. e0163602. doi: 10.1371/journal.pone.0163602.

Iossa, G. *et al.* (2007) ‘Mammal trapping: a review of animal welfare standards of killing and restraining traps’, *Citeseer*. Available at: https://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.973.5675&rep=rep1&type=pdf (Accessed: 28 August 2021).

IPBES (2019) ‘Summary for policymakers of the global assessment report on biodiversity and ecosystem services’, in S. Díaz, J. Settele, E. S. Brondízio E.S., H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A, and C. N. Z. (eds. . (ed.). doi: 10.5281/ZENODO.3553579.

IUCN (2014) ‘IUCN - Protected Area Categories’, *Iucn*, p. 1994. Available at: https://www.iucn.org/theme/protected-areas/about/protected-area-categories (Accessed: 19 July 2021).

IUCN (2021) *The IUCN Red List of Threatened Species*. Available at: https://www.iucnredlist.org/fr/search/list?taxonomies=100091&searchType=species.

Jackson, H. B. and Fahrig, L. (2015) ‘Are ecologists conducting research at the optimal scale?’, *Global Ecology and Biogeography*. Blackwell Publishing Ltd, 24(1), pp. 52–63. doi: 10.1111/geb.12233.

Jahn, O. *et al.* (2017) ‘Automated Sound Recognition Provides Insights into the Behavioral Ecology of a Tropical Bird’, *PLOS ONE*. Public Library of Science, 12(1), p. e0169041. doi: 10.1371/JOURNAL.PONE.0169041.

James, G. *et al.* (2013) ‘Moving Beyond Linearity’, in *An Introduction to Statistical Learning*, pp. 265–301. doi: 10.1007/978-1-4614-7138-7_7.

Jaramillo-Legorreta, A. *et al.* (2017) ‘Passive acoustic monitoring of the decline of Mexico’s critically endangered vaquita’, *Conservation Biology*. John Wiley & Sons, Ltd, 31(1), pp. 183–191. doi: 10.1111/COBI.12789.

Jennings, N., Parsons, S. and Pocock, M. (2008) ‘Human vs. machine: identification of bat species from their echolocation calls by humans and by artificial neural networks', *Canadian Journal of Zoology*, 86(5), pp. 371–377. doi: 10.1139/Z08-009.

Joo, W., Gage, S. H. and Kasten, E. P. (2011) 'Analysis and interpretation of variability in soundscapes along an urban-rural gradient', *Landscape and Urban Planning*. Elsevier B.V., 103(3–4), pp. 259–276. doi: 10.1016/j.landurbplan.2011.08.001.

Junker, J. *et al.* (2020) 'A Severe Lack of Evidence Limits Effective Conservation of the World's Primates', *BioScience*. Oxford University Press, 70(9), pp. 794–803. doi: 10.1093/biosci/biaa082.

Kalan, A. K. *et al.* (2015) 'Towards the automated detection and occupancy estimation of primates using passive acoustic monitoring', *Ecological Indicators*. Elsevier Ltd, 54, pp. 217–226. doi: 10.1016/j.ecolind.2015.02.023.

Kalan, A. K. *et al.* (2016) 'Passive acoustic monitoring reveals group ranging and territory use: A case study of wild chimpanzees (Pan troglodytes)', *Frontiers in Zoology*. Frontiers in Zoology, 13(1), pp. 1–11. doi: 10.1186/s12983-016-0167-8.

Kappelle, M. (2016) 'Costa Rica ' s Ecosystems : Setting the Stage Chapter 1 Costa Rica ' s Ecosystems : Setting the Stage', *Costa Rican Ecosistems*, (October).

Kasten, E. P. *et al.* (2012) 'The remote environmental assessment laboratory's acoustic library: An archive for studying soundscape ecology', *Ecological Informatics*. Elsevier B.V., 12, pp. 50–67. doi: 10.1016/j.ecoinf.2012.08.001.

Kiskin, I. *et al.* (2017) 'Mosquito Detection with Neural Networks: The Buzz of Deep Learning', pp. 1–16. Available at: http://arxiv.org/abs/1705.05180.

Kleyn, T., da Cruz Kaizer, M. and Passos, L. F. (2021) 'Sharing sound: Avian acoustic niches in the Brazilian Atlantic Forest', *Biotropica*, 53(2), pp. 658–670. doi: 10.1111/btp.12907.

Kosmidis, I. (2020) 'Bias Reduction in Generalized Linear Models'. Available at: https://cran.r-project.org/package=brglm2.

Krause, B. (1987) 'Bioacoustics, habitat ambience in ecological balance', *Whole Earth Rev*, 57, pp. 14–18.

Krause, B., Gage, S. H. and Joo, W. (2011) 'Measuring and interpreting the temporal variability in the soundscape at four places in Sequoia National Park', *Landscape Ecology 2011 26:9*. Springer, 26(9), pp. 1247–1256. doi: 10.1007/S10980-011-9639-6.

Kupsch, D. *et al.* (2019) 'High critical forest habitat thresholds of native bird communities in Afrotropical agroforestry landscapes', *Biological Conservation*. Elsevier, 230, pp. 20–28. doi: 10.1016/J.BIOCON.2018.12.001.

Lacerda, L. (2004) 'Are protected areas working?', *Wilderness*, 269(6), pp. 1–5.

Lapp, S. *et al.* (2021) 'Automated detection of frog calls and choruses by pulse repetition rate', *Conservation Biology*, 35(5), pp. 1659–1668. doi: 10.1111/cobi.13718.

Laurance, W. F., Carolina Useche, D., *et al.* (2012) 'Averting biodiversity collapse in tropical forest protected areas', *Nature 2012 489:7415*. Nature Publishing Group, 489(7415), pp. 290–294. doi: 10.1038/nature11318.

Laurance, W. F., Useche, D. C., *et al.* (2012) 'Averting biodiversity collapse in tropical forest protected areas', *Nature 2012 489:7415*. Nature Publishing Group, 489(7415), pp. 290–294. doi: 10.1038/nature11318.

Laurance, W. F., Goosem, M. and Laurance, S. G. W. (2009) 'Impacts of roads and linear clearings on tropical forests', *Trends in Ecology and Evolution*. Trends Ecol Evol, pp. 659–669. doi: 10.1016/j.tree.2009.06.009.

Laurance, W. F., Sayer, J. and Cassman, K. G. (2014) 'Agricultural expansion and its impacts on tropical nature', *Trends in Ecology and Evolution*, 29(2), pp. 107–116. doi: 10.1016/j.tree.2013.12.001.

Lecun, Y., Bengio, Y. and Hinton, G. (2015) 'Deep learning', *Nature*, 521(7553), pp. 436–444. doi: 10.1038/nature14539.

Lee, J. G. H., MacGregor-Fors, I. and Yeh, P. J. (2017) 'Sunrise in the city: disentangling drivers of the avian dawn chorus onset in urban greenspaces', *Journal of Avian Biology*, 48(7), pp. 955–964. doi: 10.1111/jav.01042.

Lee, M. B. and Goodale, E. (2018) 'Crop heterogeneity and non-crop vegetation can enhance avian diversity in a tropical agricultural landscape in southern China', *Agriculture, Ecosystems and Environment*. Elsevier, 265(February), pp. 254–263. doi: 10.1016/j.agee.2018.06.016.

Lees, A. C. *et al.* (2015) 'Poor prospects for avian biodiversity in amazonian oil palm', *PLoS ONE*, 10(5), pp. 1–17. doi: 10.1371/journal.pone.0122432.

Lees, A. C. and Peres, C. A. (2008) 'Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals', *Conservation Biology*, 22(2), pp. 439–449. doi: 10.1111/j.1523-1739.2007.00870.x.

Legge, S. *et al.* (2018) *Monitoring threatened species and ecological communities*, *Monitoring threatened species and ecological communities*. Edited by S. Legge et al. CSIRO Publishing.

Lenske, A. K. and La, V. T. (2014) 'White-throated sparrows alter songs differentially in response to chorusing anurans and other background noise', *Behavioural Processes*. Elsevier, 105, pp. 28–35. doi: 10.1016/j.beproc.2014.02.015.

Lewis, S. L. *et al.* (2019) 'Restoring natural forests is the best way to remove atmospheric carbon', *Nature*. Nature Publishing Group, 568(7750), pp. 25–28. doi: 10.1038/d41586-019-01026-8.

Lindshield, S. M. (2016) 'Protecting Nonhuman Primates in Peri-Urban Environments: A Case Study of Neotropical Monkeys, Corridor Ecology, and Coastal Economy in the Caribe Sur of Costa Rica', in. Springer, Cham, pp. 351–369. doi: 10.1007/978-3-319-30469-4_19.

Link, A. and Di Fiore, A. (2006) 'Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity', *Journal of Tropical Ecology*, 22(03), pp. 235–246. doi: 10.1017/S0266467405003081.

Lopez Gutierrez, B. *et al.* (2020) 'Ecotourism: the "human shield" for wildlife conservation in the Osa Peninsula, Costa Rica', *Journal of Ecotourism*, 19(3), pp. 197–216. doi: 10.1080/14724049.2019.1686006.

Luckett, J. *et al.* (2004) 'Planted Trees as Corridors for Primates at El Zota Biological Field Station, Costa Rica', *Neotropical Primates*, 12(3), pp. 143–146. doi: 10.1896/1413-4705.12.3.143.

Luther, D. (2009) 'The influence of the acoustic community on songs of birds in a neotropical rain forest', *Behavioral Ecology*, 20(4), pp. 864–871. doi: 10.1093/beheco/arp074.

Maciej, P., Fischer, J. and Hammerschmidt, K. (2011) 'Transmission characteristics of primate vocalizations: Implications for acoustic analyses', *PLoS ONE*, 6(8), pp. 30–36. doi: 10.1371/journal.pone.0023015.

MacLean, I. *et al.* (2003) 'Effects of habitat degradation on avian guilds in East African papyrus Cyperus papyrus swamps', *Bird Conservation International*, 13(4), pp. 283–297. doi: 10.1017/S0959270903003216.

Magura, T., Tóthmérész, B. and Molnár, T. (2008) 'A species-level comparison of occurrence patterns in carabids along an urbanisation gradient', *Landscape and Urban Planning*. Elsevier, 86(2), pp. 134–140. doi: 10.1016/j.landurbplan.2008.01.005.

Mammides, C. *et al.* (2017) 'Do acoustic indices correlate with bird diversity? Insights from two biodiverse regions in Yunnan Province, south China', *Ecological Indicators*. Elsevier, 82(July), pp. 470–477. doi: 10.1016/j.ecolind.2017.07.017.

De Marco, P. and Nóbrega, C. C. (2018) 'Evaluating collinearity effects on species distribution models: An approach based on virtual species simulation', *PLoS ONE*. Public Library of Science, 13(9), p. e0202403. doi: 10.1371/journal.pone.0202403.

Marmion, M. *et al.* (2009) 'Evaluation of consensus methods in predictive species distribution modelling', *Diversity and Distributions*. John Wiley & Sons, Ltd, 15(1), pp. 59–69. doi: 10.1111/j.1472-4642.2008.00491.x.

McRae, B. H. (2012) 'Pinchpoint Mapper Connectivity Analysis Software'. Seattle WA.: The Nature Conservancy. Available at: http://www.circuitscape.org/linkagemapper.

McRae, B. H. and Kavanagh, D. M. (2011) 'Linkage Mapper Connectivity Analysis Software'. Seattle WA: Nature Conservancy. Available at: http://www.circuitscape.org/linkagemapper.

Méndez-Rojas, D. M., Cultid-Medina, C. and Escobar, F. (2021) 'Influence of land use change on rove beetle diversity: A systematic review and global meta-analysis of a mega-diverse insect group', *Ecological Indicators*, 122. doi: 10.1016/j.ecolind.2020.107239.

Mendoza, E. *et al.* (2013) 'A preliminary assessment of the effectiveness of the Mesoamerican Biological Corridor for protecting potential Baird's tapir (Tapirus bairdii) habitat in southern Mexico', *Integrative Zoology*, 8(1), pp. 35–47. doi: 10.1111/1749-4877.12005.

Mennill, D. J. *et al.* (2012) 'Field test of an affordable, portable, wireless microphone array for spatial monitoring of animal ecology and behaviour', *Methods in Ecology and Evolution*. John Wiley & Sons, Ltd, 3(4), pp. 704–712. doi: 10.1111/j.2041-210X.2012.00209.x.

Mielke, A. and Zuberbühler, K. (2013) 'A method for automated individual, species and call type recognition in free-ranging animals', *Animal Behaviour*. Elsevier Ltd, 86(2), pp. 475–482. doi: 10.1016/j.anbehav.2013.04.017.

Mulero-Pázmány, M., D'Amico, M. and González-Suárez, M. (2016) 'Ungulate behavioral responses to the heterogeneous road-network of a touristic protected area in Africa', *Journal of Zoology*.

Blackwell Publishing Ltd, 298(4), pp. 233–240. doi: 10.1111/jzo.12310.

Naimi, B. and Araújo, M. B. (2016) ‘Sdm: A reproducible and extensible R platform for species distribution modelling’, *Ecography*, 39(4), pp. 368–375. doi: 10.1111/ecog.01881.

Mac Nally, R. and Walsh, C. (2004) ‘Hierarchical partitioning public-domain software’, *Biodiversity and Conservation*, pp. 659–660. Available at: https://search.proquest.com/openview/6f19c4d612b6cf75b106c479e7084a58/1.

Napoletano, B. M. *et al.* (2011) ‘Soundscape Ecology: The Science of Sound in the Landscape’, *BioScience*, 61(3), pp. 203–216. doi: 10.1525/bio.2011.61.3.6.

Navarro-Fernández, E., Carmen, P. and Escobedo-Cabrera, E. (2003) ‘Afinidad ecológica y distribución actual de Primates (Cebidae) en Campeche, México’, *Revista de Biologia Tropical*, 51(2), pp. 591–600.

Newbold T., Hudson L.N., Hill S.L.L., Contu S., Lysenko I., S. R. A. *et al.* (2016) ‘Global effects of land use on local terrestrial biodiversity’, *Nature*, 520, pp. 45–50. doi: 10.1038/nature14324.

Ng, M. Le, Butler, N. and Woods, N. (2018) ‘Soundscapes as a surrogate measure of vegetation condition for biodiversity values: A pilot study’, *Ecological Indicators*. Elsevier B.V., 93, pp. 1070–1080. doi: 10.1016/j.ecolind.2018.06.003.

