Using remote surveying technology and acoustic analysis tools to infer the impact of infrastructure expansion on bird biodiversity in the tropical rainforests of Brunei, Borneo.

EBERHARDT, LUCY,MARTHE,JOYCE

How to cite:

EBERHARDT, LUCY,MARTHE,JOYCE (2023) *Using remote surveying technology and acoustic analysis tools to infer the impact of infrastructure expansion on bird biodiversity in the tropical rainforests of Brunei, Borneo.*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/15326/

Using remote surveying technology and acoustic analysis tools to infer the impact of infrastructure expansion on bird biodiversity in the tropical rainforests of Brunei, Borneo.

By Lucy Marthe Joyce Eberhardt

General Abstract

Tropical rainforests are the world's most biodiverse biome but are increasingly threatened by anthropogenic stressors, such as urbanisation. Considering the current biodiversity crisis, gaining a deeper ecological understanding of the effects of such stressors on ecosystems, and the wildlife they harbour, is crucial. Due to its recent linkage to the more developed districts of the country, Temburong, a largely forested region of Brunei, presents an opportunity to collect baseline data to explore how infrastructure expansion impacts biodiversity. Using Autonomous Recording Units (ARUs) and camera traps, we deployed a wildlife monitoring network across current infrastructure expansion gradients in Temburong. Firstly, we examined spatial-temporal changes in soundscapes using the Acoustic Complexity Index and found unexpected results, with higher acoustic diversity at night and in less remote areas. Then, using Kaleidoscope Pro, we constructed and evaluated the performance of six Helmeted Hornbill (*Rhinoplax vigil*) recognisers – trainable algorithms capable of automatic detection of target calls – with each recogniser trained on different types of audio data. We found that a recogniser trained using a sample of calls of varying quality collected from within the study region performed best. Next, we applied species-specific recognisers and explored the impact of infrastructure expansion on the Helmeted Hornbill and the Great Argus (*Argusianus argus*), a ground-dwelling pheasant. We found that both species occurred more frequently in areas further from road and buildings, and with higher vegetation biomass. Finally, we compared the detection rates of Great Argus between ARUs and camera traps and found that, despite ARUs having a higher detection rate, using both surveying methods simultaneously provided a more holistic understanding of the species' ecology. This project showcases the use of two remote surveying technologies, coupled with acoustic analysis tools, to infer the impact of infrastructure expansion on birds in tropical rainforest ecosystems and highlights their contribution to eco-acoustics.

Using remote surveying technology and acoustic analysis tools to infer the impact of infrastructure expansion on bird biodiversity in the tropical rainforests of Brunei, Borneo.

Lucy Marthe Joyce Eberhardt

Thesis for MSc by Research

Supervised by Prof. Stephen Willis

Department of Biological and Biomedical Sciences

Durham University

2023

Table of contents

Acknowledgements

Firstly, I would like to thank my supervisor Steve Willis for the constant guidance he provided throughout this project. I would also like to thank the Conservation Ecology Group (CEG) at Durham University for all their support over the last year and creating a dynamic working environment. A special thank you goes to Christine and Beth G. for helping with R.

Additionally, I would like to show my gratitude to the Newcastle University and Universiti of Brunei Darussalam teams, particularly Ferry, Tasha, Beth H., Bekah, Jerry, and Sawai for their help undertaking fieldwork. Thanks also go to Shalizan and Sumi for welcoming us during our stay in Brunei.

Lastly, I want to thank my Mum and Dad, family, and friends for their unwavering support throughout my thesis. A special thank you goes to Ali as well as Adam, Andrew, and Ace for the moral support and dog walk breaks during the last stages of the project.

Chapter 1

General Introduction

1.1 Context

Unlike much of science, the study of biodiversity has a time limit (Wilson 1992). More than 30 years after E.O. Wilson made this statement, it is now truer than ever. The world is currently experiencing mass biodiversity loss, which some have labelled the *Anthropocene* or *sixth mass extinction* event (Ceballos *et al.*, 2010; Ceballos *et al*., 2017; Cook *et* al., 2023). This anthropogenic erosion of biodiversity is occurring primarily due to unsustainable use of natural resources resulting in – but not limited to – habitat loss and climate change. One of the leading causes behind these issues is the large and rapidly growing human population, which surpassed 8 billion individuals in November 2022 (United Nations, 2022). Furthermore, approximately half of the global population lives in urban areas (Brenner & Schmid, 2014). The impact of such unprecedented urbanisation and infrastructure expansion on the environment remains uncertain. Urbanisation has been proposed as a major driver of biodiversity declines. Aside from direct land use change leading to habitat loss, recent research has suggested, for example, that some species are less successful in urbanised environments are they do not possess the necessary adaptations to find resources and avoid risks (Sol *et al*., 2014). The issue of biodiversity loss through urbanisation and infrastructure expansion is particularly concerning in the tropics as this zone simultaneously harbours the largest and fastest growing human population (Harding *et al.*, 2020) and the highest species richness (Pillay *et al*., 2022; Wilson & Peter, 1988) worldwide. There is therefore an urgent need to protect biodiversity against the threat of urbanisation and infrastructure expansion – and deleterious anthropogenic impacts as a whole – not only for moral and fundamental scientific purposes, but also to maintain global ecosystem functioning. Hence, it is critical to gain further knowledge about the potential impacts of infrastructure expansion on natural systems. To do this requires new and better methods of monitoring wildlife. This thesis will focus on testing relatively novel monitoring methods in a tropical rainforest habitat and exploring bird biodiversity in relation to human infrastructure and natural habitat variability in Brunei Darussalam (henceforth abbreviated to 'Brunei'), an independent state on the island of Borneo.

1.2 What is a rainforest?

Typically, rainforests are divided into two types: temperate and tropical. Temperate rainforests are characterised by cool summers, strong wind disturbance and wet weather throughout the year. Temperate rainforests are found in high latitude zones on the East and West coast of the Pacific as well as North-Western Europe (Alaback, 1991). Tropical rainforests, however, are located at low latitudes, typically between 10 degrees north and south of the equator, and experience high temperatures and humidity year-round with heavy, yet seasonally varying amounts of rainfall (Park, 2002). This thesis will focus solely on tropical rainforests, and more specifically the avian wildlife they harbour and how best to monitor them.

Tropical rainforests stretch across the equatorial regions of all four continents which overlap this latitudinal band, namely Central and South America, Africa, Asia, and Oceania (Hazarika, 2013). Tropical rainforests are complex and diverse ecosystems, providing valuable habitat for numerous species across many taxa. Indeed, tropical rainforests are a global hub of biodiversity. Although only covering one-fifth of Earth's continental surface (Pillay *et al*., 2021), tropical rainforests are thought to harbour over half of the planet's biodiversity (Pillay *et al*., 2022; Wilson & Peter, 1988). This is in part due to their age and climatic stability. Tropical rainforests are Earth's oldest continuous habitat, first appearing as early as 300 million years ago in the Carboniferous period (Falcon-Lang *et al*., 2009), with some – like the Daintree rainforest in Australia – having resembled their present form for over 180 million years (Pierce & Roosevelt, 2021). Although all tropical rainforests have some common features, this is partly the result of convergent evolution seen between phylogenetically distinct organisms (Corlett & Primack, 2006).

Most tropical rainforests have experienced an extremely stable climate of high temperatures, humidity, and rainfall over millions of years. Such long-lasting, stable conditions have allowed extensive evolution, leading to highly specific niche partitioning (Voskamp *et al*., 2017). Moreover, intra-annual climatic stability results in high productivity and no 'rest period', in terms of reproduction or activity level, in animals and plants. For instance, trees in tropical rainforests are deciduous by nature but evergreen in habit (Park, 2002), meaning they shed and grow leaves continuously throughout the year, a process at the heart of the tight nutrient cycling seen in such forests (Vitousek & Sanford, 1986). Without the constant presence of a rapidly decomposing leaf litter creating a thin layer of nutrient rich soil, plants in tropical rainforests would struggle to grow as the deeper soil is, in fact, very infertile (Place, 2001). Vegetation in tropical rainforests also plays a key role in creating these forests' distinctive structural features. Plant life is organised into four vertical layers or 'strata': emergent trees, canopy, understory, and forest floor (Park, 2002). Each vegetative stratum has unique biotic and abiotic characteristics, creating a series of micro-habitats throughout tropical rainforests (Basham *et al.*, 2019). Complex habitats provide many refuges and niches for wildlife (Pace *et al.*, 1999), which has been shown to increase levels of biodiversity (Niklaus *et al.*, 2017). Tropical rainforests also proved to be important ecological refuges for many species during the ice-ages as they survived these periods relatively unchanged (Haffer & Prance, 2001).

1.3 Why are tropical rainforests important?

Tropical rainforests are both socially and aesthetically valuable as well as paramount for ecosystem functioning. Firstly, tropical rainforests are vital assets for local livelihoods, with many indigenous people reliant on them for food, shelter, and cultural identity (Ellen, 1998). Furthermore, tropical rainforests are a major source of raw materials, such as timber (Shearman *et al.*, 2012), ores (Costa *et al.*, 1999), and pharmaceuticals (Mendelsohn & Balick, 1995), essential to many aspects of modern society. Moreover, tropical rainforests have intrinsic value; with their unique biological make up, history and beauty, they are worthy of protection from anthropogenic impacts, irrespective of more direct service values (Park, 2002; Zhou *et al.*, 1997).

As well as providing both vital habitats for over 50% of global biota (Wilson & Peter, 1988; Pillay *et al*., 2022) and crucial resources for human use, tropical rainforests provide numerous ecosystem services without which Earth could not continue to function as it does. Akin to how the loss of one species in a given ecosystem can have cascading effects on the ecological community (Lundberg *et al.*, 2000; Petchey *et al.*, 2008; Dunne & Williams, 2009), the loss of tropical rainforests would be devastating for the global ecosystem. Tropical rainforests play a key role in regulating the climate, both globally and locally, through the process of cloud formation and maintaining the water cycle (Foley *et al.*, 2002). The vegetation in tropical rainforests also protects the land from erosion (Zuazo & Pleguezuelo, 2009), floods (Wenhua, 2004) and droughts (Staal *et al.*, 2020). Tropical rainforests often act simultaneously as a carbon sinks (Young, 2021) and oxygen sources (Belcher *et al*., 2021), thus significantly influencing atmospheric composition and potentially proving to be helpful in combating climate change. Nevertheless, studies have shown that some tropical rainforests might be becoming carbon sources due to deforestation and the burning of organic matter (Gatti *et al.*, 2021; Baccini *et al.*, 2017). A recent study revealed that only one major tropical rainforest – that of central Africa – remains a strong carbon sink (Harris *et al.*, 2021). Harris *et al.* (2021) argues that the forests in the Amazon remain a net carbon sink for now but that they are on the verge of becoming a net carbon source, thus following in the footsteps of the forests of Southeast Asia. Therefore, conservation efforts in tropical rainforests are not only needed to prevent biodiversity loss but also but maintain global ecosystem functioning.

1.4 Threats

As permanent and vast as tropical rainforests may seem, these valuable ecosystems are vulnerable as they are extremely sensitive to external pressures. Tropical rainforests have taken millions of years to evolve yet can be destroyed within a century due to anthropogenic impacts. Not only is the destruction of tropical rainforests detrimental to global ecosystem functioning, but it is also catastrophic in terms of species loss. Considering that tropical rainforests contain higher levels of biodiversity than all other habitats on Earth combined, it is reasonable to surmise that the damage done in these regions will contribute significantly to the anthropogenic extinction crisis we are currently experiencing (Ceballos *et al.*, 2010; Ceballos *et al*., 2017; Cook *et* al., 2023). Identifying and understanding the reasons behind, and impacts of, the threats faced by tropical rainforests is paramount as this is the first step towards protecting these precious ecosystems.