Nguyen, A. T. *et al.* (2020) ‘Efficacy of camera traps in detecting primates in Hue Saola Nature Reserve’, *Primates 2020 61:5*. Springer, 61(5), pp. 697–705. doi: 10.1007/S10329-020-00823-4.

Norris, D., Michalski, F. and Peres, C. a (2010) ‘Habitat patch size modulates terrestrial mammal activity patterns in Amazonian forest fragments Habitat patch size modulates terrestrial mammal activity patterns in Amazonian forest fragments’, *Journal of Mammalogy*, 91(3), pp. 551–560. doi: 10.1644/09-MAMM-A-199.1.Key.

Norris, K. *et al.* (2010) ‘Biodiversity in a forest-agriculture mosaic - The changing face of West African rainforests’, *Biological Conservation*. Elsevier Ltd, 143(10), pp. 2341–2350. doi: 10.1016/j.biocon.2009.12.032.

Novacek, M. J. and Cleland, E. E. (2001) ‘The current biodiversity extinction event: Scenarios for mitigation and recovery’, *Proceedings of the National Academy of Sciences of the United States of America*. National Academy of Sciences, 98(10), pp. 5466–5470. doi: 10.1073/pnas.091093698.

Ocampo-Ariza, C. *et al.* (2019) ‘Extinction thresholds and negative responses of Afrotropical ant-following birds to forest cover loss in oil palm and agroforestry landscapes’, *Basic and Applied Ecology*. Elsevier GmbH, 39, pp. 26–37. doi: 10.1016/j.baae.2019.06.008.

Ochoa-Quintero, J. M. *et al.* (2015) ‘Thresholds of species loss in Amazonian deforestation frontier landscapes’, *Conservation Biology*. John Wiley & Sons, Ltd, 29(2), pp. 440–451. doi: 10.1111/COBI.12446.

Oksanen, J. *et al.* (2019) ‘vegan: Community Ecology Package’. Available at: https://cran.r-project.org/package=vegan.

Oliveira, A. T. M. *et al.* (2019) ‘Primate and ungulate responses to teak agroforestry in a southern Amazonian landscape’, *Mammalian Biology*, 96, pp. 45–52. doi: 10.1016/j.mambio.2019.03.015.

de Oliveira Roque, F. *et al.* (2018) ‘Warning signals of biodiversity collapse across gradients of tropical forest loss’, *Scientific Reports 2018 8:1*. Nature Publishing Group, 8(1), pp. 1–7. doi: 10.1038/s41598-018-19985-9.

Oliver, T. H. *et al.* (2015) ‘Declining resilience of ecosystem functions under biodiversity loss’, *Nature Communications*. Nature Publishing Group, 6(1), pp. 1–8. doi: 10.1038/ncomms10122.

Osa Conservation (2016) *About the Osa*.

Osipova, E. *et al.* (2020) *IUCN World Heritage Outlook 3*, *IUCN World Heritage Outlook 3*. doi: 10.2305/iucn.ch.2020.16.en.

Ottewell, K. *et al.* (2019) ‘Remnant vegetation provides genetic connectivity for a critical weight range mammal in a rapidly urbanising landscape’, *Landscape and Urban Planning*. Elsevier, 190, p. 103587. doi: 10.1016/J.LANDURBPLAN.2019.103587.

Paoletti, A. *et al.* (2018) ‘Amphibian and reptile communities of upland and riparian sites across Indonesian oil palm, rubber and forest’, *Global Ecology and Conservation*. Elsevier Ltd, 16, p. e00492. doi: 10.1016/j.gecco.2018.e00492.

Paradis, E. and Schliep, K. (2019) ‘ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R’, *Bioinformatics*, 35, pp. 526–528.

Pardo Vargas, L. E. *et al.* (2016) ‘Assessing species traits and landscape relationships of the mammalian carnivore community in a neotropical biological corridor’, *Biodiversity and Conservation*. Springer Netherlands, 25(4), pp. 739–752. doi: 10.1007/s10531-016-1089-7.

Van Parijs, S. M., Smith, J. and Corkeron, P. J. (2002) ‘Using calls to estimate the abundance of inshore dolphins: A case study with Pacific humpback dolphins Sousa chinensis’, *Journal of Applied Ecology*, 39(5), pp. 853–864. doi: 10.1046/j.1365-2664.2002.00756.x.

Parry, L., Barlow, J. and Peres, C. A. (2007) ‘Large-vertebrate assemblages of primary and secondary forests in the Brazilian Amazon’, *Journal of Tropical Ecology*, 23(06), pp. 653–662. doi: 10.1017/S0266467407004506.

Pebesma, E. (2004) ‘ultivariable geostatistics in S: the gstat package’, *Computers & Geosciences*, 30, pp. 683–691.

Penar, W., Magiera, A. and Klocek, C. (2020) ‘Applications of bioacoustics in animal ecology’, *Ecological Complexity*. Elsevier B.V., p. 100847. doi: 10.1016/j.ecocom.2020.100847.

Peres, C. (1997) ‘Evaluating the sustainability of subsistence hunting in tropical forests’, *Working Paper - Centre for Social and Economic Research on the Global Environment*, GEC 97-22(June). doi: ISSN 0967-8875.

Peres, C. A. (1990) ‘Effects of hunting on western Amazonian primate communities’, *Biological Conservation*, 54(1), pp. 47–59. doi: 10.1016/0006-3207(90)90041-M.

Peres, C. A. (2001) ‘Synergistic effects of subsistence hunting and habitat fragmentation on amazonian forest vertebrates’, *Conservation Biology*, 15(6), pp. 1490–1505. doi: 10.1046/j.1523-1739.2001.01089.x.

Pérez-Granados, C. *et al.* (2019) ‘Vocal activity rate index: a useful method to infer terrestrial bird abundance with acoustic monitoring', *Ibis*. Blackwell Publishing Ltd, 161(4), pp. 901–907. doi: 10.1111/ibi.12728.

Pérez-Granados, C. and Schuchmann, K.-L. (2021) 'Passive acoustic monitoring of the diel and annual vocal behavior of the Black and Gold Howler Monkey', *American Journal of Primatology*. John Wiley & Sons, Ltd, 83(3), p. e23241. doi: 10.1002/AJP.23241.

Pieretti, N. *et al.* (2015) 'Determining temporal sampling schemes for passive acoustic studies in different tropical ecosystems', *Tropical Conservation Science*. Mongaby.com e-journal, 8(1), pp. 215–234. doi: 10.1177/194008291500800117.

Pieretti, N., Farina, A. and Morri, D. (2011) 'A new methodology to infer the singing activity of an avian community: The Acoustic Complexity Index (ACI)', *Ecological Indicators*. Elsevier Ltd, 11(3), pp. 868–873. doi: 10.1016/j.ecolind.2010.11.005.

Pijanowski, B. C., Villanueva-Rivera, L. J., *et al.* (2011) 'Soundscape ecology: The science of sound in the landscape', *BioScience*, 61(3), pp. 203–216. doi: 10.1525/bio.2011.61.3.6.

Pijanowski, B. C., Farina, A., *et al.* (2011) 'What is soundscape ecology? An introduction and overview of an emerging new science', *Landscape Ecology*, 26(9), pp. 1213–1232. doi: 10.1007/s10980-011-9600-8.

Pinheiro, J. and Bates, D. (2000) *Mixed-Effects Models in S and S-PLUS*, *Mixed-Effects Models in S and S-PLUS*. Springer-Verlag. doi: 10.1007/b98882.

Pinheiro, J., Bates, D. and DebRoy, S. (2020) 'nlme: Linear and Nonlinear Mixed Effects Models'. R Core Team. Available at: https://cran.r-project.org/package=nlme.

Pinto, F. A. S., Clevenger, A. P. and Grilo, C. (2020) 'Effects of roads on terrestrial vertebrate species in Latin America', *Environmental Impact Assessment Review*. Elsevier Inc., p. 106337. doi: 10.1016/j.eiar.2019.106337.

Planqué, R. and Slabbekoorn, H. (2008) 'Spectral overlap in songs and temporal avoidance in a peruvian bird assemblage', *Ethology*, 114(3), pp. 262–271. doi: 10.1111/j.1439-0310.2007.01461.x.

Pozzi, L., Gamba, M. and Giacoma, C. (2010) 'The use of artificial neural networks to classify primate vocalizations: A pilot study on black lemurs', *American Journal of Primatology*, 72(4), pp. 337–348. doi: 10.1002/ajp.20786.

Proctor, S., McClean, C. J. and Hill, J. K. (2011) 'Protected areas of Borneo fail to protect forest landscapes with high habitat connectivity', *Biodiversity and Conservation*, 20(12), pp. 2693–2704. doi: 10.1007/s10531-011-0099-8.

Pruetz, J. D. and Leasor, H. C. (2002) 'Survey of three primate species in forest fragments at La Suerte biological field station, Costa Rica', *Neotropical Primates*, 10(1), pp. 4–9.

Ramos-Fernandez, G. *et al.* (2013) 'Site Fidelity in Space Use by Spider Monkeys (Ateles geoffroyi) in the Yucatan Peninsula, Mexico', *PLoS ONE*, 8(5). doi: 10.1371/journal.pone.0062813.

Ramos-Fernández, G. (2008) 'Communication in spider monkeys: the function and mechanisms underlying the use of the whinny', *Spider Monkeys: The Biology, Behavior and Ecology of the Genus Ateles*, (January), pp. 220–235. doi: 10.1017/CBO9780511721915.008.

Ramos-Fernández, G. and Ayala-Orozco, B. (2003) ‘Population Size and Habitat use of Spider Monkeys at Punta Laguna, Mexico’, in *Primates in Fragments*. Springer US, pp. 191–209. doi: 10.1007/978-1-4757-3770-7_13.

Ramos-Fernández, G. and Wallace, R. B. (2010) ‘Spider monkey conservation in the twenty-first century: recognizing risks and opportunities’, in *Spider Monkeys*, pp. 351–376. doi: 10.1017/cbo9780511721915.013.

Rizos, G. *et al.* (2021) ‘Multi-Attentive Detection of the Spider Monkey Whinny in the (Actual) Wild’, *Interspeech 2021*.

Rocha, L. H. S. *et al.* (2015) ‘An evaluation of manual and automated methods for detecting sounds of maned wolves (Chrysocyon brachyurus Illiger 1815)’, *Bioacoustics*, 24(2), pp. 185–198. doi: 10.1080/09524622.2015.1019361.

van Roosmalen, M. G. M. (1980) ‘Habitat preferences, diet, feeding strategy and social organisation of the black spider monkey (Ateles panisius paniscus L.) in Surinam’, *Acta Amazonica*, 15, pp. 1–238. doi: 10.1590/1809-43921985155238.

da Rosa, C. A. *et al.* (2018) ‘Edge effects on small mammals: Differences between arboreal and ground-dwelling species living near roads in Brazilian fragmented landscapes’, *Austral Ecology*. Blackwell Publishing, 43(1), pp. 117–126. doi: 10.1111/aec.12549.

Ross, S. R. P. J. *et al.* (2018) ‘Listening to ecosystems: data-rich acoustic monitoring through landscape-scale sensor networks’, *Ecological Research*. Springer Tokyo, 33(1), pp. 135–147. doi: 10.1007/s11284-017-1509-5.

Ross, S. R. P. J. *et al.* (2021) ‘Utility of acoustic indices for ecological monitoring in complex sonic environments’, *Ecological Indicators*. Elsevier B.V., 121, p. 107114. doi: 10.1016/j.ecolind.2020.107114.

Van Rossum, G. and Drake, F. (2009) ‘Python 3 Reference Manual’. Scotts Valley, CA: CreateSpace.

Rota, C. T. *et al.* (2009) ‘Occupancy estimation and the closure assumption’, *Journal of Applied Ecology*. John Wiley & Sons, Ltd, 46(6), pp. 1173–1181. doi: 10.1111/j.1365-2664.2009.01734.x.

Rudnick, D. a *et al.* (2012) ‘Published by the Ecological Society of America esa’, *Issues in Ecology*, (16).

Sánchez-Azofeifa, A. G. *et al.* (2002) ‘Integrity and isolation of Costa Rica’s national parks and biological reserves: Examining the dynamics of land-cover change’, *Biological Conservation*, 109(1), pp. 123–135. doi: 10.1016/S0006-3207(02)00145-3.

Saura, S. *et al.* (2017) ‘Protected areas in the world’s ecoregions: How well connected are they?’, *Ecological Indicators*. Elsevier, 76, pp. 144–158. doi: 10.1016/J.ECOLIND.2016.12.047.

Saura, S. *et al.* (2018) ‘Protected area connectivity: Shortfalls in global targets and country-level priorities’, *Biological Conservation*. Elsevier, 219, pp. 53–67. doi: 10.1016/J.BIOCON.2017.12.020.

Schroeder, J. *et al.* (2012) ‘Passerine birds breeding under chronic noise experience reduced fitness’, *PLoS ONE*, 7(7). doi: 10.1371/journal.pone.0039200.

Shrestha, S. *et al.* (2018) ‘Utilizing NASA Earth Observations to Evaluate Effects of Land Use Change on Watershed Health and Carbon Sequestration in the Osa Peninsula, Costa Rica’. NASA DEVELOP National Program.

Da Silva, A. and Kempenaers, B. (2017) ‘Singing from North to South: Latitudinal variation in timing of dawn singing under natural and artificial light conditions’, *Journal of Animal Ecology*. Edited by E. Derryberry. Blackwell Publishing Ltd, 86(6), pp. 1286–1297. doi: 10.1111/1365-2656.12739.

Da Silva, A., Valcu, M. and Kempenaers, B. (2016) ‘Behavioural plasticity in the onset of dawn song under intermittent experimental night lighting’, *Animal Behaviour*. Academic Press, 117, pp. 155–165. doi: 10.1016/j.anbehav.2016.05.001.

Da Silva, L. G. *et al.* (2015) ‘Patch size, functional isolation, visibility and matrix permeability influences neotropical primate occurrence within highly fragmented landscapes’, *PLoS ONE*, 10(2), pp. 1–20. doi: 10.1371/journal.pone.0114025.

Smith, D. G. *et al.* (2020) ‘Do acoustically detectable species reflect overall diversity? A case study from Australia’s arid zone’, *Remote Sensing in Ecology and Conservation*, 6(3), pp. 286–300. doi: 10.1002/rse2.173.