1.4.1 Habitat loss: land use change & deforestation

The main cause of environmental damage and species decline in tropical rainforests is habitat loss and fragmentation (Püttker *et al*., 2020). The pressures on the land, and competition between different land uses, is immense. Land use change is sometimes defined as the shift from untouched natural landscapes to anthropogenically modified land, usually to benefit human economic activities (Paul & Rashid, 2017). In the case of tropical rainforests, this usually leads to the removal of vegetation (deforestation) to leave space for food production, infrastructure development, as well as the extraction of raw materials and energy production (Hartemink, 2010). Tropical rainforests across the globe are suffering from intense deforestation: Over 2.3 million km^2 of tree cover has been lost between 2000 and 2012, with the tropics being the biggest victims (Hansen *et al.*, 2013). Undoubtedly land use change has a negative impact on tropical rainforest ecosystems, both in terms of disrupting the ecosystem services they provide (Portela & Rademacher, 2001) but also as it reduces and fragments habitat available for wildlife. Although there is no clear consensus in the literature about whether habitat fragmentation *per se* truly has negative effects on biodiversity (Fahrig, 2017; 2019; Fletcher *et al.*, 2018), studies suggest that the ‘edge effect’ – created by having several smaller patches of habitat as opposed to one larger one – prevents smaller habitat ‘islands’ from supporting some species, decreasing overall biodiversity (Laurance *et al*., 2011). It has been stated that habitat fragmentation not only reduces biodiversity by 13-75% but that it also negatively affects the ecosystem services tropical rainforests provide (Haddad *et al*., 2015). Considering 70% of the world's remaining forest cover is less than 1km away from forest edge (Haddad *et al*., 2015), it is paramount that more research is conducted into this issue and immediate action is taken to reduce habitat fragmentation and conserve vulnerable species affected.

Once removed, primary forests are replaced by secondary forests which sometimes have difficulty becoming established, as tropical rainforest soil is very infertile once the vegetation is removed (Hartemink *et al.*, 2008). Deforestation breaks the nutrient cycle as there are no leaves falling on the forest floor to replenish the soil nutrients. Consequently, deforestation expedites further environmental damage such as soil erosion, floods, droughts, fires, and landslides (Ramos & Yamamoto, 2018). If secondary forests do manage to establish, studies have found that they are often less biodiverse as they cannot support all the species a primary forest can, due to reduced complexity of the vegetation structure (Klimes *et al.*, 2012). Despite these findings, comparative studies have shown that different species react differently to secondary forests habitat. Certain species groups' abundance and diversity were unchanged (Yoshimoto *et al.*, 2015) or even increased (Wu *et al*.,1996) in secondary as opposed to primary forests in China. Lastly, deforestation is contributing heavily towards climate change, as tropical rainforests are the primary absorber of carbon globally (Beer *et al*., 2010). The major degradations tropical rainforests are experiencing are resulting in an increase in global greenhouse gas emissions, with deforestation of tropical rainforests accounting for 11% of total emissions (Montero *et al.*, 2020).

Urbanisation and infrastructure expansion

Urbanisation and infrastructure expansion are heavily anthropogenic factors which contribute to land use change and deforestation (Ehrhardt-Martinez, 1998), particularly in countries with a rapidly growing human population and/or striving to increase their national infrastructure and development (Myers, 2021; Laurance *et al.*, 2009), which is the case in for many countries in Southeast Asia. The high human density in the tropics (Harding *et al.*, 2020) coupled with the fact that the majority of the countries in this region are considered developing countries (Park, 2002), results in great pressure on the land. Developing countries typically have larger populations, at greater densities, and have a considerable reliance on the land for their survival and economic activities. Urban sprawl is a driving factor of deforestation in the tropics both directly and indirectly (Carr *et al.*, 2005). Firstly, forest is being removed to create space for housing and other infrastructure needed in urban areas (DeFries *et al.*, 2010). Secondly, rural exodus, and consequent increase in wealth, results in increased demand for high quality lifestyle resources, such as meat and dairy products

(Delgado, 2003; Elferink & Schierhorn, 2016). These demands worsen agricultural deforestation and ultimately drive climate change. Higher levels of urbanisation often result in transport infrastructure development to link urban areas together. Developing such infrastructure requires significant areas of land to be cleared of vegetation in a linear fashion, resulting not only in deforestation but also habitat fragmentation, biological invasions, increased hunting pressure due to ease of access, changes in predator-prey interactions, and wildlife deaths through collision (Laurance *et al.*, 2009).

Brunei, although a country in the tropics looking to expand its infrastructure, does not conform to the general trends seen in most countries in Southeast Asia. Brunei has quite a low population density and the majority of the population – circa 450,000 people according to Brunei's Department of Economic planning and Statistics – is concentrated in the capital, Bandar Seri Begawan. Brunei is also a high-income country that is classified as developed and oil exporting (Ahmad, 2014). As explained in section 1.6 of this chapter, the infrastructure expansion happening in Brunei currently will facilitate commuting to rural areas but in doing so might have deleterious impacts of surrounding rainforest habitats and wildlife.

Agriculture, exploitation of raw materials, and hydroelectric dams

Although not hugely problematic in Brunei, agriculture, exploitation of raw materials, and hydroelectric dams present threats to many of the other tropical rainforests globally and awareness of these threats is important.

Agriculture is the most significant contributor to land use change and deforestation in tropical rainforests due to the vast surface areas required and adverse farming practices used. Vegetation is often removed using the slash and burn method (Brady, 1996) to grow crops – namely oil palms (Carlson & Garrett, 2018) and animal feed (Carlson & Garrett, 2018) – as well as for pastoral use, such as castle grazing (Veiga *et al.*, 2002; van Solinge, 2013). This results in habitat loss and homogeneity (Hamilton *et al.*, 2020), causing drastic declines in biodiversity. Furthermore, the soil does not remain fertile for long, so farmers who cannot afford fertilizers repeat the process every few years, resulting in drastic levels of deforested land left in very poor condition, making it harder for secondary forest to grow. Hence, this method is only sustainable at very low levels (Kleinman *et al.*, 1995). However, with approximately 40% of the world's human population living in the tropics (Harding *et al.*, 2020), agriculture is responsible for more tropical rainforest deforestation than any other factor (Jayathilake *et al.*, 2021).

Exploitation of raw materials, namely timber (Damette & Delacote, 2011) and ores (Giljum *et al.*, 2022), is a major contributor to land use change in tropical rainforests. Tropical rainforests are appealing to the logging industry as these forests have a very high density of plant biomass compared to temperate forests (Lugo & Brown, 1991), leaving them overexploited by this trade. Furthermore, felling, log decks, skid trails, and logging roads all cause collateral damage (Asner *et al.*, 2004). Mines also cause environmental issues in tropical rainforests such as further deforestation, long-lasting pollution of air, water, and soil from products used in the industry (Alvarez-Berrios & Aide, 2015). The increased ease of access created by roads to transport exploited raw materials out of the forests, exposes tropical rainforests to a plethora of other threats (Kleinschroth & Healey, 2017; Laurance *et al.*, 2009).

Although fighting climate change by providing renewable energy (Bakis, 2007), hydroelectric dams cause major land use change because of flooding, which has devastating impacts on tropical rainforests at all trophic levels. Seasonal flooding in areas adjacent to rivers is a naturally occurring phenomenon contributing to a healthy ecosystem (Ferreira & Stohlgren, 1999), but tropical rainforests are not adapted to permanent, deep flooding. Dams also obstructs vital waterways, in turn disrupting the access to natural spawning grounds of many fish species, causing negative repercussions not only on fish populations but also on all animals – and people – who depend on these fish for food (Canas & Waylen, 2012). It is vital that the benefits hydroelectricity can provide are weighed up against the impacts this type of infrastructure has on the environment.

1.4.2 Climate change

There is a positive feedback loop between climate change and tropical rainforest damage. This cycle is paving the way towards a tipping point in which the synergistic actions of climate change and deforestation will transform tropical rainforests into dry savannah ecosystems (Sales *et al.*, 2020). Climate change is weakening tropical rainforest ecosystems. Increases in temperatures are driving species to higher elevations where the climate is cooler but where weather patterns and humidity levels are dissimilar. If animals don't emigrate, they are forced either to adapt to ever higher temperatures and unusually unpredictable climates or to die. Moreover, many of the threats faced by tropical rainforests act synergistically, ultimately aggravating each other. For instance, deforestation worsens climate change as the removal of trees results in less greenhouse gases (in this case CO_2) being sequestered. Furthermore, when vegetation is burnt it releases the stored carbon (Padoch & Pinedo-Vasquez, 2010), thus actively fuelling climate change. As well as controlled fires, tropical rainforests are experiencing ever increasing frequencies of wildfires, either ignited intentionally or as a result of environmental factors, such as reduced humidity stemming from increased global temperatures (Ma *et al.*, 2022). The scale and frequency of wildfires over the last decade is causing extensive damage to tropical rainforest ecosystems and wildfires are becoming significant contributors to climate change.

1.4.3 Illegal wildlife poaching and trafficking

Poaching is the illegal hunting, capture, and subsequent trade of wildlife and presents a threat to every tropical rainforest in the world. Despite often being connected to other illicit trade activities such as arms or drugs (Van Uhm *et al*., 2021), poaching is still regarded by many governments as a relatively 'minor' crime (Anderson & Jooste, 2014). This, coupled with the fact that wildlife traders often make very high profits (Le Duc, 1996), is resulting in an increase in poaching rates in recent years as regulations, controls, and punishments are minor compared to those of other illegal trading activities. Moreover, since the COVID-19 related lockdowns, there has been sharp rises in poaching around the globe (Aditya *et al.*, 2021; Koju *et al.*, 2021; Ndlovu *et al*., 2021; Quesada-Rodríguez *et al*., 2021; Rahman *et al.*, 2021; Behera *et al*., 2022), likely a combined result of damaged economies, decrease in food security, and reduced surveillance, in turn increasing the likelihood of another zoonotic pandemic. Furthermore, animals are often kept in very poor conditions due to the traders having to smuggle them through borders, which often leads to injury or death of live cargo. Overexploitation of certain rare, and thus highly sought after, species leaves their wild populations in a precarious state, rendering those species even more threatened (Challender *et al*., 2020). All charismatic taxa are targeted in tropical rainforests, from herpetofauna (Jestrzemski *et al*., 2013) and mammals (Wiafe, 2018) to birds (Pires & Clarke, 2011), with young birds often being taken straight from the nests (Wright *et al*., 2001). Poaching is creating additional ecological stressors to tropical rainforest ecosystems by removing keystone species and generating further holes in food chains, further weakening tropical rainforests and exacerbating the effects of other threats. However, new monitoring methods are providing affective poaching control techniques, such as the use of Autonomous Recording Units (ARUs) to automatically detect gunshot noise (Katsis *et al*., 2022) and camera traps to identify poaching hotspots (de Matos Dias *et al.*, 2020).

1.5 Monitoring biodiversity in tropical rainforests

The first step in protecting tropical rainforests and the wildlife their harbour is gaining deeper ecological knowledge about the species, their behaviours, and their interconnectivity. Scientific monitoring of tropical rainforests can provide vital insights. A variety of monitoring methods for biodiversity have been used in tropical rainforests, which differ in their accuracy, scale, and the type of data they collect, with some being more adapted to certain species than others. To monitor overall ecosystem health, biodiversity is a useful metric, as more biodiverse sites tend to be more stable, resistant, and productive (Johnson *et al.*, 1996; Tilman, 1999). There are two common ways of undertaking such measurements: field surveys and remote sensing.