Sorensen, T. C. and Fedigan, L. M. (2000) ‘Distribution of three monkey species along a gradient of regenerating tropical dry forest’, *Biological Conservation*, 92(2), pp. 227–240. doi: 10.1016/S0006-3207(99)00068-3.

Soto, J. S. V. *et al.* (2021) ‘Human disturbance and shifts in vertebrate community composition in a biodiversity hotspot’, *Conservation Biology*. John Wiley & Sons, Ltd. doi: 10.1111/COBI.13813.

Spaan, D. *et al.* (2019) ‘Thermal infrared imaging from drones offers a major advance for spider monkey surveys’, *Drones*, 3(2), pp. 1–19. doi: 10.3390/drones3020034.

Spaan, D. *et al.* (2020) ‘Anthropogenic habitat disturbance and food availability affect the abundance of an endangered primate: a regional approach’, *Mammalian Biology*. Springer International Publishing, 100(3), pp. 325–333. doi: 10.1007/s42991-020-00025-x.

Spillmann, B. *et al.* (2015) ‘Validation of an acoustic location system to monitor Bornean orangutan (Pongo pygmaeus wurmbii) long calls’, *American Journal of Primatology*, 77(7), pp. 767–776. doi: 10.1002/ajp.22398.

Stanley, C. Q. *et al.* (2016) ‘Insect noise avoidance in the dawn chorus of Neotropical birds’, *Animal Behaviour*. Academic Press, 112, pp. 255–265. doi: 10.1016/j.anbehav.2015.12.003.

STEM, C. *et al.* (2005) ‘Monitoring and Evaluation in Conservation: a Review of Trends and Approaches’, *Conservation Biology*. John Wiley & Sons, Ltd, 19(2), pp. 295–309. doi: 10.1111/J.1523-1739.2005.00594.X.

Stewart, F. E. C. *et al.* (2019) ‘Corridors best facilitate functional connectivity across a protected area network’, *Scientific Reports 2019 9:1*. Nature Publishing Group, 9(1), pp. 1–9. doi: 10.1038/s41598-019-47067-x.

Stolton, S. *et al.* (2014) ‘The futures of privately protected areas’, *Protected Area Technical Report Series No.1 International Union For Consevation Nature (IUCN)*, (1), p. 128. Available at: http://www.iucn.org/about/work/programmes/gpap_home/gpap_ (Accessed: 1 June 2021).

Sueur, J. *et al.* (2008) ‘Rapid acoustic survey for biodiversity appraisal’, *PLoS ONE*, 3(12). doi:

10.1371/journal.pone.0004065.

Sueur, J. *et al.* (2014) ‘Acoustic indices for biodiversity assessment and landscape investigation’, *Acta Acustica united with Acustica*, 100(4), pp. 772–781. doi: 10.3813/AAA.918757.

Sueur, J. and Farina, A. (2015) ‘Ecoacoustics: the Ecological Investigation and Interpretation of Environmental Sound’, *Biosemiotics*, 8(3), pp. 493–502. doi: 10.1007/s12304-015-9248-x.

Sugai, L. S. M. *et al.* (2019) ‘Terrestrial Passive Acoustic Monitoring: Review and Perspectives’, *BioScience*. Oxford Academic, 69(1), pp. 15–25. doi: 10.1093/BIOSCI/BIY147.

Tangmitcharoen, S. *et al.* (2006) ‘Insect biodiversity in flowering teak (Tectona grandis L.f.) canopies: Comparison of wild and plantation stands’, *Forest Ecology and Management*, 222(1–3), pp. 99–107. doi: 10.1016/j.foreco.2005.10.040.

Taylor, B. D. *et al.* (2010) ‘Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia’, *Wildlife Research*. CSIRO PUBLISHING, 37(4), pp. 320–331. doi: 10.1071/WR09171.

Taylor, B. D. and Goldingay, R. L. (2010) ‘Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia’, *Wildlife Research*, 37(4), p. 320. doi: 10.1071/wr09171.

Teixeira, F. *et al.* (2013) *Canopy bridges as road overpasses for wildlife in urban fragmented landscapes*, *Biota Neotrop*. Available at: http://www.biotaneotropica.org.br/v13n1/en/abstract?article+bn02713012013http://www.biotaneotropica.org.brhttp://www.ecologia.ufrgs.br/ppgeco/http://www.ufrgs.br/macacosurbanoshttp://www.biotaneotropica.org.br/v13n1/en/abstract?article+bn02713012013 (Accessed: 5 July 2021).

Teixidor, P. and Byrne, R. W. (1999) *The ‘Whinny’ of Spider Monkeys: Individual Recognition before Situational Meaning*, *Source: Behaviour*.

Thompson, M. E. *et al.* (2010) ‘Acoustic estimation of wildlife abundance: Methodology for vocal mammals in forested habitats’, *African Journal of Ecology*, 48(3), pp. 654–661. doi: 10.1111/j.1365-2028.2009.01161.x.

Thuiller, W. *et al.* (2009) ‘BIOMOD - A platform for ensemble forecasting of species distributions’, *Ecography*. John Wiley & Sons, Ltd, 32(3), pp. 369–373. doi: 10.1111/j.1600-0587.2008.05742.x.

Towsey, M. *et al.* (2014) ‘The use of acoustic indices to determine avian species richness in audio-recordings of the environment’, *Ecological Informatics*. Elsevier B.V., 21(100), pp. 110–119. doi: 10.1016/j.ecoinf.2013.11.007.

Towsey, M. (2018) *The calculation of acoustic indices derived from long-duration recordings of the natural environment*.

Towsey, M. *et al.* (2020) ‘QutEcoacoustics/audio-analysis: Ecoacoustics Audio Analysis Software v20.11.2.0’. Zenodo. Available at: http://doi.org/10.5281/zenodo.1188744.

Trombulak, S. C. and Frissell, C. A. (2000) *Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities*, *Conservation Biology*.

Tucker, D. *et al.* (2014) *Linking ecological condition and the soundscape in fragmented Australian forests*, *Landscape Ecology*. doi: 10.1007/s10980-014-0015-1.

Tucker, M. A. *et al.* (2018) 'Moving in the Anthropocene: Global reductions in terrestrial mammalian movements', *Science*. American Association for the Advancement of Science, 359(6374), pp. 466–469. doi: 10.1126/SCIENCE.AAM9712.

Turesson, H. K. *et al.* (2016) 'Machine learning algorithms for automatic classification of marmoset vocalizations', *PLoS ONE*. Public Library of Science, 11(9), p. e0163041. doi: 10.1371/journal.pone.0163041.

UNEP-WCMC and IUCN (2016) *Protected Planet Report*, *Protected Planet Report 2016.How Protected Areas contribute to achieving Global Targets for Biodiversity*. Available at: https://livereport.protectedplanet.net/ (Accessed: 16 July 2021).

Urquiza-Haas, T., Peres, C. A. and Dolman, P. M. (2009) 'Regional scale effects of human density and forest disturbance on large-bodied vertebrates throughout the Yucatán Peninsula, Mexico', *Biological Conservation*. Elsevier, 142(1), pp. 134–148. doi: 10.1016/j.biocon.2008.10.007.

Vallejos, M. A. V., Padial, A. A. and Vitule, J. R. S. (2016) 'Human-induced landscape changes homogenize atlantic forest bird assemblages through nested species loss', *PLoS ONE*, 11(2), pp. 1–17. doi: 10.1371/journal.pone.0147058.

Villanueva-Rivera, L. J. *et al.* (2011) 'A primer of acoustic analysis for landscape ecologists', *Landscape Ecology*, 26(9), pp. 1233–1246. doi: 10.1007/s10980-011-9636-9.

Waldron, A. *et al.* (2020) 'Protecting 30% of the planet for nature: costs, benefits and economic implications', *Campaign for Nature*, 49, p. undefined-58. Available at: https://www.conservation.cam.ac.uk/files/waldron_report_30_by_30_publish.pdf (Accessed: 16 July 2021).

Wallace, R. B. (2001) 'Diurnal activity budgets of black spider monkeys, aleles chamek in a southern Amazonian tropical forest', *Neotropical Primates*, 9(3), pp. 101-.

Wallace, R. B. (2005) 'Seasonal variations in diet and foraging behavior of Ateles chamek in a southern Amazonian tropical forest', *International Journal of Primatology*, 26(5), pp. 1053–1075. doi: 10.1007/s10764-005-6458-4.

Wallace, R. B. (2008a) 'Factors influencing spider monkey habitat use and ranging patterns', *Spider monkeys: Behavior, ecology and evolution of the Genus Ateles*, (January 2008), pp. 138–154. doi: 10.5860/CHOICE.48-1788.

Wallace, R. B. (2008b) 'The influence of feeding patch size and relative fruit density on the foraging behavior of the black spider monkey ateles chamek', *Biotropica*, 40(4), pp. 501–506. doi: 10.1111/j.1744-7429.2007.00392.x.

Ward, M. *et al.* (2020) 'Just ten percent of the global terrestrial protected area network is structurally connected via intact land', *Nature Communications 2020 11:1*. Nature Publishing Group, 11(1), pp. 1–10. doi: 10.1038/s41467-020-18457-x.

Watson, J. E. M. *et al.* (2014) 'The performance and potential of protected areas', *Nature 2014 515:7525*. Nature Publishing Group, 515(7525), pp. 67–73. doi: 10.1038/nature13947.

Watson, J. E. M. *et al.* (2018) 'The exceptional value of intact forest ecosystems', *Nature Ecology and Evolution*, pp. 599–610. doi: 10.1038/s41559-018-0490-x.

Weghorst, J. A. (2007) ‘High population density of black-handed spider monkeys (Ateles geoffroyi) in Costa Rican lowland wet forest’, *Primates*, 48(2), pp. 108–116. doi: 10.1007/s10329-006-0025-y.

Weston, N. *et al.* (2011) ‘Using canopy bridges to link habitat for arboreal mammals: Successful trials in the Wet Tropics of Queensland’, *Australian Mammalogy*, 33(1), pp. 93–105. doi: 10.1071/AM11003.

Whitworth, A. *et al.* (2019) ‘Spider monkeys rule the roost: Ateline sleeping sites influence rainforest heterogeneity’, *Animals*, 9(12). doi: 10.3390/ani9121052.

Wich, S. A. and Marshall, A. J. (2016) ‘An introduction to primate conservation’, in Wich, S. A. and Marshall, A. J. (eds) *An Introduction to Primate Conservation*. Oxford University Press, pp. 1–12. doi: 10.1093/ACPROF:OSO/9780198703389.003.0001.

Willacy, R. J., Mahony, M. and Newell, D. A. (2015) ‘If a frog calls in the forest: Bioacoustic monitoring reveals the breeding phenology of the endangered Richmond Range mountain frog (Philoria richmondensis)’, *Austral Ecology*. Blackwell Publishing, 40(6), pp. 625–633. doi: 10.1111/aec.12228.

Williams, E. M., O’Donnell, C. F. J. and Armstrong, D. P. (2018) ‘Cost-benefit analysis of acoustic recorders as a solution to sampling challenges experienced monitoring cryptic species’, *Ecology and Evolution*. John Wiley and Sons Ltd, 8(13), pp. 6839–6848. doi: 10.1002/ece3.4199.

Wong, M. K. *et al.* (2016) ‘Comparison of soil macro-invertebrate communities in Malaysian oil palm plantations with secondary forest from the viewpoint of litter decomposition’, *Forest Ecology and Management*. Elsevier B.V., 381, pp. 63–73. doi: 10.1016/j.foreco.2016.09.011.

Wood, M. A. *et al.* (2017) ‘Comparison of land use change in payments for environmental services and National Biological Corridor Programs’, *Land Use Policy*. Elsevier Ltd, 63, pp. 440–449. doi: 10.1016/j.landusepol.2017.02.005.

Wood, S. N. (2017) *Generalized additive models: An introduction with R, second edition*. 2nd edn, *Generalized Additive Models: An Introduction with R, Second Edition*. 2nd edn. Chapman and Hall/CRC. doi: 10.1201/9781315370279.

Wrege, P. H. *et al.* (2017) ‘Acoustic monitoring for conservation in tropical forests: examples from forest elephants’, *Methods in Ecology and Evolution*. Edited by J. Matthiopoulos. Wiley/Blackwell (10.1111), 8(10), pp. 1292–1301. doi: 10.1111/2041-210X.12730.

Yue, S. *et al.* (2015) ‘Oil palm plantations fail to support mammal diversity’, *Ecological Applications*, 25(8), pp. 2285–2292. doi: 10.1890/14-1928.1.

Zaldívar, M. E. *et al.* (2004) ‘Distribution, ecology, life history, genetic variation, and risk of extinction of nonhuman primates from Costa Rica’, *Revista de biología tropical*, 52(3), p. 679. Available at: http://file//localhost(null)%5Cnpapers3://publication/uuid/43533379-7B70-4BD3-AAF9-F280C6C87BCA.

Zambrano, A. M. A., Broadbent, E. N. and Durham, W. H. (2010) ‘Social and environmental effects of ecotourism in the Osa Peninsula of Costa Rica: The Lapa Rios case’, *Journal of Ecotourism*, 9(1), pp. 62–83. doi: 10.1080/14724040902953076.

Zemanova, M. A. (2020) ‘Towards more compassionate wildlife research through the 3Rs principles: Moving from invasive to non-invasive methods’, *Wildlife Biology*. Nordic Council for Wildlife

Research, 2020(1). doi: 10.2981/wlb.00607.

Zhou, T. *et al.* (2020) ‘Quantifying the effects of road width on roadside vegetation and soil conditions in forests’, *Landscape Ecology*. Springer, 35(1), pp. 69–81. doi: 10.1007/s10980-019-00930-8.

Zilli, D. *et al.* (2014) ‘A Hidden Markov Model-Based Acoustic Cicada Detector for Crowdsourced Smartphone Biodiversity Monitoring’, *Journal of Artificial Intelligence Research*, 51, pp. 805–827.

Znidersic, E. *et al.* (2021) ‘Eastern Black Rail detection using semi-automated analysis of long-duration acoustic recordings’, *Avian Conservation and Ecology, Published online: Mar 19, 2021 | doi:10.5751/ACE-01773-160109*. The Resilience Alliance, 16(1). doi: 10.5751/ACE-01773-160109.