Field surveys are in-person observations made by researchers whilst physically in the location being studied, with the aims of collecting data on the object of study (Eberhardt & Thomas, 1991). Field surveys are a more traditional monitoring method and can be undertaken in various forms such as linear transect lines, quadrats, point counts, trapping, or sampling substrates for further laboratory testing (Anderson, 1976; Karr, 1981; Ralph *et al.*, 1995; Woodcock, 2005; Janečka *et al.*, 2008; Lucci Freitas *et al.*, 2014; Mancini *et al.*, 2022). According to the literature, field surveys are the dominant monitoring system employed to date (Mulatu *et al.*, 2017), however this is because – until relatively recently – this was the only survey method available to scientists. Traditional field surveys do not necessarily require extensive and advanced hardware, but rather rely on field time, effort, and expertise. Although traditional surveying methods have provided invaluable baseline data in many habitats across the globe – including tropical rainforests, where, for example, mist nets have been used to study avifauna (Rahman, 2002) – they have many limitations. Despite not being resource intensive in terms of hardware, they require biological experts to spend a great amount of time in the field to gather relatively restricted spatial-temporal data. This significantly raises research costs as well as producing data at risk of being biased by the observer and limits monitoring to areas which are easily accessible.

Remote sensing surveying methods have revolutionised the field of biological monitoring. Not only do they allow remote locations to be easily surveyed (Lim & Lee, 2017), but they are also unbiased, non-intrusive, systematic, usable by non-expert biologists, and applicable to vast spatial-temporal scales (Sethi *et al.*, 2020). Remote sensing technologies can be left in the field for long periods of time, thus further reducing research costs (Lyra-Jorge *et al.,* 2008). Additionally, this survey method provides digital data which can be stored and analysed with greater ease. These data can be used to gain a comprehensive and general understanding of the overall biodiversity and environment studied, something that is hard to achieve using traditional surveying methods that are typically focused on smaller scale ecological questions. Remoting sensing encompasses several different surveying techniques, each providing a unique insight into the state of biodiversity and its changes in the studied areas.

Large scale remote sensing technologies, such as high-resolution satellite imaging and various types of electromagnetic radiation, can be used to examine ecologically relevant aspects of the globe's surface. Remote sensing using satellites provides essential information on land use and cover over large geographic areas. For instance, satellite imagery has helped in mapping global wetlands (Ozesmi & Bauer, 2002), fires (Roy *et al.*, 2013), and sea-ice (Kwok, 2010) amongst other things. Both optical and laser sensors are currently being used to map forest coverage and detect land use changes (Sica *et al.*, 2019), providing critical data for tropical rainforest conservation. Although there are maps available in the literature presenting data on tropical rainforest coverage, studies are often focused on a local area (Delgado-Aguilar *et al.*, 2019), or at best on one biogeographic realm (Pulella *et al.*, 2020) and many are outdated (Saatchi *et al.*, 1997). Considering the urgency and rate of change tropical rainforests are experiencing currently, it is essential to have up-to-date global level mapping available of all tropical rainforests. Nevertheless, this technology requires the use of satellite imagery, and is therefore not accessible to researchers who lack the necessary budget or expertise.

Smaller scale remote sensing technologies – such as camera traps, ARUs, and tracking devices such as Radio-frequency identification (RFID) tags – also provide vital monitoring data whilst being more accessible to smaller budget projects. Although these ground-based sensors do not solve the accessibility challenge of surveying remote areas as they need to be set up in the field, they nevertheless reduce the amount of time researchers must spend on the ground, and therefore in difficult conditions, without impairing the amount of data collected. Moreover, these devices allow finer-scale monitoring of individual animals and their interactions with their environment and each other, than satellite remote sensing does, enabling scientists to implement targeted conservation plans. For example, in the last few years, camera traps have helped delineate ecological corridors for Spectacled bears (*Tremarctos ornatus*) in the Peruvian Amazon (Sánchez *et al.*, 2022) and estimate the endangered Amur leopard (*Panthera pardus orientalis*) population to 84 individuals (Vitkalova *et al.*, 2018). ARUs have aided in the identification of eight previously unrecorded Dupont's Lark populations (*Chersophilus duponti*) (Pérez-Granados *et al.*, 2018) as well as proving to be a promising tool to detect cryptic mammals such as the black lion tamarin (*Leontopithecus chrysopygus*) (Zambolli *et al.*, 2022). RFID tags helped to shed light on how personality influences seed dispersal in small mammals (Brehm *et al.*, 2019) as well as to study interspecific paper wasp interactions (Sumner *et al.*, 2007). Although RFID tags are useful to track individuals, giving incredibly high-resolution data (Rafiq *et al.*, 2021), they require baseline information on the environment studied and are more suited to answer very specific research questions about a relatively narrow field - often focusing on a few individuals of one species. Camera traps and ARUs present themselves as more well-rounded technologies, enabling users to study animals at an individual scale whilst also offering the possibility of conducting wider scale ecological surveys. Additionally, ARUs provide a unique way of monitoring overall biodiversity, without necessarily having to focus on keystone species as a proxy, by studying the soundscape (Pijanowski *et al.*, 2011). This novel analysis technique provides a systematic assessment metric of overall biodiversity by summarising certain traits in audio datasets. Thus, camera traps and ARUs are useful for environments which have been minimally monitored in the past – such as Brunei – as they survey all mobile or vocal species present in that environment, providing largescale but high-resolution data.

1.6 Case study details

Brunei is a small country situated on the island of Borneo and is one of Asia's leading producers of liquefied natural gas, crude oil, and petroleum products (Ahmad, 2014), making the nation financially prosperous. This removes the need to exploit the local rainforest's raw materials or exploit the land for agricultural reasons, unlike neighbouring Malaysia and Indonesia. The country's Eastern exclave, Temburong, contains particularly pristine rainforests due to its historic geographical isolation from the capital city. According to the 2020 population census conducted by Brunei's Ministry of Finance and Economy, 97.5% of the population lives in the Western part of the country, leaving only 11 200 people living in Temburong. Unsurprisingly, Temburong is far less developed in terms of infrastructure (fewer roads and buildings), thus retaining more forest cover. Brunei's only national park, Ulu Temburong, is located in the southern part of this sparsely populated district. However, in March 2020, Temburong was, for the first time, directly connected by road to the Western part of the country via the 27 km Sultan Haji Omar Ali Saifuddien (SOAS) bridge (Taylor, 2022). This new, increased level of connection between the more populated side of Brunei and Temburong will likely bring about an increase in traffic and infrastructure development, including new roads and buildings in this Eastern district. Hence, it is anticipated that Temburong will become increasingly urbanised and will experience high levels of infrastructure expansion. One of the primary aims of this thesis is to document current biodiversity in the region in relation to infrastructure, prior to further development.

Birds were chosen as the focal taxon in this study as they are good indicators of ecosystem health and are sensitive to environmental changes (Mekonen, 2017). Although not all species of birds are negatively affected by urbanisation (Møller, 2009; Maklakov *et al.,* 2011), it is thought that overall species richness and evenness decreases in response to urbanisation (Marzluff, 2001). Parts of this study focus specifically of two species of birds: the Helmeted

Hornbill and the Great Argus. These species were chosen as they are charismatic and emblematic of Borneo's tropical rainforests, often deeply embedded in local culture, making them key flagship species for conservation efforts (Philovenny & Mohd-Azlan, 2021; Aihara *et al*., 2008). Additionally, the Helmeted Hornbill is a canopy specialist whereas the Great Argus is a ground dwelling bird, thus allowing the study to explore the effect of infrastructure expansion on both extremes of avian ecologies.

1.7 Aims and objectives

Our study focused on the current infrastructure expansion in the Temburong district of Brunei, with a particular focus on the avian wildlife found in the tropical rainforest of this region. The biodiversity in Temburong has been understudied in the past and, to the best of our knowledge, there is little wildlife monitoring data for this region in the scientific literature. Thus, in this study, we use the remote sensing technologies of ARUs and camera traps to assess the biodiversity of Temburong's TR, with a focus on avian diversity, and explore the potential impacts of infrastructure expansion on birds in this region.

<u>This thesis aims to:</u>

(i) Assess the impact of infrastructure expansion (main roads, presence of buildings, and forest quality) on overall bird biodiversity in Temburong's tropical rainforest.

(ii) Assess the impact of infrastructure expansion on two focal species of special conservation value (Helmeted Hornbill *(Rhinoplax vigil*) and Great Argus (*Argusianus argus*)) in Temburong's tropical rainforest.

(iii) Compare two remote surveying technologies (camera traps and ARUs), and associated audio analysis tools, to inform best practice for their use in tropical rainforest ecosystems.

1.8 Thesis plan

This thesis has been written in the format of chapters as stand-alone manuscripts as much as possible, to expediate potential paper publication. This necessarily results in some repetition of reference material amongst chapters. Repetition of methods has been avoided by extracting common methods to a single 'General Materials and Methods' chapter following the introduction.

In Chapter 2, we provide background to the project, present fieldwork details, and lay out sampling protocols which apply to all four data chapters. ARUs and camera traps are paired and placed along infrastructure expansion gradients, spanning from near roads and urban areas, into undisturbed tropical rainforest.

In Chapter 3, we analyse the soundscapes to explore the impact of infrastructure expansion on overall bird biodiversity in Temburong's tropical rainforest using the Acoustic Complexity Index. The level of infrastructure expansion is measured according to distance from main roads, distance from buildings and above ground biomass at recording sites.

In Chapter 4, we construct and compare the performance of six semi-automated acoustic recognisers built to detect Helmeted Hornbill calls contained in an audio dataset. We vary the training data and the recogniser 'learning' methods to assess which yields the best results.

In Chapter 5, we explore the impact of infrastructure expansion on Helmeted Hornbills and Great Argus in Temburong's tropical rainforest. Their distribution and regularity of persistence at sites is explored according to distance to main roads, distance to buildings, and above ground biomass at recording sites using call count data extracted from the audio dataset using custom made species-specific recognisers.

In Chapter 6, we compare ARUs and camera traps detection rates of Great Argus. Great Argus call count data from the audio dataset is quantitatively compared to paired camera trap images of Great Argus. The advantages and disadvantages of each remote sensing survey methods are discussed.

1.9 References

Aditya, V., Goswami, R., Mendis, A. and Roopa, R., 2021. Scale of the issue: Mapping the impact of the COVID-19 lockdown on pangolin trade across India. *Biological Conservation*, *257*, p.109136.

Alaback, P.B., 1991. Comparative ecology of temperate rainforests of the Americas along analogous climatic gradients. *Revista Chilena de Historia Natural*, 64, pp.399-412.

Alvarez-Berríos, N.L. and Aide, T.M., 2015. Global demand for gold is another threat for tropical forests. *Environmental Research Letters, 10*(1), p.014006.

Anderson, D.R., 1976. *Guidelines for Line Transect Sampling of Biological Populations* (No. 9-76). Utah Cooperative Wildlife Research Unit. Utah State University. Logan, Utah.

Anderson, B. and Jooste, J., 2014. *Wildlife poaching: Africa's surging trafficking threat*. National defense univ fort mcnair dc africa center for strategic studies.

Asner, G.P., Keller, M. and Silva, J.N., 2004. Spatial and temporal dynamics of forest canopy gaps following selective logging in the eastern Amazon. *Global Change Biology, 10*(5), pp.765-783.

Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D. and Houghton, R.A., 2017. Tropical forests are a net carbon source based on aboveground measurements of gain and loss. *Science, 358*(6360), pp.230-234.

Bakis, R., 2007. The current status and future opportunities of hydroelectricity*. Energy Sources, Part B, 2*(3), pp.259-266.

Basham, E.W., Seidl, C.M., Andriamahohatra, L.R., Oliveira, B.F. and Scheffers, B.R., 2019. Distance–decay differs among vertical strata in a tropical rainforest. *Journal of Animal Ecology*, 88(1), pp.114-124.

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Arain, M.A., Baldocchi, D., Bonan, G.B. and Bondeau, A., 2010. Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science*, *329*(5993), pp.834-838.

Behera, A.K., Kumar, P.R., Priya, M.M., Ramesh, T. and Kalle, R., 2022. The impacts of COVID-19 lockdown on wildlife in Deccan Plateau, India. *Science of the Total Environment*, *822*, p.153268.

Belcher, C.M., Mills, B.J., Vitali, R., Baker, S.J., Lenton, T.M. and Watson, A.J., 2021. The rise of angiosperms strengthened fire feedbacks and improved the regulation of atmospheric oxygen. *Nature Communications*, 12(1), pp.1-9.

Brady, N.C., 1996. Alternatives to slash-and-burn: a global imperative. *Agriculture, Ecosystems & Environment, 58*(1), pp.3-11.

Brehm, A.M., Mortelliti, A., Maynard, G.A. and Zydlewski, J., 2019. Land-use change and the ecological consequences of personality in small mammals. *Ecology Letters*, *22*(9), pp.1387-1395.

Brenner, N. and Schmid, C., 2014. The ‘urban age’ in question. *International Journal of Urban and Regional Research*, *38*(3), pp.731-755.

Canas, C.M. and Waylen, P.R., 2012. Modelling production of migratory catfish larvae (Pimelodidae) on the basis of regional hydro-climatology features of the Madre de Dios Basin in southeastern Peru. *Hydrological Processes*, 26(7), pp.996-1007.

Carlson, K.M. and Garrett, R.D., 2018. Environmental impacts of tropical soybean and palm oil crops. In *Oxford Research Encyclopedia of Environmental Science*.

Carr, D.L., Suter, L. and Barbieri, A., 2005. Population dynamics and tropical deforestation: state of the debate and conceptual challenges. *Population and Environment, 27*(1), pp.89-113.

Ceballos, G., García, A. and Ehrlich, P.R., 2010. The sixth extinction crisis: Loss of animal populations and species*. Journal of Cosmology*, 8(1821), p.31.

Ceballos, G., Ehrlich, P.R. and Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, *114*(30), pp.E6089-E6096.

Challender, D.W., Heinrich, S., Shepherd, C.R. and Katsis, L.K., 2020. International trade and trafficking in pangolins, 1900–2019. In *Pangolins* (pp. 259-276). Academic Press.

Cooke, R., Mancini, F., Boyd, R.J., Evans, K.L., Shaw, A., Webb, T.J. and Isaac, N.J., 2023. Protected areas support more species than unprotected areas in Great Britain but lose them equally rapidly. *Biological Conservation*, *278*, p.109884.

Corlett, R.T. and Primack, R.B., 2006. Tropical rainforests and the need for cross-continental comparisons. *Trends in Ecology & Evolution, 21*(2), pp.104-110.

Costa, M.L., Angélica, R.S. and Costa, N.C., 1999. The geochemical association Au–As–B–(Cu)–Sn–W in latosol, colluvium, lateritic iron crust and gossan in Carajás, Brazil: importance for primary ore identification. *Journal of Geochemical Exploration*, 67(1-3), pp.33-49.

Damette, O. and Delacote, P., 2011. Unsustainable timber harvesting, deforestation and the role of certification. *Ecological Economics*, *70*(6), pp.1211-1219.

DeFries, R.S., Rudel, T., Uriarte, M. and Hansen, M., 2010. Deforestation driven by urban population growth and agricultural trade in the twenty-first century. *Nature Geoscience, 3*(3), pp.178-181.

de Matos Dias, D., Ferreguetti, Á.C. and Rodrigues, F.H.G., 2020. Using an occupancy approach to identify poaching hotspots in protected areas in a seasonally dry tropical forest. *Biological Conservation*, *251*, p.108796.

Delgado, C.L., 2003. Rising consumption of meat and milk in developing countries has created a new food revolution. *The Journal of Nutrition*, *133*(11), pp.3907S-3910S.

Delgado-Aguilar, M.J., Hinojosa, L. and Schmitt, C.B., 2019. Combining remote sensing techniques and participatory mapping to understand the relations between forest degradation and ecosystems services in a tropical rainforest. *Applied Geography, 104*, pp.65-74.

Dunne, J.A. and Williams, R.J., 2009. Cascading extinctions and community collapse in model food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1524), pp.1711-1723.

Eberhardt, L.L. and Thomas, J.M., 1991. Designing environmental field studies. *Ecological monographs*, *61*(1), pp.53-73.

Ehrhardt-Martinez, K., 1998. Social determinants of deforestation in developing countries: A cross-national study. *Social Forces, 77*(2), pp.567-586.

Elferink, M. and Schierhorn, F., 2016. Global demand for food is rising. Can we meet it. *Harvard Business Review, 7*(04), p.2016.

Ellen, R.F., 1998. Indigenous Knowledge of the Rainforest. In *Human activities and the tropical rainforest* (pp. 87-99). Springer, Dordrecht.

Fahrig, L., 2019. Habitat fragmentation: A long and tangled tale. *Global Ecology and Biogeography, 28*(1), pp.33-41.

Falcon-Lang, H.J., DiMichele, W.A., Elrick, S. and Nelson, W.J., 2009. Going underground: in search of Carboniferous coal forests. *Geology Today*, *25*(5), pp.181-184.

Fearnside, P.M., 2016. Greenhouse gas emissions from hydroelectric dams in tropical forests. *Alternative Energy and Shale Gas Encyclopedia*, pp.426-436.

Ferreira, L.V. and Stohlgren, T.J., 1999. Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. *Oecologia, 120*(4), pp.582-587.

Fletcher Jr, R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., Holt, R.D., Gonzalez, A., Pardini, R., Damschen, E.I. and Melo, F.P., 2018. Is habitat fragmentation good for biodiversity? *Biological conservation, 226*, pp.9-15.

Foley, J.A., Botta, A., Coe, M.T. and Costa, M.H., 2002. El Niño–Southern oscillation and the climate, ecosystems and rivers of Amazonia. *Global Biogeochemical Cycles*, 16(4), pp.79-1.

Gatti, L.V., Basso, L.S., Miller, J.B., Gloor, M., Gatti Domingues, L., Cassol, H.L., Tejada, G., Aragão, L.E., Nobre, C., Peters, W. and Marani, L., 2021. Amazonia as a carbon source linked to deforestation and climate change. *Nature, 595*(7867), pp.388-393.

Giljum, S., Maus, V., Kuschnig, N., Luckeneder, S., Tost, M., Sonter, L.J. and Bebbington, A.J., 2022. A pantropical assessment of deforestation caused by industrial mining. *Proceedings of the National Academy of Sciences*, *119*(38), p.e2118273119.

Guérin, F., Abril, G., Tremblay, A. and Delmas, R., 2008. Nitrous oxide emissions from tropical hydroelectric reservoirs. *Geophysical Research Letters, 35*(6).

Gunkel, G., 2009. Hydropower–A green energy? Tropical reservoirs and greenhouse gas emissions. *CLEAN–Soil, Air, Water, 37*(9), pp.726-734.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D. and Cook, W.M., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances, 1*(2), p.e1500052.

Haffer, J. and Prance, G.T., 2001. Climatic forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation. *Amazoniana: Limnologia et Oecologia Regionalis Systematis Fluminis Amazonas*, 16(3/4), pp.579-607.

Hamilton, H., Henry, R., Rounsevell, M., Moran, D., Cossar, F., Allen, K., Boden, L. and Alexander, P., 2020. Exploring global food system shocks, scenarios and outcomes. *Futures, 123*, p.102601.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R. and Kommareddy, A., 2013. High-resolution global maps of 21st-century forest cover change. *Science, 342*(6160), pp.850-853.

Harding, S., Penny, A., Hunt, E., Diop, H., Kalanzi, B., Touitha, Y., Archer, C., Jackson, A., McHugh, J., Chang, O. and Mohamed, A., 2020. State of the tropics report.

Harris, N.L., Gibbs, D.A., Baccini, A., Birdsey, R.A., De Bruin, S., Farina, M., Fatoyinbo, L., Hansen, M.C., Herold, M., Houghton, R.A. and Potapov, P.V., 2021. Global maps of twenty-first century forest carbon fluxes. *Nature Climate Change, 11*(3), pp.234-240.

Hartemink, A.E., Veldkamp, T. and Bai, Z., 2008. Land cover change and soil fertility decline in tropical regions. *Turkish Journal of Agriculture and Forestry, 32*(3), pp.195-213.

Hartemink, A.E., 2010. Land use change in the tropics and its effect on soil fertility. In *Proceedings 19th World Congress of Soil Science, Brisbane, Australia, 01-06 August, 2010* (pp. 55-58).

Hazarika, S., 2013. Rainforests and migration. In *The Encyclopaedia of Global Human Migration.* Blackwell Publishing Ltd. Oxford.

Janečka, J.E., Jackson, R., Yuquang, Z., Diqiang, L., Munkhtsog, B., Buckley-Beason, V. and Murphy, W.J., 2008. Population monitoring of snow leopards using noninvasive collection of scat samples: a pilot study. *Animal Conservation*, *11*(5), pp.401-411.Jayathilake, H.M., Prescott, G.W., Carrasco, L.R., Rao, M. and Symes, W.S., 2021. Drivers of deforestation and degradation for 28 tropical conservation landscapes. *Ambio, 50*(1), pp.215-228.

Jestrzemski, D., Schütz, S., Nguyen, T.Q. and Ziegler, T., 2013. A survey of amphibians and reptiles in Chu Mom Ray National Park, Vietnam, with implications for herpetofaunal conservation. *Asian Journal of Conservation Biology*, *2*(2), pp.88-110.

Johnson, K.H., Vogt, K.A., Clark, H.J., Schmitz, O.J. and Vogt, D.J., 1996. Biodiversity and the productivity and stability of ecosystems. *Trends in Ecology & Evolution*, *11*(9), pp.372-377.

Karr, J.R., 1981. Surveying birds with mist nets. *Studies in Avian Biology*, *6*, pp.62-67.

Katsis, L.K., Hill, A.P., Pina-Covarrubias, E., Prince, P., Rogers, A., Doncaster, C.P. and Snaddon, J.L., 2022. Automated detection of gunshots in tropical forests using convolutional neural networks. *Ecological Indicators*, *141*, p.109128.

Kleinman, P.J.A., Pimentel, D. and Bryant, R.B., 1995. The ecological sustainability of slash-and-burn agriculture*. Agriculture, Ecosystems & Environment, 52*(2-3), pp.235-249.

Kleinschroth, F. and Healey, J.R., 2017. Impacts of logging roads on tropical forests. *Biotropica, 49*(5), pp.620-635.

Klimes, P., Idigel, C., Rimandai, M., Fayle, T.M., Janda, M., Weiblen, G.D. and Novotny, V., 2012. Why are there more arboreal ant species in primary than in secondary tropical forests? *Journal of Animal Ecology, 81*(5), pp.1103-1112.