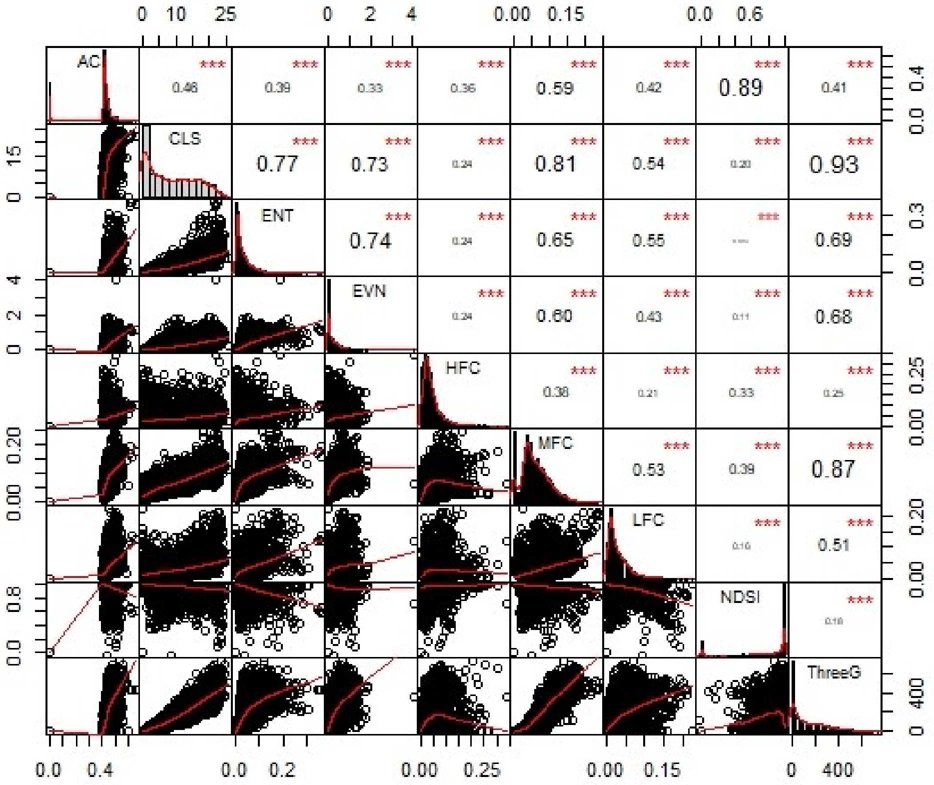
Zuur, A. F. *et al.* (2009a) ‘Required Pre-knowledge : A Linear Regression’, *Mixed Effects Models and Extensions in Ecology with R*, 1(January 2016), pp. 531–561. doi: 10.1007/978-0-387-87458-6.

Zuur, A. F. *et al.* (2009b) ‘Required Pre-knowledge : A Linear Regression’, *Mixed Effects Models and Extensions in Ecology with R*, 1, pp. 531–561. doi: 10.1007/978-0-387-87458-6.

Supplementary Information One: Chapter Two

1.1. Detailed Explanation of Principal Component Analysis

Results indicate that biotic indices are generally correlated, with an R^2 value of between 0.4 and 1 (Supplementary Figure.1.1), confirming that Principal Component Analysis (PCA) is suitable for reducing the dimensionality of the nine acoustic indices into PC axis. Eigenvalues indicate that we should retain PC1, and that PC2 may also contain some interesting information. PC1 alone accounts for more than 56% of the variation in the data and cumulative variance across PC1 and PC2 is almost 70%, therefore we are unlikely to lose important information by discarding the other PCs (Supplementary Table.1.1).



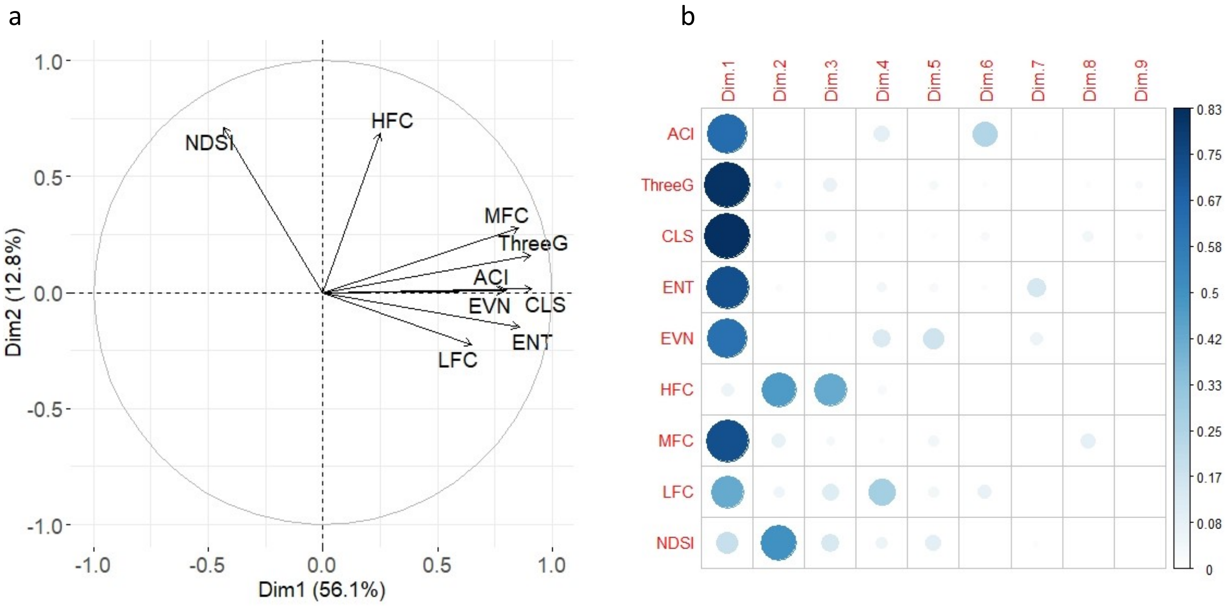
Supplementary Figure 1.1. Correlation Plot. Correlation plot showing the correlation between acoustic indices. Correlation values indicate the level of correlation between each of the indices.

Supplementary Table 1.1. Eigenvalues and Explained Variance. Eigenvalues, variance explained and cumulative variance for each PC. PC's to be retained are highlighted in grey. PC1 and PC2 both have eigenvalues over 1 and together account for 69% of variance.

Principal Component	**eigenvalue**	**Variance (%)**	**Cumulative Variance (%)**
Dim.1	5.049277	56.10307	56.10307
Dim .2	1.152307	12.80341	68.90649
Dim .3	0.84507	9.38967	78.29616
Dim .4	0.674869	7.49854	85.7947
Dim .5	0.447408	4.971205	90.7659
Dim .6	0.38383	4.264777	95.03068
Dim .7	0.239444	2.660488	97.69117
Dim .8	0.161413	1.793483	99.48465
Dim .9	0.046381	0.51535	100

The variable correlation plot (Supplementary Figure. 1.2.a) shows the relationship between the indices and their relationship to PC1 and PC2. It confirms that most biotic indices are correlated, with the exception of HFC index that is negatively correlated to the biotic indices and correlated to the NDSI index, which represents anthropogenic sound. From inspection of the LDFC spectrograms we conclude that across our landscape, HFC index is dominated by insect sounds, mainly cicadas, and anthropogenic sounds, which is likely why we see little correlation to other biotic indices and more correlation to the NDSI index (Supplementary Figure. 1.7). The biotic indices are represented across PC1, with ThreeG, MFC, CLS and ENT indices showing a stronger effect and NDSI and HFC index are represented across PC2 (Supplementary Figure. 1.2.a & b). The separation of the biotic and anthropogenic indices across PC1 and PC2 shows that as anthropogenic sound increases, biotic sound decreases (Supplementary Figure. 1.2.a). Supplementary Figure 1.2.b highlights which indices are represented across all nine PCA axis and the contribution of each index, with larger and darker circles indicating increased strength. Here we see again that biotic indices are represented across PC1, the most important being ThreeG and CLS indices, and to a lesser extent LFC index (Supplementary Fig. 1.2.b). This is likely due to LFC containing less biotic sounds and more left-over geophony and anthrophony than other biotic indices. This is further highlighted in the loading values, where larger values represent a stronger influence along that PC axis (Supplementary Table 1.2).

From these results we can conclude that PC1 can be considered an index of biotic sound and PC2 an index of anthropogenic sound. Some precaution must be taken with the interpretation of PC2 since HFC does represent both anthropogenic and biotic sounds. Further investigation of other PC's would be of little benefit since they contain little variation, PC3 is mainly represented by HFC and PC4 represented by LFC, making it more beneficial to study the actual index itself (Supplementary Figure 1.2.b).



Supplementary Figure 1.2.a. Variable Correlation Plot. Variable correlation plot showing the relationship between the indices, closer vectors are more highly correlated and those on opposite quadrants are negatively correlated. The x-axis represents PC1 and y-axis PC2, with % of variance explained. **b. Variable Correlation Plot All Axis.** Correlation plot showing the contribution of each index to a PC, larger darker circles represent a stronger contribution.

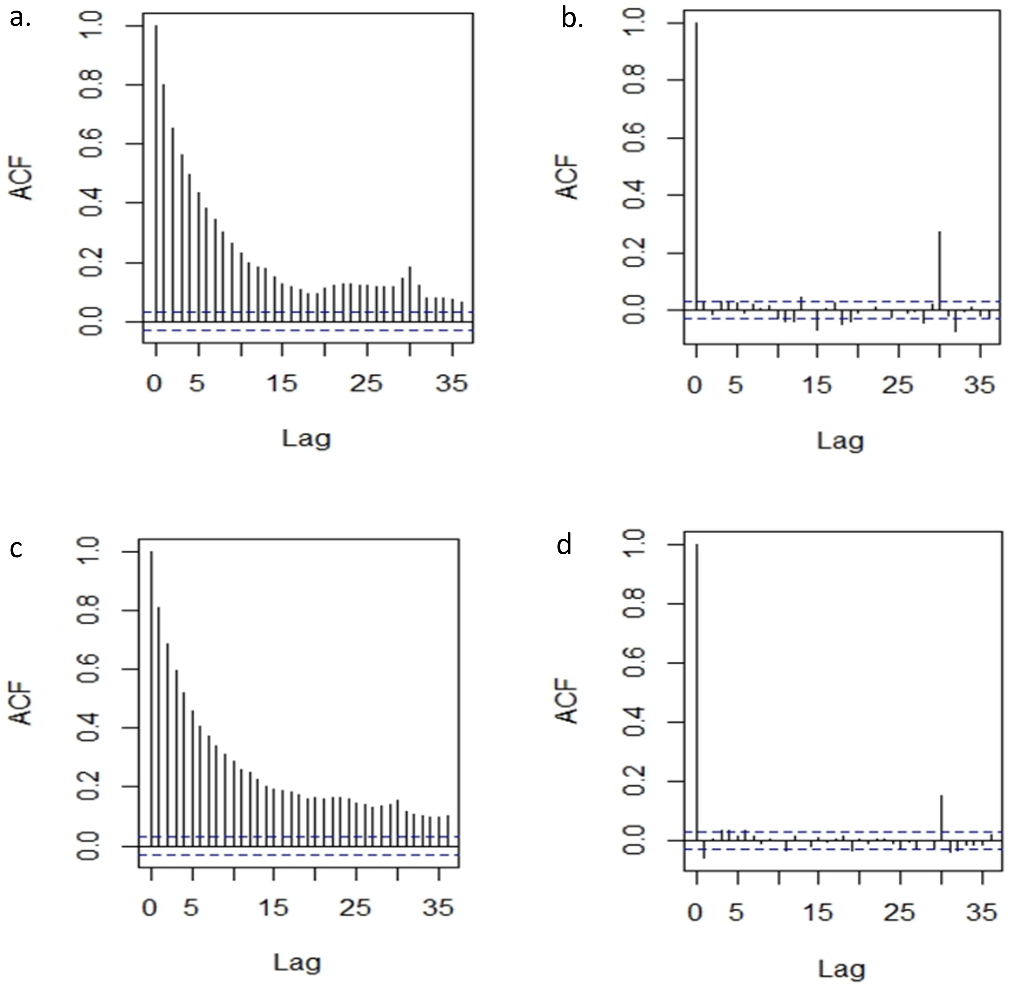
Supplementary Table 1.2. Loading Values. Loading values indicating the strength of contribution of each index to the PC's. Higher values show a stronger contribution. Indices that represent PC1 and PC2 are highlighted.

Index	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
ACI	0.355791	0.009918	-0.07503	0.37573	-0.01756	0.797949	0.185951	0.21514	-0.09283
ThreeG	0.40249	0.14967	0.294838	0.02026	-0.2746	-0.17039	0.087723	0.249754	0.744143
CLS	0.406131	0.01404	0.235143	-0.13529	-0.16079	-0.28448	-0.11641	0.529525	-0.60045
ENT	0.380919	-0.13802	-0.07901	-0.25263	0.260905	0.189232	-0.7871	-0.1488	0.142249
EVN	0.351479	0.006377	0.08028	-0.43963	0.618439	-0.01702	0.526435	-0.12956	-0.00548
HFC	0.111292	0.639137	-0.70809	-0.22195	-0.12692	-0.05107	0.012169	0.097855	0.005046
MFC	0.380102	0.257638	0.203652	0.155853	-0.32878	-0.07035	0.040619	-0.74399	-0.23486
LFC	0.289532	-0.20855	-0.37049	0.647123	0.325746	-0.45786	0.009115	0.000666	0.028588
NDSI	-0.19272	0.663209	0.399167	0.301166	0.466453	0.00465	-0.21361	0.094414	-0.02882

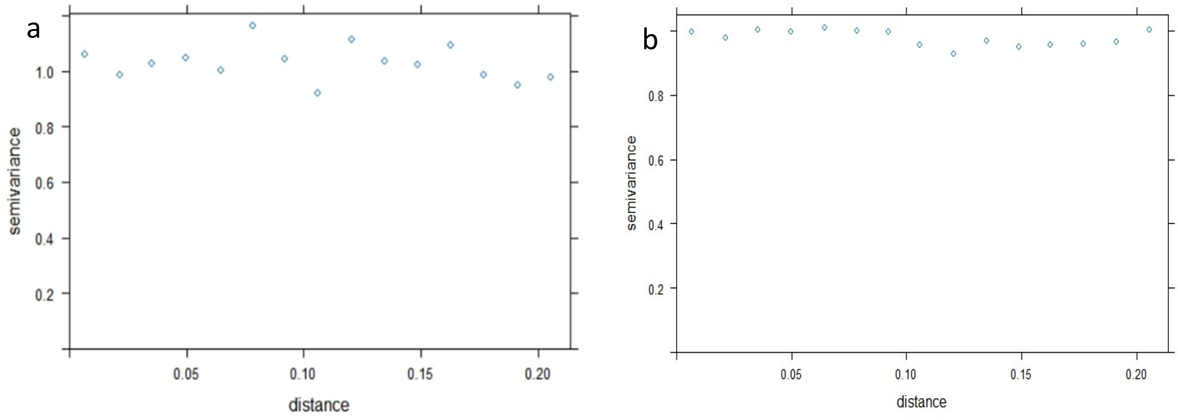
1.2. GAMM’s and LMM’s

Supplementary Table 1.3. Model Selection for GAMM’s. Model selection for all GAMM’s showing model df, AIC, LogLik and R-sq values for PC1 and PC2 separately. The best models are highlighted in grey and contain month as a random effect and a corCAR correlation structure.

Model	df	AIC (PC1)	AIC (PC2)	LogLik (PC1)	LogLik (PC2)	R-sq.(adj) PC1	R-sq.(adj) PC2
Basic Gam_k9	16	16240.85	12370.680	-8104.424	-6169.340	0.558	0.158
Gam_k12	16	16218.68	12371.093	-8093.341	-6169.546	0.561	0.158
Gam_k15	16	16166.26	12371.345	-8067.128	-6169.672	0.569	0.158
Gam_k20	16	16158.35	12371.400	-8063.173	-6169.700	0.571	0.158
Gamm_Month	17	15954.47	x	-7991.723	x	0.542	x
Gamm_ARMA	22	16230.68	12382.680	-8093.341	-6169.340	0.561	0.158
Gamm_AR1	17	16220.68	12372.680	-8093.341	-6169.340	0.561	0.158
Gamm_ corCAR	17	11673.31	7100.300	-5819.654	-3533.165	0.561	0.158
Gamm_Final	17	11643.42	7061.983	-5803.710	-3512.991	0.544	0.166



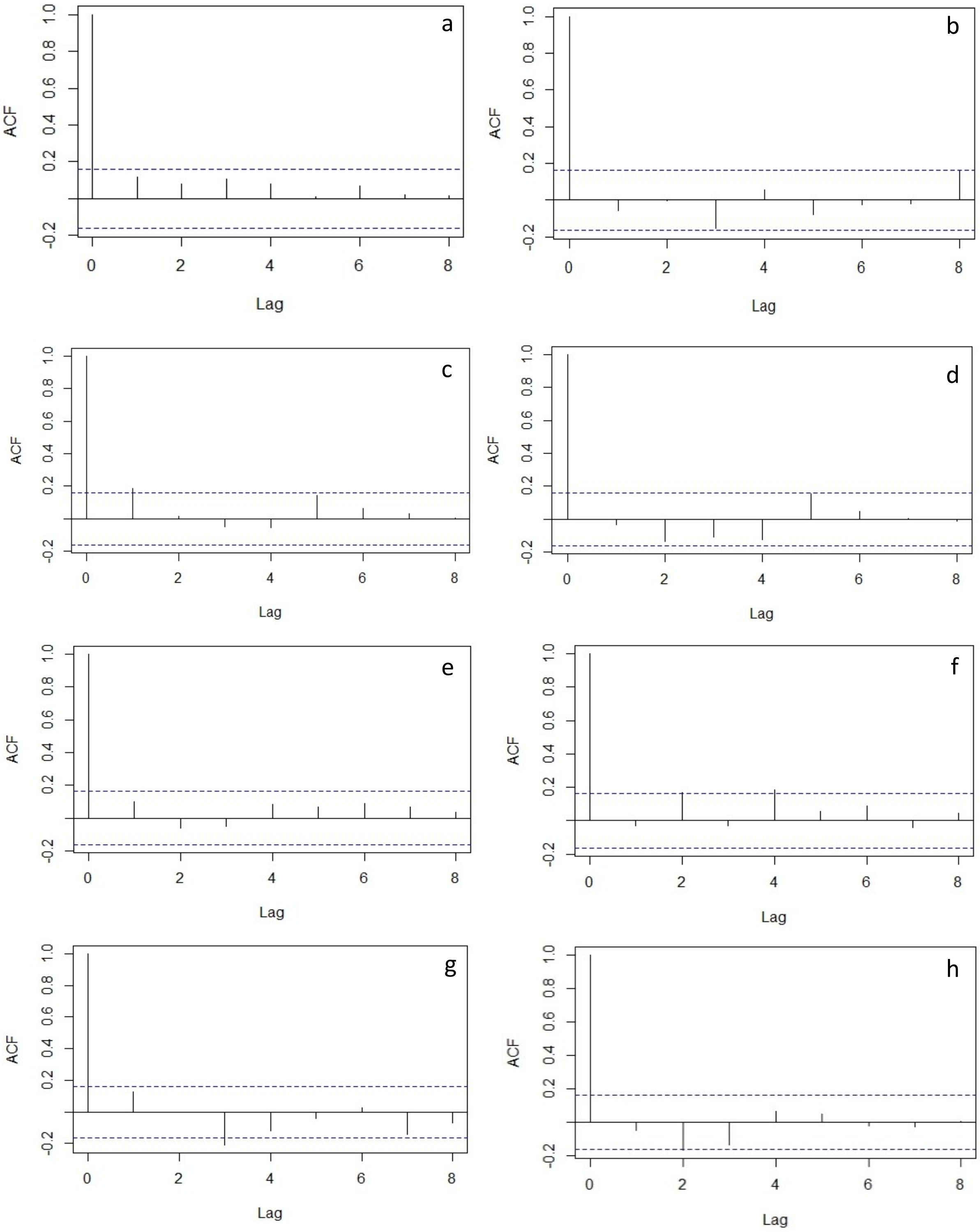
Supplementary Figure 1.3. Autocorrelation Plots for GAMM's. Autocorrelation plots for GAMM's showing the level of temporal autocorrelation between each 30-minute period in the diel cycle. Each lag represents one 30-minute period. Lag at zero is always 1, subsequent lags closer to zero suggest less autocorrelation. The blue dashed horizontal line represents the significance boundary, with all lags falling within that boundary showing insignificant levels of correlation. a. PC1 GAMM before corCAR correlation structure added b. PC1 GAMM after corCAR correlation structure added. c. PC2 GAMM before corCAR correlation structure added. d. PC2 GAMM after corCAR correlation structure added.



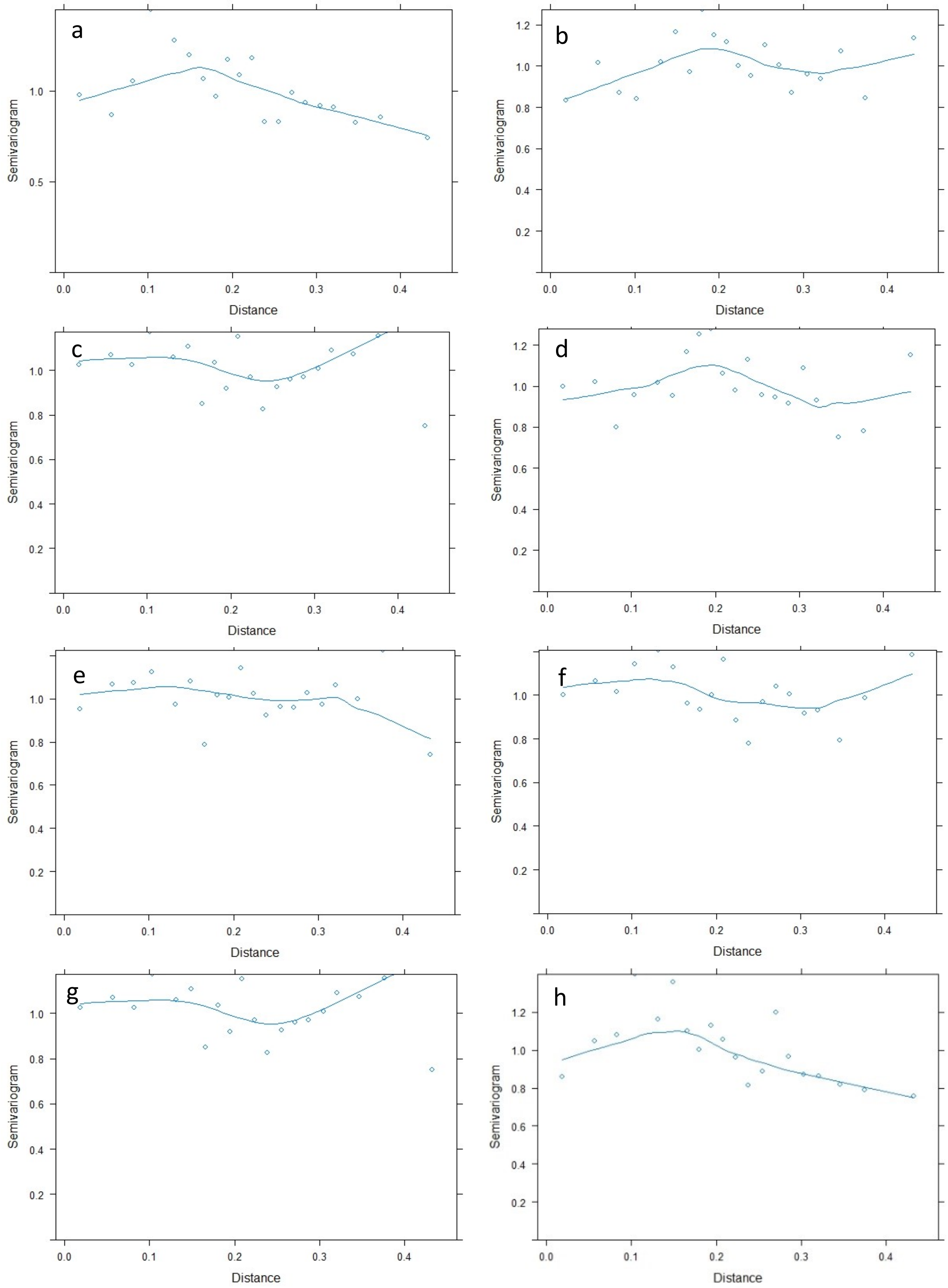
Supplementary Figure 1.4. Variogram Plots for GAMM's. Variogram plots showing the absence of spatial autocorrelation for the best GAMM model for a. PC1 and b. PC2. All points run along the horizontal at 1.0 indicating no significant spatial autocorrelation for either model.

Supplementary Table 1.4. Moran's I Statistic for GAMM's. Results for Moran's I Statistic showing insignificant spatial autocorrelation for the best GAMM model for PC1 and PC2. If no significant autocorrelation is present, then the observed and expected values should be similar and the *p*-value insignificant.

GAMM	**Observed correlation**	**Expected correlation**	***p* Value**
PC1	-0.0008051865	-0.000226808	0.486
PC2	-0.0008372966	-0.000232288	0.680



Supplementary Figure 1.5. **Autocorrelation Plots for LMM's.** Autocorrelation plots showing insignificant temporal autocorrelation between months for each LMM. Each lag represents one month. Lag at zero is always 1, subsequent lags closer to zero suggest less autocorrelation. The blue dashed horizontal line represents the significance boundary, with all lags falling within that boundary showing insignificant levels of correlation, a. PC1 at 06:30, b. PC2 at 06:30, c. PC1 at 14:00, d. PC2 at 14:00, e. PC1 at 16:30, f. PC2 at 16:30, g. PC1 at 00:00, h. PC2 at 00:00.



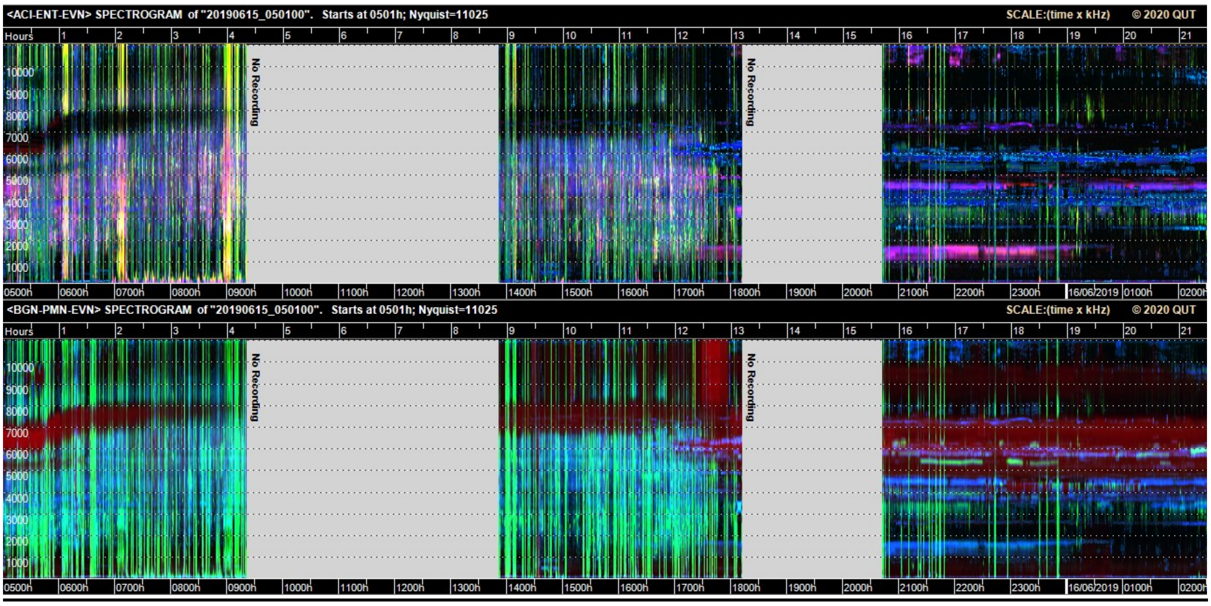
Supplementary Figure 1.6. Variogram Plots for LMM's. Variogram plots showing the absence of spatial autocorrelation for. a. PC1 at 00:00, b. PC2 at 00:00, c. PC1 at 06:30, d. PC2 at 06:30, e. PC1 at 14:00, f. PC2 at 14:00, g. PC1 at 16:30, h. PC2 at 16:30. All points run along the horizontal at 1.0 indicating no significant spatial autocorrelation.