Koju, N.P., Kandel, R.C., Acharya, H.B., Dhakal, B.K. and Bhuju, D.R., 2021. COVID-19 lockdown frees wildlife to roam but increases poaching threats in Nepal. *Ecology and Evolution*, *11*(14), pp.9198-9205.

Kwok, R., 2010. Satellite remote sensing of sea-ice thickness and kinematics: a review. *Journal of Glaciology*, *56*(200), pp.1129-1140.

Laurance, W.F., Goosem, M. and Laurance, S.G., 2009. Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution, 24*(12), pp.659-669.

Laurance, W.F., Camargo, J.L., Luizão, R.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., Stouffer, P.C., Williamson, G.B., Benítez-Malvido, J., Vasconcelos, H.L. and Van Houtan, K.S., 2011. The fate of Amazonian forest fragments: a 32-year investigation*. Biological Conservation, 144*(1), pp.56-67.

Le Duc, J.P., 1996. Trafficking in animals and plants: a lucrative form of crime. *International Criminal Police*, *458*(459), pp.19-31.

Lim, J. and Lee, K.S., 2017. Investigating flood susceptible areas in inaccessible regions using remote sensing and geographic information systems. *Environmental monitoring and assessment*, *189*, pp.1-13.

Lucci Freitas, A.V., Agra Iserhard, C., Pereira Santos, J., Oliveira Carreiral, J.Y., Bandini Ribeiro, D., Alves Melo, D.H., Batista Rosa, A.H., Marini-Filho, O.J., Mattos Accacio, G. and

Uehara-Prado, M., 2014. Studies with butterfly bait traps: an overview. *Revista Colombiana de Entomología*, *40*(2), pp.203-212.

Lugo, A.E. and Brown, S., 1991. Comparing tropical and temperate forests. In *Comparative Analyses of Ecosystems* (pp. 319-330). Springer, New York, NY.

Lundberg, P., Ranta, E. and Kaitala, V., 2000. Species loss leads to community closure. *Ecology Letters*, 3(6), pp.465-468.

Lyra-Jorge, M.C., Ciocheti, G., Pivello, V.R. and Meirelles, S.T., 2008. Comparing methods for sampling large-and medium-sized mammals: camera traps and track plots. *European Journal of Wildlife Research*, *54*, pp.739-744.

Ma, C., Pu, R., Downs, J. and Jin, H., 2022. Characterizing Spatial Patterns of Amazon Rainforest Wildfires and Driving Factors by Using Remote Sensing and GIS Geospatial Technologies. *Geosciences*, *12*(6), p.237.

Maklakov, A.A., Immler, S., Gonzalez-Voyer, A., Rönn, J. and Kolm, N., 2011. Brains and the city: big-brained passerine birds succeed in urban environments. *Biology letters*, *7*(5), pp.730-732.

Mancini, M.C.S., Hintze, F., de Souza Laurindo, R., de Macêdo Mello, R. and Gregorin, R., 2022. Tradition vs. innovation: comparing bioacoustics and mist-net results to bat sampling. *Bioacoustics*, *31*(5), pp. 575-593.

Marzluff, J.M., 2001. Worldwide urbanization and its effects on birds. *Avian ecology and conservation in an urbanizing world*, pp.19-47.

Mekonen, S., 2017. Birds as biodiversity and environmental indicator. *Indicator*, *7*(21).

Mendelsohn, R. and Balick, M.J., 1995. The value of undiscovered pharmaceuticals in tropical forests. *Economic Botany*, 49(2), pp.223-228.

Møller, A.P., 2009. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*, *159*(4), pp.849-858.

Montero, S.A., Ellis, E.A., Ellis, P.W., Manson, R.H., Binnqüist, C.L. and Pérez, J.A.V., 2020. Carbon emissions from selective logging in the southern Yucatan Peninsula, Mexico. *Madera y Bosques, 26*(1), p.2.

Mulatu, K.A., Mora, B., Kooistra, L. and Herold, M., 2017. Biodiversity monitoring in changing tropical forests: a review of approaches and new opportunities. *Remote Sensing*, *9*(10), p.1059.

Myers, G., 2021. Urbanisation in the Global South*. Urban ecology in the Global South. Springer, Cham*, pp.27-49.

Ndlovu, M., Matipano, G. and Miliyasi, R., 2021. An analysis of the effect of COVID-19 pandemic on wildlife protection in protected areas of Zimbabwe in 2020. *Scientific African*, *14*, p.e01031.

Nellemann, C.I.E.C.P., 2012. Green carbon, black trade: illegal logging, tax fraud and laundering in the world's tropical forests*. Green carbon, black trade: illegal logging, tax fraud and laundering in the world's tropical forests.*

Niklaus, P.A., Baruffol, M., He, J.S., Ma, K. and Schmid, B., 2017. Can niche plasticity promote biodiversity–productivity relationships through increased complementarity? *Ecology, 98*(4), pp.1104-1116.

Ozesmi, S.L. and Bauer, M.E., 2002. Satellite remote sensing of wetlands. *Wetlands Ecology and Management*, *10*(5), pp.381-402.

Pace, M.L., Cole, J.J., Carpenter, S.R. and Kitchell, J.F., 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution, 14*(12), pp.483-488.

Padoch, C. and Pinedo-Vasquez, M., 2010. Saving slash-and-burn to save biodiversity. *Biotropica*, *42*(5), pp.550-552.

Paul, B.K. and Rashid, H., 2017. Climatic Hazards in Coastal Bangladesh*. Salinity intrusion and impacts, pp.153-182.*

Park, C.C., 2002. *Tropical rainforests*. Routledge. Oxford.

Pérez-Granados, C., Bustillo-De La Rosa, D., Gómez-Catasús, J., Barrero, A., Abril-Colón, I. and Traba, J., 2018. Autonomous recording units as effective tool for monitoring of the rare and patchily distributed Dupont's Lark Chersophilus duponti. *Ardea*, *106*(2), pp.139-146.

Petchey, O.L., Eklöf, A., Borrvall, C. and Ebenman, B., 2008. Trophically unique species are vulnerable to cascading extinction. *The American Naturalist*, 171(5), pp.568-579.

Pierce, J. and Roosevelt, F.D., 2021. 13. Trees are our past and our future: Lessons from pollution of forests in Australia*. Journal of the Commonwealth Human Ecology Council Spring 2021 Issue 31*, (31), p.47.

Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H. and Pieretti, N., 2011. Soundscape ecology: the science of sound in the landscape. *BioScience*, *61*(3), pp.203-216.

Pillay, R., Venter, M., Aragon-Osejo, J., González-del-Pliego, P., Hansen, A.J., Watson, J.E. and Venter, O., 2022. Tropical forests are home to over half of the world’s vertebrate species*. Frontiers in Ecology and the Environment, 20(1),* pp.10-15.

Pires, S.F. and Clarke, R.V., 2011. Sequential foraging, itinerant fences and parrot poaching in Bolivia. *The British Journal of Criminology*, 51(2), pp.314-335.

Place, S.E. ed., 2001. *Tropical rainforests: Latin American nature and society in transition* (Vol. 2). Rowman & Littlefield. Blue Ridge Summit.

Portela, R. and Rademacher, I., 2001. A dynamic model of patterns of deforestation and their effect on the ability of the Brazilian Amazonia to provide ecosystem services. *Ecological Modelling*, *143*(1-2), pp.115-146.

Pulella, A., Aragão Santos, R., Sica, F., Posovszky, P. and Rizzoli, P., 2020. Multi-temporal sentinel-1 backscatter and coherence for rainforest mapping. *Remote Sensing, 12*(5), p.847.

Püttker, T., Crouzeilles, R., Almeida-Gomes, M., Schmoeller, M., Maurenza, D., Alves-Pinto, H., Pardini, R., Vieira, M.V., Banks-Leite, C., Fonseca, C.R. and Metzger, J.P., 2020. Indirect effects of habitat loss via habitat fragmentation: A cross-taxa analysis of forest-dependent species*. Biological Conservation, 241*, p.108368.

Quesada-Rodríguez, C., Orientale, C., Diaz-Orozco, J. and Sellés-Ríos, B., 2021. Impact of 2020 COVID-19 lockdown on environmental education and leatherback sea turtle (Dermochelys coriacea) nesting monitoring in Pacuare Reserve, Costa Rica. *Biological Conservation*, *255*, p.108981.

Rafiq, K., Appleby, R.G., Edgar, J.P., Radford, C., Smith, B.P., Jordan, N.R., Dexter, C.E., Jones, D.N., Blacker, A.R. and Cochrane, M., 2021. WildWID: An open-source active RFID system for wildlife research. *Methods in Ecology and Evolution*, *12*(9), pp.1580-1587.

Rahman, M.A., 2002. Using mist-nets on canopy walkways in Malaysia to study canopy avifauna. *Raffles Bulletin of Zoology*, *50*(2), pp.499-506.

Rahman, M.S., Alam, M.A., Salekin, S., Belal, M.A.H. and Rahman, M.S., 2021. The COVID-19 pandemic: A threat to forest and wildlife conservation in Bangladesh? *Trees, Forests and People*, *5*, p.100119.

Ralph, C.J., Sauer, J.R. and Droege, S., 1995. *Monitoring bird populations by point counts*. Pacific Southwest Research Station. Albany, California.

Ramos, E.P. and Yamamoto, L., 2018. Deforestation, drought and environmental migration in Brazil: An overview. Routledge Handbook of *Environmental Displacement and Migration,* pp.216-224.

Roy, D.P., Boschetti, L. and Smith, A.M., 2013. Satellite remote sensing of fires. *Fire Phenomena and the Earth System: An Interdisciplinary Guide to Fire Science*, pp.77-93.

Saatchi, S.S., Soares, J.V. and Alves, D.S., 1997. Mapping deforestation and land use in Amazon rainforest by using SIR-C imagery. *Remote Sensing of Environment, 59*(2), pp.191-202.

Sales, L.P., Galetti, M. and Pires, M.M., 2020. Climate and land-use change will lead to a faunal “savannization” on tropical rainforests. *Global Change Biology, 26(12),* pp.7036-7044.

Sánchez, A.C., Salazar, A., Oviedo, C., Bandopadhyay, S., Mondaca, P., Valentini, R., Briceño, N.B.R., Guzmán, C.T., Oliva, M., Guzman, B.K. and Mori, G.M., 2022. Integrated cloud computing and cost-effective modelling to delineate the ecological corridors for Spectacled bears (Tremarctos ornatus) in the rural territories of the Peruvian Amazon. *Global Ecology and Conservation*, 36, p.e02126.

Sethi, S.S., Ewers, R.M., Jones, N.S., Signorelli, A., Picinali, L. and Orme, C.D.L., 2020. SAFE Acoustics: An open-source, real-time eco-acoustic monitoring network in the tropical rainforests of Borneo. *Methods in Ecology and Evolution*, *11*(10), pp.1182-1185.

Shearman, P., Bryan, J. and Laurance, W.F., 2012. Are we approaching ‘peak timber’ in the tropics? *Biological Conservation, 151*(1), pp.17-21.

Sica, F., Pulella, A., Nannini, M., Pinheiro, M. and Rizzoli, P., 2019. Repeat-pass SAR interferometry for land cover classification: A methodology using Sentinel-1 Short-Time-Series. *Remote Sensing of Environment, 232*, p.111277.

Sol, D., González-Lagos, C., Moreira, D., Maspons, J. and Lapiedra, O., 2014. Urbanisation tolerance and the loss of avian diversity. *Ecology Letters*, *17*(8), pp.942-950.