Supplementary Table 1.5. Moran's I Statistic for LMM's. Results for Moran's I Statistic showing absence of significant spatial autocorrelation in LMM's for PC1 and PC2. If no significant autocorrelation is present, then the observed and expected values should be similar and the *p*-value insignificant.

Model	**Observed correlation**	**Expected correlation**	**p-value**
PC1 06:30	0.01	-0.006	0.23
PC2 06:30	-0.02	-0.006	0.34
PC1 14:00	-0.03	-0.006	0.06
PC2 14:00	0.01	-0.006	0.19
PC1 16:30	-0.01	-0.006	0.53
PC2 16:30	-0.02	-0.006	0.38
PC1 00:00	-0.006	-0.006	0.97
PC2 00:00	-0.03	-0.006	0.13

1.3. Results

1.3.1. Dimensionality Reduction



Supplementary Figure 1.7. **Long Duration False Colour Spectrogram (LDFC Spectrogram)**. Created using Analysis Programmes software, developed by Towsey *et al* (2018)**.** This process combines the spectral data from six indices, ACI, EVN, ENT, BGN, PMN and EVN to visually summarise the content of 24 hours of audio recording. In the example above we can see hues of blue and pink representing biotic sounds, overlaid by anthropogenic sounds in yellow and green covering the full frequency range of the spectrogram. HFC index only detects sounds above 8000kHz, we can see how this section is dominated by anthropogenic sounds, causing this index to be more closely related to NDSI index, the index of anthropogenic sound.

Supplementary Table 1.6. Model Results PC1. Edf, *F* values and *p* values for each smooth term for the best model PC1 'Gamm_Final'

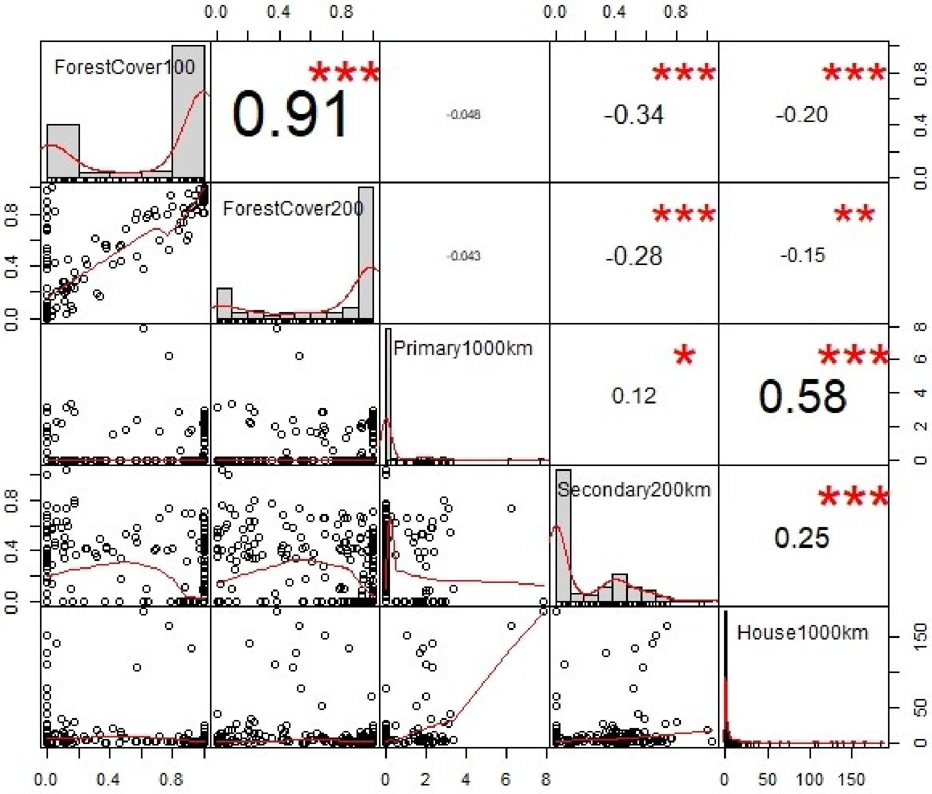
Model terms	**Edf**	***SE***	***F* value**	***p* value**
s(Time*Grassland)	9.616	0.21	47.181	<0.0001
s(Time*Old Growth)	10.379	0.2	20.929	<0.0001
s(Time*Palm)	4.294	0.21	5.443	<0.0001
s(Time*Secondary)	10.702	0.17	60.069	<0.0001
s(Time*Teak)	5.887	0.28	3.572	<0.0001

Supplementary Table 1.7. Model Results PC2. Edf, F values and P values for each smooth term in best model PC2- 'Gamm_Final'

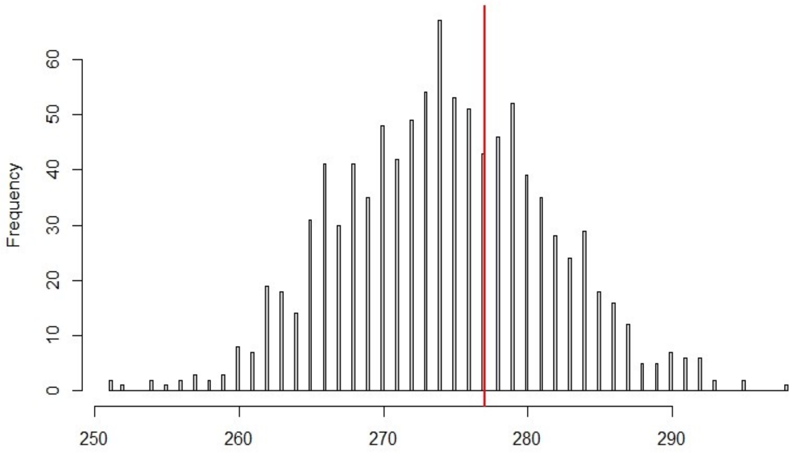
Model terms	**edf**	***F* value**	***P* value**
s(Time*Grassland)	7.430	12.436	<0.001
s(Time*Old Growth)	3.345	3.526	<0.05
s(Time*Palm)	4.836	8.265	<0.001
s(Time*Secondary)	6.844	3.036	<0.01
s(Time*Teak)	3.233	5.365	<0.01

Supplementary Information Two: Chapter Three

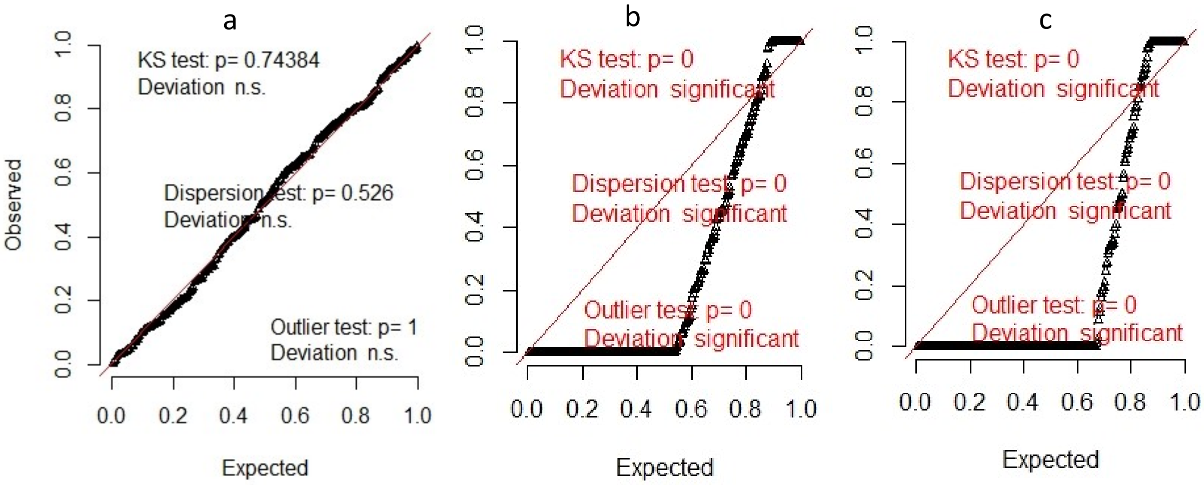
2.1. Methods



Supplementary Figure 2.1. Explanatory Variables Correlation Plot. Correlation plot for each of the explanatory variables. Correlation values indicate the level of correlation between each of the variables.



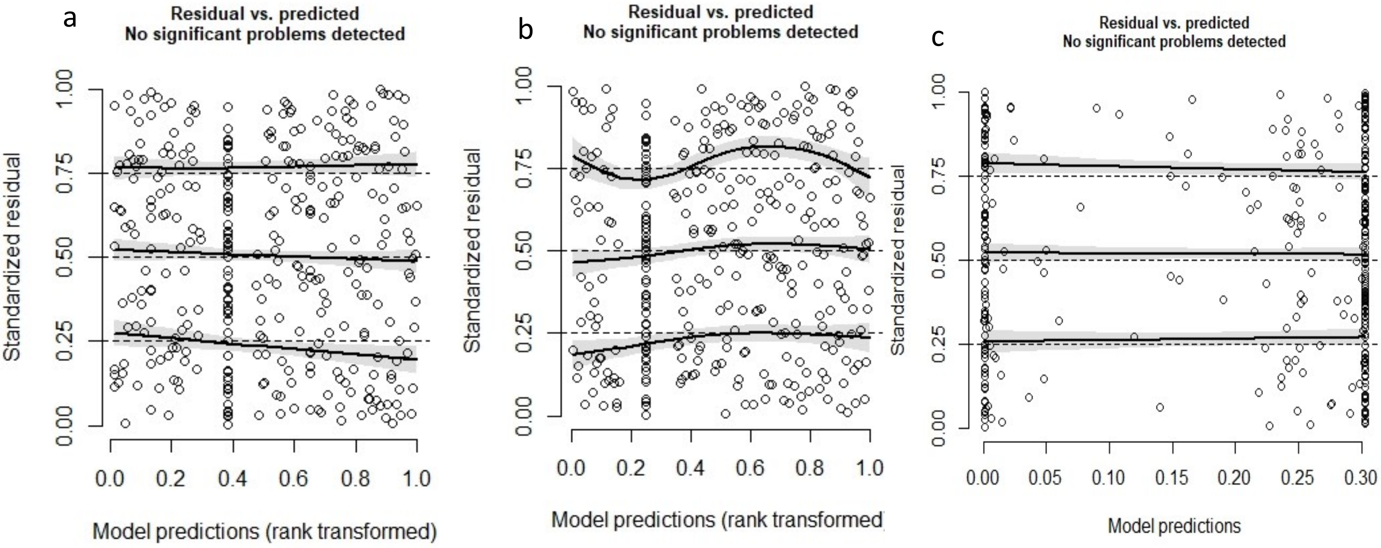
Supplementary Figure 2.2. Zero Inflation Plot. Plot showing no zero-inflation for negative binomial model with call rate as the response variable and forest cover, secondary road and buildings as the explanatory variables.



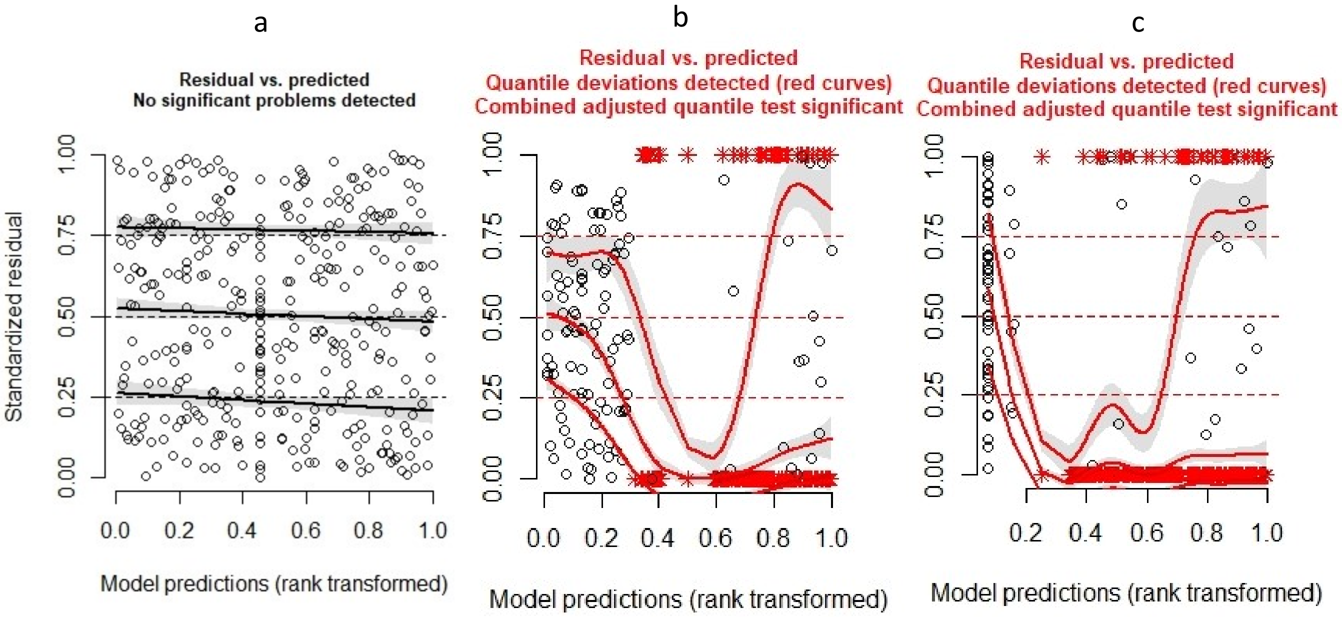
Supplementary Figure 2.3. Test for Overdispersion. a. Plot indicating insignificant overdispersion for the negative binomial model with call rate as the response variable and forest cover, secondary road and buildings as the explanatory variables. b. Plot indicating significant overdispersion for Poisson model with call rate as the response variable and land use as the explanatory variable and c. primary road as the explanatory variable

Supplementary Table 2.1. Model Fit for Poisson and Negative Binomial Model. Shows AIC and Log Likelihood results for Poisson and negative binomial models with call rate as the response variable and forest cover, secondary road and buildings as the explanatory variables. *** indicates whether this difference was significant.