Staal, A., Flores, B.M., Aguiar, A.P.D., Bosmans, J.H., Fetzer, I. and Tuinenburg, O.A., 2020. Feedback between drought and deforestation in the Amazon*. Environmental Research Letters, 15*(4), p.044024.

Sumner, S., Lucas, E., Barker, J. and Isaac, N., 2007. Radio-tagging technology reveals extreme nest-drifting behavior in a eusocial insect. *Current Biology*, 17(2), pp.140-145.

Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, *80*(5), pp.1455-1474.

Tsuji, S.R., McCarthy, D.D. and Quilley, S., 2021. Green Energy—Green for Whom? A Case Study of the Kabinakagami River Waterpower Project in Northern Canada. *Sustainability, 13*(16), p.9445.

United Nations (2022). *Population*. [online] United Nations. Available at: https://www.un.org/en/global-issues/population.

van Solinge, T.B., 2013. Equatorial deforestation as a harmful practice and a criminological issue. In *Global Environmental Harm* (pp. 38-54). Willan. London.

Van Uhm, D., South, N. and Wyatt, T., 2021. Connections between trades and trafficking in wildlife and drugs. *Trends in Organized Crime*, pp.1-22.

Veiga, J.B., Tourrand, J.F., Poccard-Chapuis, R. and Piketty, M.G., 2002. Cattle ranching in the amazon rainforest. *Animal Production*, *24*, pp.253-256.

Vitkalova, A.V., Feng, L., Rybin, A.N., Gerber, B.D., Miquelle, D.G., Wang, T., Yang, H., Shevtsova, E.I., Aramilev, V.V. and Ge, J., 2018. Transboundary cooperation improves endangered species monitoring and conservation actions: A case study of the global population of Amur leopards. *Conservation Letters*, *11*(5), p.e12574.

Vitousek, P.M. and Sanford Jr, R.L., 1986. Nutrient cycling in moist tropical forest. *Annual review of Ecology and Systematics, 17*(1), pp.137-167*.*

Voskamp, A., Baker, D.J., Stephens, P.A., Valdes, P.J. and Willis, S.G., 2017. Global patterns in the divergence between phylogenetic diversity and species richness in terrestrial birds. *Journal of Biogeography*, 44(4), pp.709-721.

Wenhua, L., 2004. Degradation and restoration of forest ecosystems in China. *Forest Ecology and Management, 201*(1), pp.33-41*.*

Wiafe, E.D., 2018. Hunted species and hunting equipment used by rainforest poachers in Ghana. *Journal of Threatened Taxa*, *10*(2), pp.11285-11289.

Wilson, E.O., Peter, F.M., National Academy Of Sciences (U.S. and Smithsonian Institution, 1988. *Biodiversity*. Washington, D.C.: National Academy Press.

Wilson, E.O., 1992. The diversity of life. Allen Lane. *The Penguin Press*, *178*, pp.6-7.

Woodcock, B.A., 2005. Pitfall trapping in ecological studies. *Insect Sampling in Forest Ecosystems*, *5*, pp.37-57.

Wright, T.F., Toft, C.A., Enkerlin-Hoeflich, E., Gonzalez-Elizondo, J., Albornoz, M., Rodríguez-Ferraro, A., Rojas-Suárez, F., Sanz, V., Trujillo, A., Beissinger, S.R. and Brice, A.T., 2001. Nest poaching in Neotropical parrots. *Conservation Biology*, 15(3), pp.710-720.

Wu, D.L., Luo, J. and Fox, B.J., 1996. A comparison of ground-dwelling small mammal communities in primary and secondary tropical rainforests in China. *Journal of Tropical Ecology, 12*(2), pp.215-230.

Young, C.E.F., 2021. The Economics of Tropical rainforest Preservation. In *Oxford Research Encyclopedia of Environmental Science.* Oxford. Oxford.

Yoshimoto, J., Hisamatsu, S.T., Kishimoto-Yamada, K., Hyodo, F., Hashimoto, Y. And Itioka, T., 2015. Faunal studies of sap beetles (Coleoptera: Nitidulidae) in primary and secondary tropical rainforests in the middle reaches of the Baram River Basin, Borneo*. Contributions from the Biological Laboratory Kyoto University,* 30(2), pp.77-84.

Zambolli, A.H., Manzano, M.C.R., Honda, L.K., Rezende, G.C. and Culot, L., 2022. Performance of autonomous recorders to detect a cryptic and endangered primate species, the black lion-tamarin (Leontopithecus chrysopygus). *American Journal of Primatology*, p.e23454.

Zhou, B.N., Baj, N.J., Glass, T.E., Malone, S., Werkhoven, M.C., van Troon, F., David, Wisse, J.H., Kingston, D.G. and Kingston, D.G., 1997. Bioactive labdane diterpenoids from Renealmia alpinia collected in the Suriname rainforest*. Journal of Natural Products, 60*(12), pp.1287-1293*.*

Zuazo, V.H.D. and Pleguezuelo, C.R.R., 2009. Soil-erosion and runoff prevention by plant covers: a review. *Sustainable agriculture,* pp.785-811.

Chapter 2

General Materials and Methods

2.1 Study site

The study was conducted in the Temburong district of Brunei. Brunei is a small country on the northern coast of the island of Borneo, Southeast Asia (Figure 2.1A), with a total land area of 5 765 km^2 (Ahmad, 2014). Situated 4 degrees North of the equator, Brunei has a wet tropical climate, with an annual mean temperature of 27°C and annual rainfall of 2300 - 4000 mm (Becek & Odihi, 2008). Approximately 72% of the land cover is forest (FAO, 2022), principally made up of mixed dipterocarp forest (Becek & Odihi, 2008). Brunei has remarkably pristine rainforest, likely as an indirect effect of the nation's oil-based economy (Ahmad, 2014). Furthermore, Brunei is geographically split into two distinct regions: the districts of Belait, Tutong, and Brunei-Muara to the west and the – until recently – geographically isolated district of Temburong to the East (Figure 2.1B) where the study was conducted.

2.2 Study design

2.2.1 Recording sites

To assess the current impact of infrastructure expansion on biodiversity in Temburong's tropical rainforest environment, we deployed a series of ARUs and camera traps along infrastructure expansion gradients in this district. In total, 27 SongMeter Micros and 3 SongMeter Minis from Wildlife Acoustics were deployed, each of which was paired with a Browning Recon Force Edge 4K camera trap (See Appendix A for equipment details). The recording pairs were set up at 69 randomly generated pre-determined GPS points, created using ArcMaps (details below), along infrastructure pressure gradients. Original grid generation did not take paths into account, as no map data was available on them. Later, in the field, we used existing trails where possible to hike as near as possible to the GPS coordinates without needing to cut trails, before going off trail to navigate closer to the randomly generated point.

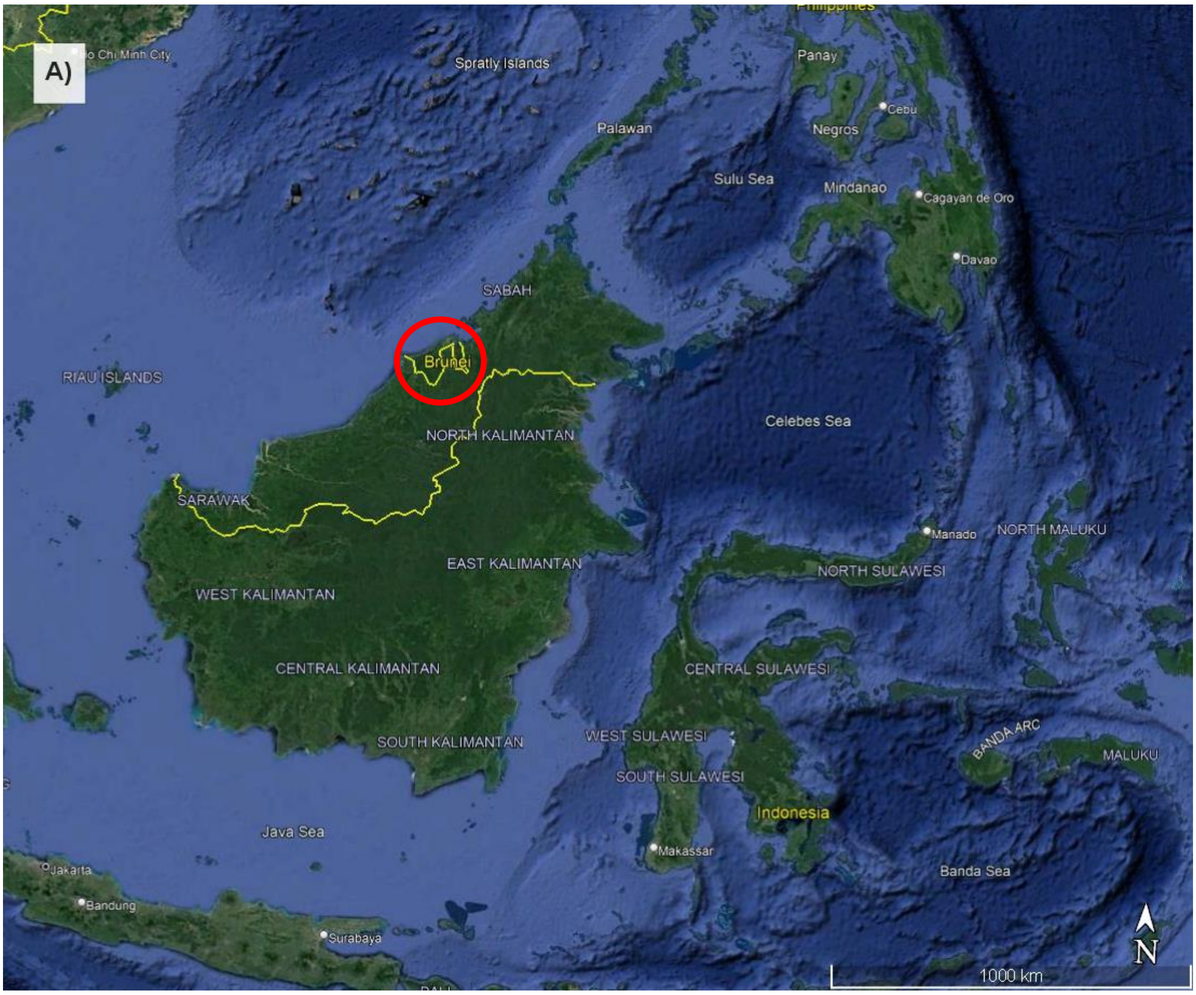
Effects of roads (ecological edge effects, likelihood of roadkill, access for hunters, etc.) can extend kilometres into the forest but generally expected to be strongest closest to the road

(Laurance *et al*., 2009). The study design was therefore created in a way to survey forest patches with varying levels of disturbance by placing the recorders near different types of roads, as well as different distances from these roads (as there could be potential interaction between the two). Thus, the recording sites were stratified to encompass three zones of varying general infrastructure pressure, classified into high, intermediate, and low infrastructure pressure (Figure 2.1C). The zone of high infrastructure pressure (HIP) was defined as the area in which the closest main road is Jalan Labu, a paved and well-maintained highway with 80 km/hour speed limit for most of its length. This road also connects the East and West borders of Temburong as well as Bangar (capital of Temburong) and the SOAS bridge. It is the busiest road in Temburong. The zone of intermediate (or medium) infrastructure pressure (MIP) was defined as the area in which the closest main road was Jalan Batang Duri, a less well-maintained road with a speed limit of 65 km/hour. This road also links Bangar to Batang Duri, the last village accessible by road (when driving South in Temburong, towards Ulu Temburong National Park). This road has less traffic and is less frequently used than the highway. The zone of low infrastructure pressure (LIP) was situated in and around Ulu Temburong National Park and was accessed by boat as there are no roads in this area. Within the HIP and MIP zones, the recording sites were distributed along an infrastructure pressure gradient ranging from beside the road, to further into the forest in order to collect data from across the gradient. As there were no roads in the LIP zone, these study sites were conceived as a baseline with as little impact from roads as possible.