Model	AIC Poisson	AIC Negative binomial	LogLik Poisson	LogLik Negative binomial
Forest Cover /Secondary Road/ Building	9330.04	920.28	-4661.0	-455.1***



Supplementary Figure 2.4. Residual Plots for Binomial Models. Plots indicating good model fit for binomial models with presence as the response variable and a. Land use b. Primary road and c. Forest cover, secondary road and buildings as the explanatory variables



Supplementary Figure 2.5. Residual Plots for Poisson and Negative Binomial Models. a. Plot indicating good model fit for negative binomial model with call rate as the response variable and forest cover, secondary road and buildings as the explanatory variables. b. Plot indicating poor model fit for Poisson model with call rate as the response variable and land use as the explanatory variable and c. primary road as the explanatory variable.

Supplementary Table 2.2 Spatial Autocorrelation Results: Occurrence. Results for Moran's I Statistic showing insignificant spatial autocorrelation for logistic regression. If no significant autocorrelation is present then the observed values should be close to zero and similar to the expected values and the p-value insignificant.

Model	**Observed correlation**	**Expected correlation**	**p-value**
Land Use	-0.006	-0.002	0.059
Primary Road	-0.006	-0.002	0.058
Forest Cover/Secondary Road/ Building	-0.005	-0.002	0.09

Supplementary Table 2.3 Spatial Autocorrelation Results: Call rate. Results for Moran's I Statistic showing insignificant spatial autocorrelation in Poisson and negative binomial models. If no significant autocorrelation is present then the observed values should be close to zero and similar to the expected values and the p-value insignificant.

Model	**Observed correlation**	**Expected correlation**	**p-value**
Land Use	-0.004	-0.002	0.26
Primary Road	-0.003	-0.002	0.83
Forest Cover/Secondary Road/ Building	-0.007	-0.002	0.07

Supplementary Table 2.4. Model Selection: Occurrence. Showing AIC and Log Likelihood results for logistic regression models without and with an auto covariate function added to account for spatial autocorrelation in the data. *** indicates whether this difference was significant.

Model	**AIC (without ac function)**	**AIC (with ac function)**	**LogLik (without ac function)**	**LogLik (with ac function)**
Habitat	293.75	292.63	-129.64	-140.88
Primary Road	311.36	307.67	-139.31	-150.84*
Forest Cover/Secondary Road/ Building	280.59	231.69	-136.30	-110.85 ***

Supplementary Table 2.5. Model Selection: Call rate. Showing AIC and Log Likelihood results for Poisson and negative binomial models without and with an auto covariate function added to account for spatial autocorrelation in the data. *** indicates whether this difference was significant.

Model	AIC (without ac function)	AIC (with ac function)	LogLik (without ac function)	LogLik (with ac function)
Habitat	9645.568	9055.147	-4816.8	4520.6 ***
Primary Road	10581.273	9949.455	-5288.6	-4971.7***
Forest Cover/Secondary Road/ Building	920.28	916.46	-455.14	452.23*

Supplementary Table 2.6. Scale of Effect. Scale of effect for Occurrence (Occ) and call rate (CF) for each explanatory variable: Forest cover, primary and secondary roads and buildings, measured using a buffer around each site at a scale of 50:5000 m radius for forest cover and 50:1000 all for other variables. X indicates non-convergence of the model

Scale (m)	Forest: Occ	Forest: CF	Primary Road: Occ	Primary Road: CF	Secondary Road: Occ	Secondary Road: CF	Buildings: Occ	Buildings: CF
50	0.66	0.96	x	0.225	0.073	0.237	0.002	0.021
100	0.69	0.96	x	0.225	0.082	0.272	0.000	0.379
200	0.77	0.97	x	0.543	0.091	0.305	0.002	0.025
300	0.71	0.96	x	0.651	0.083	0.191	0.010	0.235
400	0.63	0.95	0.185	0.720	0.072	0.182	0.049	0.368
500	0.66	0.94	0.244	0.799	0.051	0.158	0.027	0.400
750	0.49	0.92	0.483	0.910	0.064	0.274	0.078	0.731
1000	0.41	0.87	0.597	0.951	0.071	x	0.228	0.819
2000	0.33	0.821						
3000	0.17	0.713						
4000	0.19	0.55						
5000	0.16	0.25						

2.2. Results: Occupancy Analysis

Our full model with p (forest cover) psi (forest cover, secondary road and buildings) shows good fit (p=0.08, c-hat=1.53) but ranked fifth within the candidate models and had a QAICc of >2. The best model according to QAICc contained only forest cover as affecting occupancy and detection probability, the second-best model contained only forest cover as affecting occupancy and detection remaining constant p(.). The third best model contained forest cover and secondary road as affecting occupancy, and forest cover affecting detection probability and the fourth best model contained forest cover and secondary road as affecting occupancy and detection remaining constant p(.). As all four models had a QAICc of <2, they are all plausible (Supplementary Table 2.7).

When considering model averaged parameter estimates and summed Akaike weights (w_i) forest cover is the most important variable in explaining site occupancy (Supplementary Table 2.7). As secondary road density is included in our third-best model, it is likely that it is also affecting site occupancy to some extent (AICw=0.13, QAICc=1.8) (Supplementary Table 2.7). Model averaged coefficients from the top four models show a significant positive effect of forest cover on occupancy, suggesting occupancy increases with increasing forest cover (Supplementary Table 2.8). The effect of forest cover on detection probability was not significant (p=0.3). Secondary road density and area cover of building show a weaker, non-significant negative effect on occupancy, suggesting occupancy decreases with increasing density of secondary roads and buildings (Supplementary Table 2.8).

Supplementary Table 2.7. Model Selection: Occupancy. Model selection results for occupancy analysis. AICc, QAICc and AIC weights show the best models.

	AICc	**QAICc**	**AICw**
p(Forest cover) Psi(Forest Cover)	891.91	0	0.33
p(.) Psi(Forest_Cover)	893.14	1.22	0.18
p(Forest cover) Psi(Forest Cover, Secondary_Road)	893.72	1.80	0.13
p(.) Psi(Forest Cover, Secondary_Road)	893.98	2.07	0.12

Supplementary Table 2.8. Model Output: Occupancy. Estimates show the direction of the correlation with standard errors and z values and p values indicate the strength and significance of that variable in its effect on site occupancy.

	Estimate	**se**	**z value**	**P value**
psi(Forest Cover)	9.47	3.11	3.04	<0.01
psi(Secondary_Road)	-0.10	0.20	0.5	0.61
psi(Building)	<-0.001	<0.01	0.01	0.98
p(Forest Cover)	3.3	3.1	1.02	0.3

2.3. Results: Generalised Linear Models

Supplementary Table 2.9. Model Results for Land Use: Occurrence. Logit scale estimates and transformed probability of occurrence estimates for each land use with standard errors (*se*)

Habitat	**Estimate (logit scale)**	**se**	**Probability of occurrence**	***se***
Old Growth	-0.83	0.28	0.30	0.05
Secondary	-0.23	0.32	0.257	0.03
Mangrove	-3.21	1.47	0.01	0.02
Teak	-2.0	1.56	0.05	0.8
Palm	-3.02	1.48	0.01	0.02
Grassland	-3.61	1.46	0.01	0.01

Supplementary Table 2.10. Model Results for Land Use: Call rate. Call rate, logit estimate and standard errors (*se*) in different land use types

Habitat	**Call rate**	**Estimate (logit scale)**	***se***
Old Growth	10.8	2.23	0.04
Secondary	11.1	0.02	0.04
Mangrove	0.01	-6.40	1.41
Teak	0.06	-5.15	1.41
Palm	0.02	-6.20	1.41
Grassland	0.01	-6.81	1.41

Supplementary Table 2.11. Model Results for Continuous Variables: Occurrence. Logit estimates showing increase or decrease in probability of occurrence with increasing values of each variable. Se, z values and p values for model covariates are shown.

Variable	**Estimate (logit scale)**	**se**	**Z value**	**P value**
Forest Cover	5.21	1.96	2.60	<0.01
Secondary Road	-0.69	0.92	-0.74	0.45
Buildings	-0.005	0.02	-0.24	0.81
Primary Road	-2.03	1.02	-1.98	<0.05

Supplementary Table 2.12. Model Results for Continuous Variables: Call rate. Logit estimates showing increase or decrease in call rate with increasing values of each variable. Se, z values and p values for model covariates are also shown.

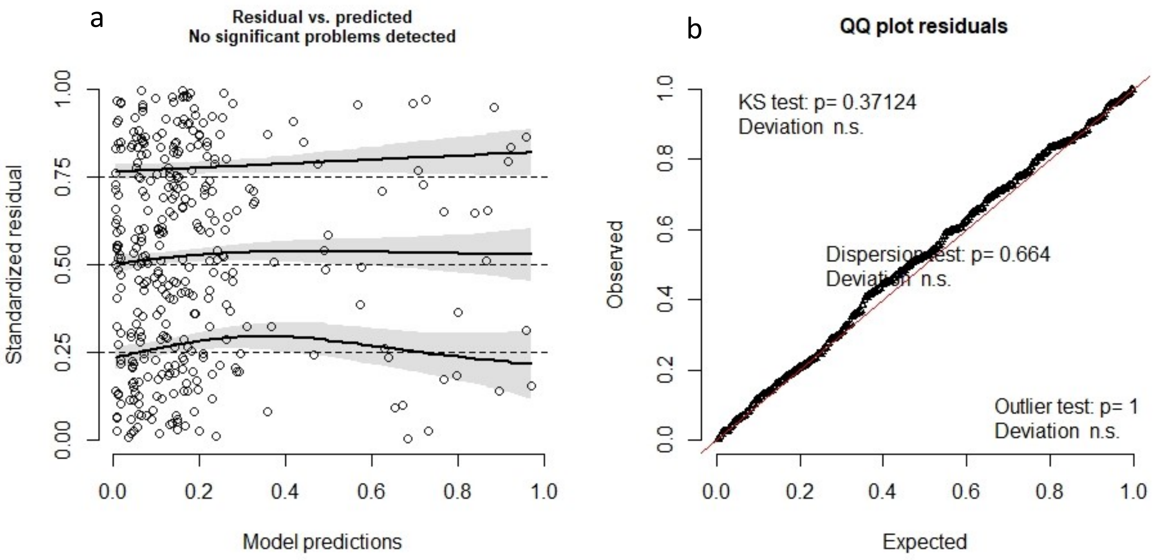
Variable	**Estimate (logit scale)**	**se**	**Z value**	**P value**
Forest Cover	3.73	0.98	3.8	<0.001
Secondary Road	-0.09	0.4	-0.23	0.81
Houses	-1.47	2.26	-0.65	0.51
Primary Road	-44.27	18.86	-2.34	<0.05

Supplementary Table 2.13. Variance Partitioning Results: Call rate. Variance partitioning analysis for call rate variables showing individual and shared variance and % individual variance for each explanatory variable. Larger values indicate more variance attributed to that variable.

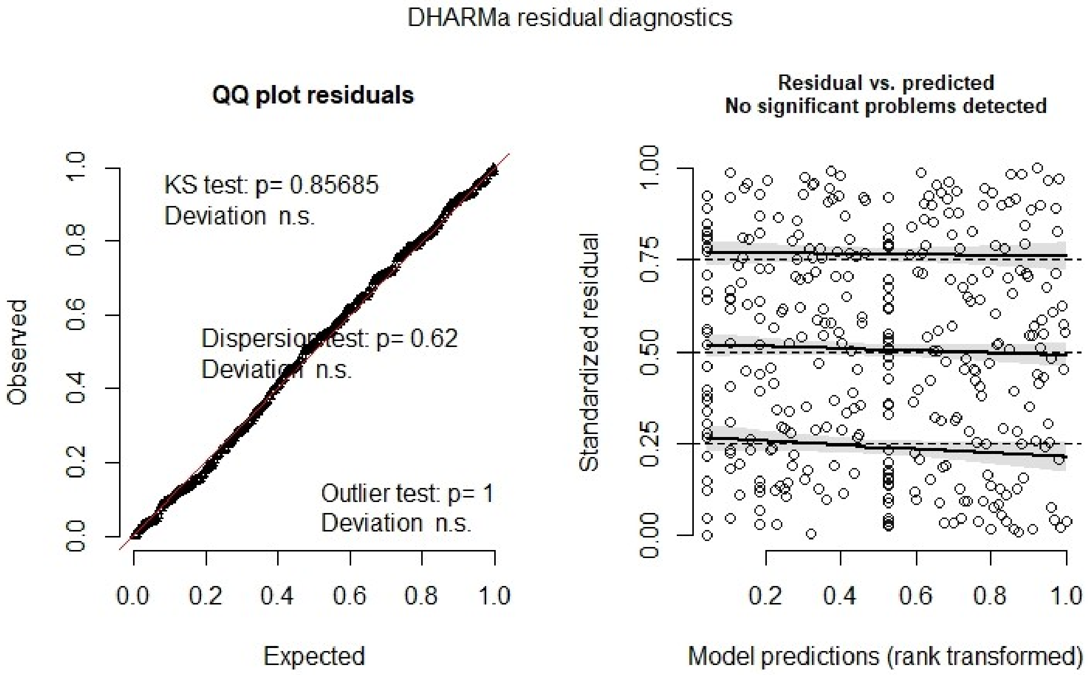
Variable	**Individual Variance**	**Shared variance**	**Individual variance (%)**
Land Use	-5.10	-4.69	27
Forest Cover	-7.02	-5.22	37
Primary Road Density	-5.6	1.2	30
Secondary Road Density	-0.91	-1.53	4.8
Area of Buildings	-0.22	-0.46	1.2

Supplementary Information Three: Chapter Four

3.1. Methods



Supplementary Figure 3.1. Diagnostic Plots for Distance to Corcovado. Plots indicating good model fit and insignificant overdispersion for binomial model with occurrence as the response variable and distance to Corcovado National Park as the explanatory variable.



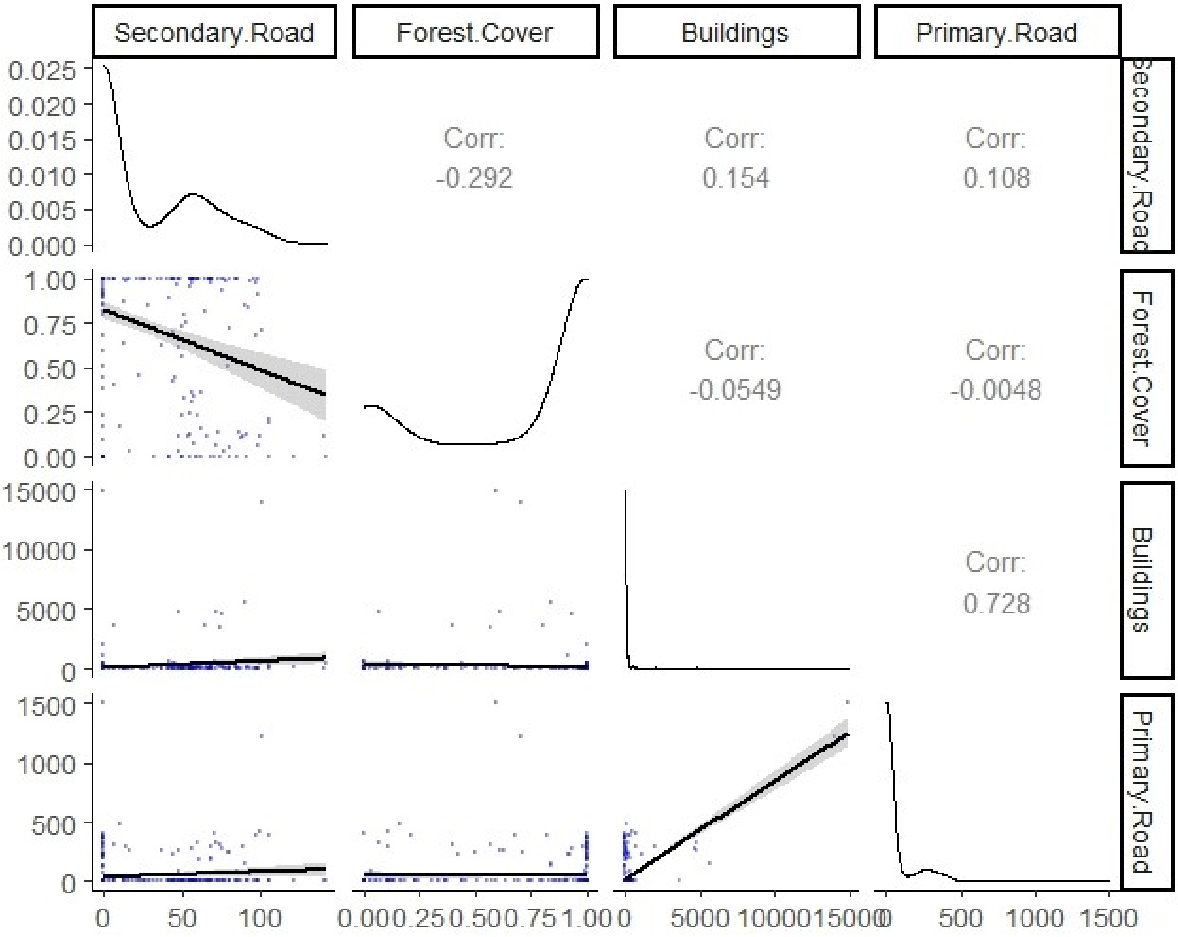
Supplementary Figure 3.2. Diagnostic Plots for Protection Level. Diagnostic plots for GLM with a binomial distribution fitted in brglm2 package with presence as the response variable and protection as the explanatory variables. Plots show good model fit and insignificant overdispersion.

Supplementary Table 3.1. Spatial Autocorrelation Results. Results for Moran's I Statistic showing insignificant spatial autocorrelation for logistic regression models. If no significant autocorrelation is present then the observed values should be close to zero and similar to expected values and the p-value insignificant.

Model	**Observed correlation**	**Expected correlation**	**p-value**
Protection	-0.007	-0.002	0.051
Distance to Corcovado	-0.004	-0.002	0.18

Supplementary Table 3.2. Model Selection. Showing AIC and Log Likelihood results for logistic regression models without and with an auto covariate function added to account for spatial autocorrelation in the data. *** indicates whether this difference was significant.

Model	**AIC (without ac function)**	**AIC (with ac function)**	**LogLik (without ac function)**	**LogLik (with ac function)**
Protection	219.32	221.33	-103.66	-103.67
Distance to Corcovado	304.29	57.47	-150.15	-125.74***



Supplementary Figure 3.3. Explanatory Variable Correlation Plot. Correlation values indicate the level of correlation between each of the explanatory variables.

3.2. Results

Supplementary Table 3.3. Model Results for Distance to Corcovado. Logit estimates showing increase or decrease in probability of occurrence with increasing values of each variable. Se, z values and p values for model covariates are also shown.

Variable	**Estimate (logit scale)**	**se**	**Z value**	**P value**
Distance to Corcovado	-0.08	0.02	-3.04	<0.01

Supplementary Table 3.4. Model Results for Protection Status. Logit scale estimates and transformed probability of occurrence estimates for each protection level with standard errors (*se*)

Protection	**Estimate (logit scale)**	**se**	**Probability of occurrence**	***se***
Corcovado NP	0.52	0.37	0.63	0.08
GD Forest Reserve	-2.15	0.43	0.16	0.03
Unprotected	-3.89	0.66	0.03	0.03
Terreba-Sierpe NP	-4.49	1.5	0.01	0.02
Piedras Blancas NP	-4.60	1.49	0.01	0.02
Wildlife Refuge	0.71	0.5	0.78	0.08

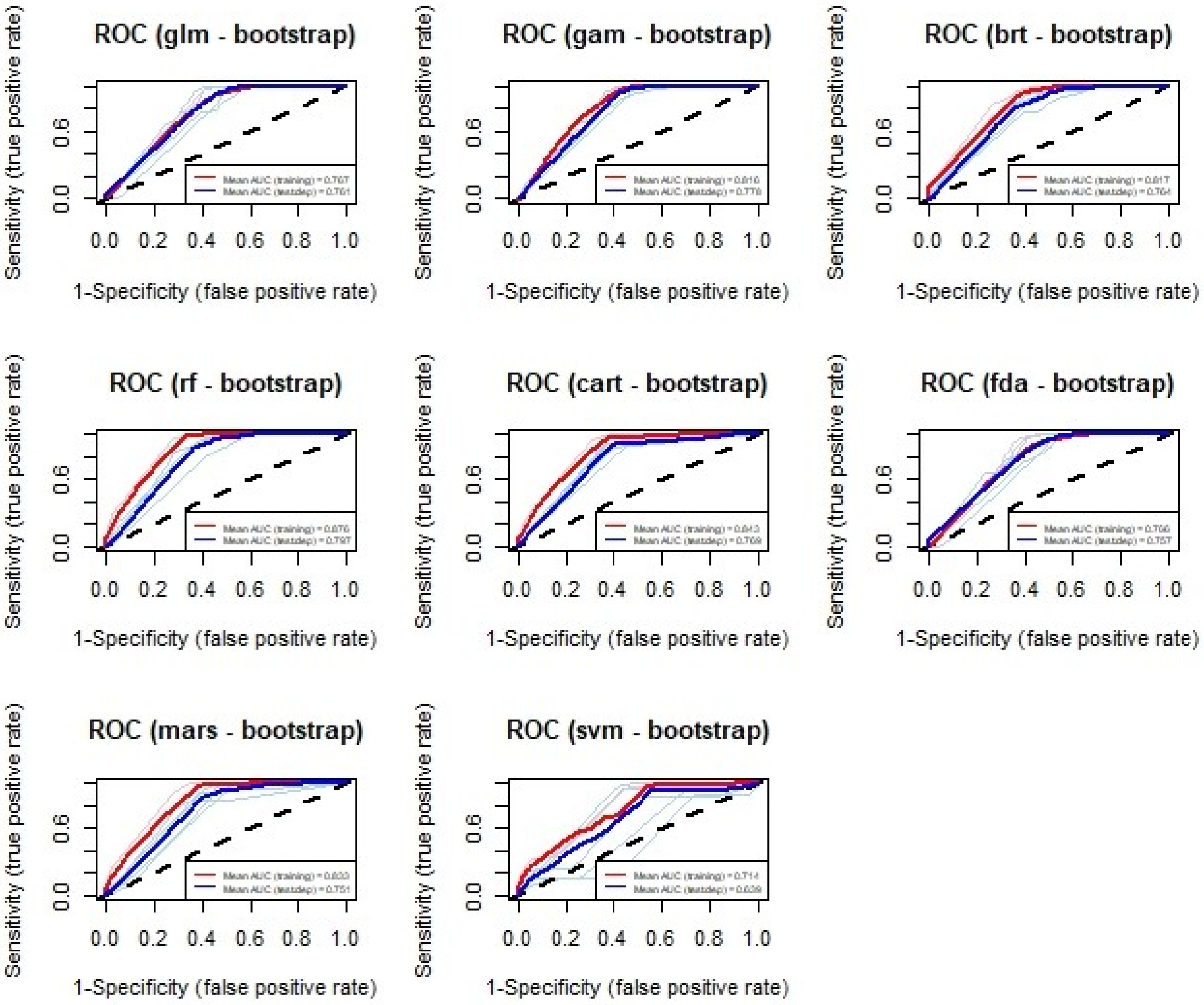
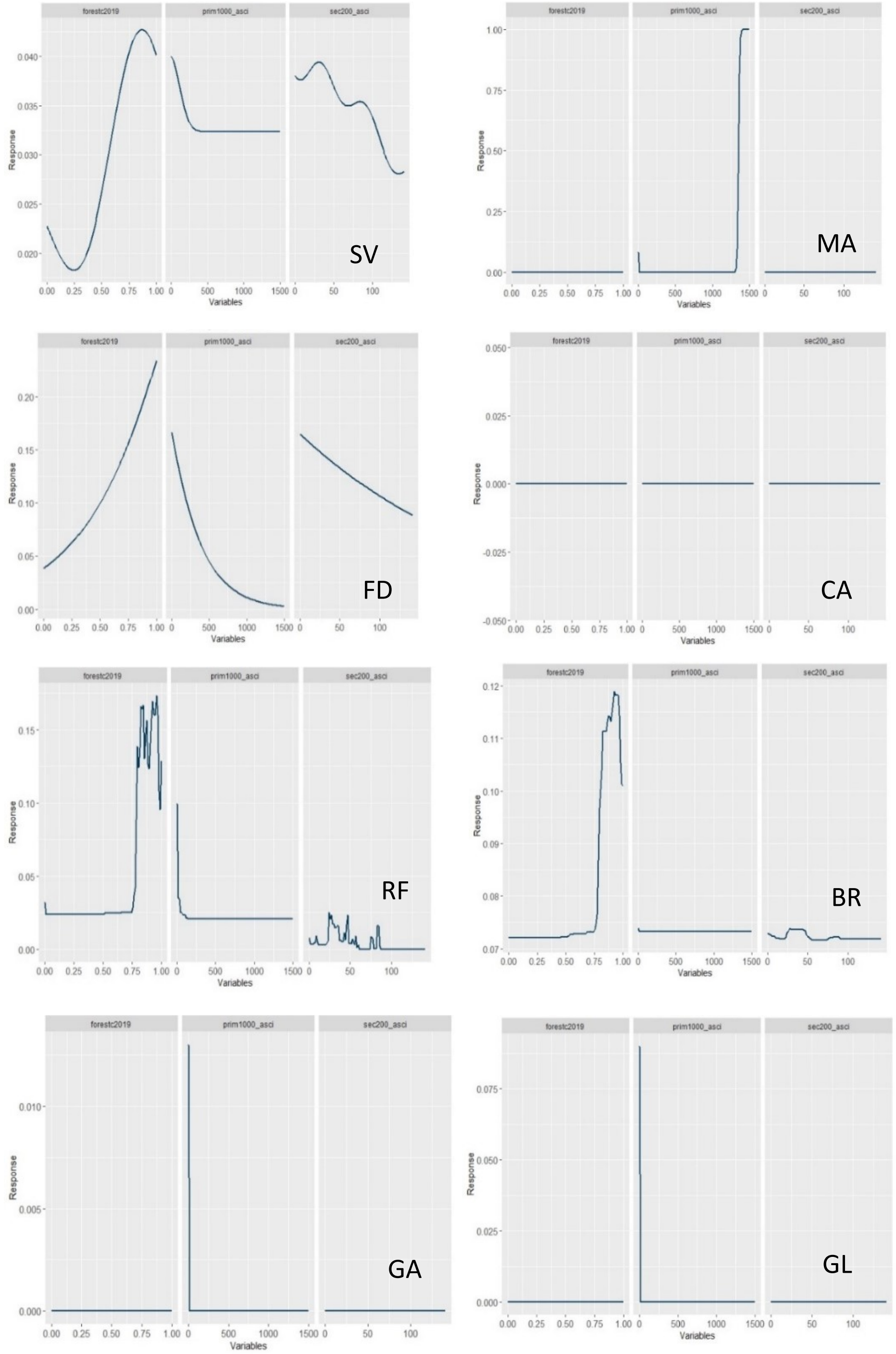


Figure 3.4. Receiver Operating Characteristic (ROC) Curve for Habitat Suitability Modelling Methods. ROC Curves for all eight modelling methods: Generalized linear models (GLM), Generalized additive models (GAM), Boosted regression trees (BRT), Multivariate adaptive regression spline (MARS), Classification and regression trees (CART), Multivariate adaptive regression spline (MARS), Random forests (RF), Support vector machine (SVM), and Flexible Discriminant Analysis (FDA). The ROC curve shows the trade-off between sensitivity (or TPR) and specificity (1 – FPR). Methods that show curves closer to the top-left corner indicate a better performance. The closer the curve comes to the 45-degree diagonal of the ROC space, the less accurate the method.



Supplementary Figure 3.5. Fitted Response Curves for Habitat Suitability Models. Plots show the fitted response curves for all eight modelling methods for each explanatory variable (forest cover, primary and secondary road): Generalized linear models (GLM), Generalized additive models (GAM), Boosted regression trees (BRT), Multivariate adaptive regression spline (MARS), Classification and regression trees (CART), Multivariate adaptive regression spline (MARS), Random forests (RF), Support vector machine (SVM), and Flexible Discriminant Analysis (FDA).

Supplementary Table 3.5. Ensemble Model Performance Metrics. AUC, TSS and deviance explained for final habitat suitability model using a combination of RF and RDA methods.

Model	**AUC**	**TSS**
RF	0.81	0.58
FDA	0.78	0.55