The study design ensured even sampling across the landscape using the *fishnets* function in ArcMaps, where a randomised grid of points was created in each infrastructure pressure zone. Recording sites were designed to be a minimum of 1 km apart (recommendations from Wearn & Glover-Kapfer, 2017), using systematic grid sampling. However, for security reasons, in the LIP zone recording sites were located within sight (no closer than 10m) of the two ‘hiking’ trails along the ridges, created by the Kuala Belalong Field Studies Centre and managed by Universiti Brunei Darussalam. This was a limitation of the study design but movement elsewhere across the landscape was severely restricted due to difficult terrain. Nevertheless, recording sites were placed in such a way as to maximise inter-trap distance.

The placement of some recording sites could not be positioned at the proposed GPS location due to inaccessibility or dangerous terrain. In such circumstances, we navigated as close as possible to the pre-generated GPS point and then positioned the units at the nearest accessible and safe point using the same standard set up method as follows. Both recording units were secured to the nearest suitable tree trunk at circa 2 m and 50 cm from ground level for ARUs and the camera traps respectively (Figure 2.2). Cameras were not placed preferentially along trails, nor pointed at interesting features but we avoided pointing them at obstructions (boulders, tree buttresses, etc). Where possible, we placed them facing the largest field of view, or if an animal trail was present near the chosen tree, then the camera was placed at a 45-degree angle to the trail. If possible, the camera traps were placed facing north or south to reduce light movement of the sun triggering the camera trap. The time needed to deploy recording units was typically 1-3 units per day. Moreover, we had fewer recording units than deployment sites, so individual units were redeployed at multiple sites. Consequently, not all data were collected concurrently causing possible time-dependence between data points. To reduce this effect, we deployed the recording pairs at randomly chosen grid locations, thus ensuring the independence of data points in terms of time.

There are risks that some of the findings might be confounded by the fact that there is spatial autocorrelation in the distribution of the different types of forests (Figure 2.1C). However, there were no alternatives as the different levels of infrastructure pressure were spatially autocorrelated. This was mainly due to the fact that there was only one of each type of road in the study area, limiting site location options. Attempts were made to reduce autocorrelation by deploying recording pairs at sites further west from the secondary main road but this was limited due to access problems and disturbances from quarries and agriculture which were thought to be possible confounding factors. However, due to correlation between some of the environmental variables (See Chapter 3: *section 3.3.4*), infrastructure pressures zones were not kept in the analysis models and a continuous variable (*Distance to Nearest Main Road*) was used instead, reducing these autocorrelative effects.


A)
Ho Chi Minh City
Spratly Islands
Philippines
Panay
Cebu
Negros
Palawan
Sulu Sea
Mindanao
Cagayan de Oro
Davao
SABAH
Brunei
RIAU ISLANDS
NORTH KALIMANTAN
Celebes Sea
SARAWAK
Manado
NORTH MALUKU
NORTH SULAWESI
EAST KALIMANTAN
WEST KALIMANTAN
CENTRAL KALIMANTAN
CENTRAL SULAWESI
WEST SULAWESI
SOUTH KALIMANTAN
BANDA ARC
MALUKU
SOUTH SULAWESI
Indonesia
Java Sea
Makassar
Jakarta
Banda Sea
Bandung
Surabaya
N
1000 km

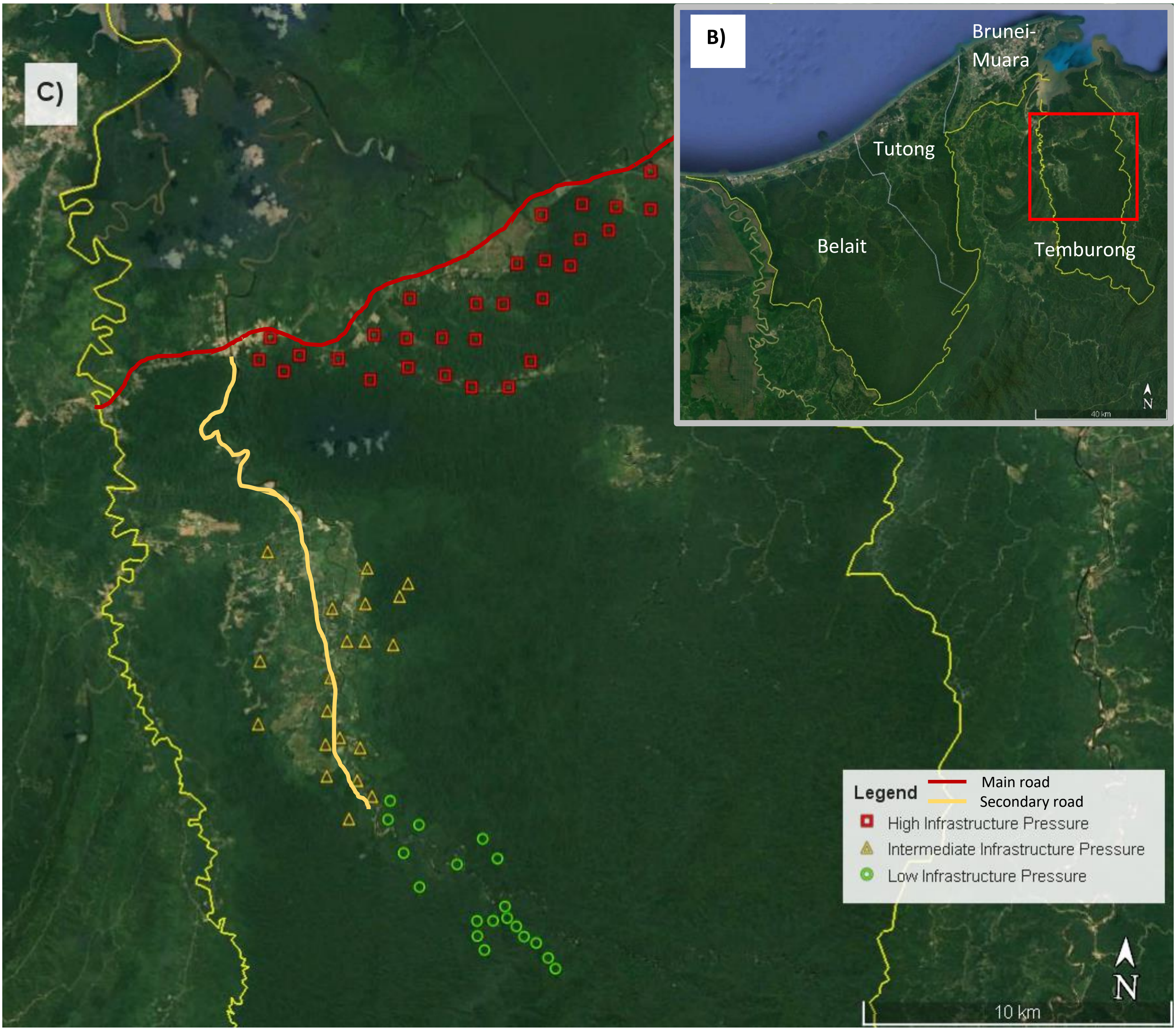


Figure 2.1 Map of study site generated using Google Earth Pro. A) Brunei (indicated by the red circle) is located on the northern coast of the island of Borneo, in South East Asia. B) Brunei has two geographically distinct regions, with the districts of Belait, Tutong, and Brunei-Muara to the west and Temburong to the East. The study site is highlighted with the red box. C) Details of the locations of each recording site (N = 69), with the legend indicating the levels of infrastructure pressure each site was situated in. The coordinates of these points were randomly generated using grid sampling in ArcMaps within each infrastructure pressure zones. A camera trap and ARU were deployed at each of these sites for 30 days. The two study roads are also shown on the map.

Figure 2.2 Photographs of the recording units used in the study namely: A) an Autonomous Recording Unit (SongMeters by Wildlife Acoustics) and B) a camera trap (Browning Recon Force Edge 4K). Recording pairs were deployed at 69 randomly generated recording sites for 30 days, with respective Python locks to prevent theft, at heights of approximately 2m and 50cm above ground level respectively to maximise efficient surveying capabilities.

2.2.2 Sampling protocols and schedules

Autonomous Recording Units

The ARUs were pre-programmed to record at fixed times of day for a fixed amount of time (Table 2.1), with a 44.1 kHz sampling rate and an 18 dB gain (standard settings and recommended for SongMeters to record best quality sound). Studies adopt a variety of different sampling regimes depending on study goal (Bradfer-Lawrence *et al*., 2019; Quinn *et al*., 2022; Towsey *et al*., 2014; Lellouch *et al*., 2014; Sueur *et al*., 2008; Depraetere *et al*., 2012). Bradfer-Lawrence *et al*., 2019 suggested that 120h of recording in tropical environments balanced deployment length whilst capturing enough of the soundscape variability. The battery life for the SongMeters is approximately 122h for our sampling rate and gain settings, which matches well with the optimal recording time. The study showed that continuous recording is more effective at capturing soundscape variability in a shorter amount of time than subsampling. However, studies have also found significant positive correlations between acoustic complexity indices acquired from continuous recordings and recordings where only one in every five or one in every ten minutes were recorded. Moreover, the latter sampling schemes required 80% and 90% less storage space respectively than data derived from continuous recordings (Pieretti *et al*. 2015).

Additionally, acoustic diurnal pattern differs among ecosystems. Indeed, different ecosystems need different sampling schedules to fully capture how acoustic activity changes over time, more precisely over a 24-hour period. Pieretti *et al*. (2015) shows that when there is a high and continuous presence of sounds in an environment, it would be better to have less dense recording regimes as sufficient information will be captured to correctly represent the community. However, in order to capture the diurnal variation of a more unpredictable soundscape, more intense sampling is necessary. A mix of both sampling intensities can be used, especially to capture more information at certain times of day, like dawn and dusk, where acoustic activity is known to peak.

There have been very few eco-acoustic studies in Temburong to date, making it difficult to assess what would be the optimal sampling protocol to capture the soundscape found in this region. However, one study (Monacchi & Farina, 2019) detected most acoustic activity between 10:00 and 18:00. Furthermore, an audio project from the SAFE Project in Sabah, Malaysian Borneo (Sethi *et al*., 2020), detected dawn and dusk choruses as well as differences in the soundscape between the hours of day and night. Given their relatively close proximity and similar habitats, we assumed Temburong’s soundscapes would be broadly similar to that of Sabah’s forest ecosystems. We therefore adopted a sampling protocol that would allow us to survey across all hours of day and nighttime, with an additional focus on dawn and dusk to ensure we captured theses key choruses. Furthermore, given the available evidence on the benefits of audio subsampling, as opposed to continuous recoding, in terms of maximising biodiversity recording (given our ARUs were deployed for 30 days due to pairing with the camera traps), we used a subsampling regime (Table 2.1). This also meant that the audio recordings could run for the entire period of camera trap deployment.

Table 2.1 Sampling schedule used for the Autonomous Recording Units used in this study (SongMeters). The protocol was designed to balance deployment length (limited by battery life and capabilities to store and process the data collected) whilst capturing enough of the soundscape variability to ensure valid representation of the surveyed location. This was further ensured by sampling at all times of day, although an emphasis was brought upon dawn and dusk, where acoustic activity is known to peak. Sunrise and sunset time shifts are horizon-based calculations based on location and shifted to match the selected time-zone.

Time of day	**Recording duration**
Dawn (circa 06:00 during the study period, though recorders were programmed to use daily sunrise data to trigger recordings)	40 mins (20 mins before and after local sunrise time)
Day time (08:00 to 17:00 included)	First 7 mins of the hour
Dusk (circa 18:00 during the study period, though recorders were programmed to use daily sunset data to trigger recordings)	20 mins (10 mins before and after local sunset time)
Night time (19:00 to 05:00 included)	First 7 mins of the hour

Camera traps

The camera traps were deployed at each of the 69 recording sites for a 30-day period, following recommended good practice (Wearn & Glover-Kapfer, 2017). Table 2.2 shows the settings used in the camera traps deployed, following general recommendations from the manufacturer, given their intended use (principally to capture mammals and ground dwelling birds).

Table 2.2 Settings used for deployed camera traps used in this study (Browning Recon Force Edge 4K), deployed at 69 recording sites for 30 days each. Settings were programmed in a way such as to best capture intended targets, namely mammals and ground dwelling birds.

Setting	**Description**
Capture mode: trail	Captures still pictures during day and night time.
Capture delay: 1 second	Shortest possible delay available: does not record images within 1 second of the final image of a previous camera burst (see below for burst setting).
Picture size: low (4 MP)	Set to balance image quality whilst maximising storage.
Multishot mode: 8 rapid fire images (0.3s between each picture)	Burst of 8 images aids detection of animals during image classification stage.
Infra-red flash: fast motion	Fast exposure time is best for fast moving animals (esp. birds).
Info strip on	Provides info on images of camera identifier, date, time etc., which aids downstream data management.
SD card management: off	Ensures oldest pictures are not deleted if the SD card becomes full.

2.2.3 Vegetation surveys

To get a quantitative measure of the habitat at each recording site, a standardised vegetation survey was conducted at each site. The survey consisted of a 20 x 20-meter plot with the camera trap and audio recorder in the centre of the plot. Occasionally (n = 11 sites) a smaller plot was used when terrain precluded assessing a full-sized plot. The plots were then sub-divided into 4 smaller plots to make recording data easier (Figure 2.3). Every tree in the plot with a Circumference at Breast Hight (CBH) greater than 30 cm was measured and the CBH recorded. Above Ground Biomass (AGB) was selected as a quantitative proxy for habitat structure and quality as higher biomass is associated with primary rainforests (Okuda *et al.*, 2004) namely as large trees, found solely in primary forests, make up nearly a quarter of biomass (Laurance *et al.*, 2000). Nevertheless, since we were unable to gather height data for trees, we used the equation provided for estimating AGB when the tree height is unavailable which is thought to be less accurate. We used an allometric equation previously used in tropical forests (below; Chave *et al.* 2014) for estimating AGB:

$$\mathrm{AGB}_{est} = \exp[-1.803 - 0.976E + 0.976\ \ln(\rho) + 2.673\ \ln(D) - 0.0299[\ln(D)]^2]$$

where E is a measure of environmental stress, ρ is wood-specific density (g/cm^3), and D is trunk diameter (cm). E increases with temperature seasonality (time plant is exposed stressful temperature) as well as being influenced by water stress. Chave *et al.* (2014) deemed this model the most appropriate for estimating AGB of tropical trees in the absence of tree height. E values for our recording sites were extracted using a global gridded raster layer and R code provided by Chave *et al.* (2014; http://chave.ups-tlse.fr/pantropical_allometry.htm). As trees at recording sites were not identified to species level, we were unable to get wood-specific density values. Therefore, we used a mean value from a dataset generated from peer-reviewed literature (Phillips *et al.*, 2019) instead. From this, the mean basal-area-weighted mean community wood density for old-growth moist forests in Asia is 0.594 g/cm^3. D values were calculated by dividing the collected CBH measurements by π. Due to tree height not being available and using a mean wood-specific density value, our measure of AGB was likely not precise. Hence, associated results need to be read with some caution.

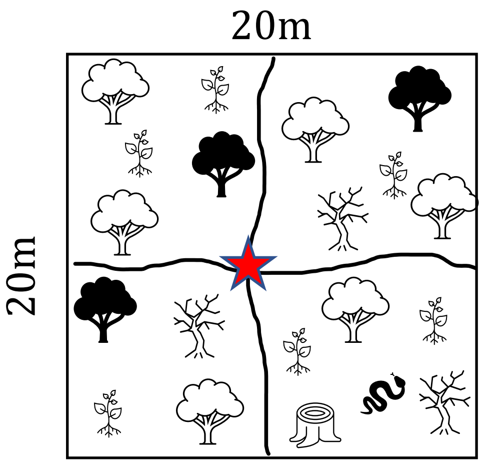


Figure 2.3 Plot set up to conduct the vegetation surveys. A 20x20m plot was measured out at each of the 69 randomly generated recording sites, which was further roughly divided into four smaller subsections using two 20m ropes (represented by the wavy lines) to facilitate data recording, especially when counting the number of trees. The red star indicates the location of the camera trap and ARU within the plot. The recording pair was placed as close to the plot centre as possible but due to the necessity of having to be fixed to a big enough tree (typically > 30 cm in diameter) this was not always perfectly central to the plot.

2.3 Data analysis: pre-processing

2.3.1 Audio data

The sampling regime chosen resulted in, on average, 103.5 hours of recording per site. Due to slight variation in battery life and occasional malfunctions, not all the ARUs recorded for exactly the same number of days. Furthermore, there were occasional shorter-duration malfunctions within the sampling regimes, even for ARUs that otherwise recorded as intended. For example, some ARUs missed occasional time slots which they were programmed to record or recorded slightly shorter clips than they were programmed to. One of the major and most common malfunctions was the length of the dawn recordings. For unknown reasons, many of the ARUs recorded dawn clips of anywhere between 41 to 46 min of dawn audio (as opposed to the 40 min duration they were programmed to record). To standardise the dawn recordings across all sites, the first 40 mins were used in analyses, and the excess time was disregarded. Similarly, some of the ARUs recorded an additional 1 min of audio data after each scheduled recording slot. These were also disregarded. A list of all the malfunctions can be found in Appendix B. However, most of these malfunctions were deemed to be minor and the data from ARUs that had malfunctioned slightly were retained and later standardised in appropriate fashion to the study questions, to avoid excessive data loss.

2.3.2 Camera trap data

As with the ARUs, some of the camera traps malfunctioned or were moved by animals (usually monkeys). Again, a list of all the non-standard recordings is provided in Appendix B. Most of the malfunctions were also deemed to be minor as the majority consisted of the cameras being moved slightly by wildlife, impeded image quality, or excessive photographs being taken, all of which did not prevent the data collected from being used. Thus, the data from the majority of camera traps were retained to avoid excessive loss of valuable data.

2.4 References

Ahmad, A., 2014. The disengagement of the tourism businesses in ecotourism and environmental practices in Brunei Darussalam. *Tourism Management Perspectives*, *10*, pp.1-6.

Becek, K. and Odihi, J.O., 2008. Identification and assessment of factors affecting forest depletion in Brunei Darussalam. *The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences*, *37*(B2), pp.209-214

Bradfer-Lawrence, T., Gardner, N., Bunnefeld, L., Bunnefeld, N., Willis, S.G. and Dent, D.H., 2019. Guidelines for the use of acoustic indices in environmental research. *Methods in Ecology and Evolution*, *10*(10), pp.1796-1807.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C. and Henry, M., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, *20*(10), pp.3177-3190.

Department of Economic Planning and Statistics, Ministry of Finance and Economy, Brunei Darussalam
https://deps.mofe.gov.bn/SitePages/Population.aspx#:~:text=%E2%80%8BLatest%20Highlights%202021,females%20(47.4%20per%20cent).

Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S. and Sueur, J., 2012. Monitoring animal diversity using acoustic indices: implementation in a temperate woodland. *Ecological Indicators*, *13*(1), pp.46-54.

Food and Agriculture Organization of the United Nations. 2022. *Brunei Darussalam*. [online] Available at: <https://www.fao.org/countryprofiles/index/en/?iso3=BRN> [Accessed 6 October 2022].

Laurance, W.F., Delamônica, P., Laurance, S.G., Vasconcelos, H.L. and Lovejoy, T.E., 2000. Rainforest fragmentation kills big trees. *Nature*, *404*(6780), pp.836-836.

Laurance, W.F., Goosem, M. and Laurance, S.G., 2009. Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution*, *24*(12), pp.659-669.

Lellouch, L., Pavoine, S., Jiguet, F., Glotin, H. and Sueur, J., 2014. Monitoring temporal change of bird communities with dissimilarity acoustic indices. *Methods in Ecology and Evolution*, *5*(6), pp.495-505.

Monacchi, D. and Farina, A., 2019. A multiscale approach to investigate the biosemiotic complexity of two acoustic communities in primary forests with high ecosystem integrity recorded with 3D sound technologies. *Biosemiotics*, *12*(2), pp.329-347.

Okuda, T., Suzuki, M., Numata, S., Yoshida, K., Nishimura, S., Adachi, N., Niiyama, K., Manokaran, N. and Hashim, M., 2004. Estimation of aboveground biomass in logged and primary lowland rainforests using 3-D photogrammetric analysis. *Forest Ecology and Management*, *203*(1-3), pp.63-75.

Phillips, O.L., Sullivan, M.J., Baker, T.R., Monteagudo Mendoza, A., Vargas, P.N. and Vásquez, R., 2019. Species matter: wood density influences tropical forest biomass at multiple scales. *Surveys in geophysics*, *40*(4), pp.913-935.

Pieretti, N., Duarte, M.H.L., Sousa-Lima, R.S., Rodrigues, M., Young, R.J. and Farina, A., 2015. Determining temporal sampling schemes for passive acoustic studies in different tropical ecosystems. *Tropical Conservation Science*, *8*(1), pp.215-234.

Quinn, J.E., Schindler, A.R., Blake, L., Kline Schaffer, S. and Hyland, E., 2022. Loss of winter wonderland: proximity to different road types has variable effects on winter soundscapes. *Landscape Ecology*, *37*(2), pp.381-391.

Sethi, S.S., Jones, N.S., Fulcher, B.D., Picinali, L., Clink, D.J., Klinck, H., Orme, C.D.L., Wrege, P.H. and Ewers, R.M., 2020. Characterizing soundscapes across diverse ecosystems using a universal acoustic feature set. *Proceedings of the National Academy of Sciences*, *117*(29), pp.17049-17055.

Sueur, J., Pavoine, S., Hamerlynck, O. and Duvail, S., 2008. Rapid acoustic survey for biodiversity appraisal. *PloS one*, *3*(12), p.e4065.

Taylor, D., 2022, February. Sultan Haji Omar Ali Saifuddien Bridge (Temburong Bridge): span by span deck erection. In *Proceedings of the Institution of Civil Engineers-Bridge Engineering* (pp. 1-24). Thomas Telford Ltd.

Towsey, M., Wimmer, J., Williamson, I. and Roe, P., 2014. The use of acoustic indices to determine avian species richness in audio-recordings of the environment. *Ecological Informatics*, *21*, pp.110-119.

Wearn, O.R. and Glover-Kapfer, P., 2017. Camera-trapping for conservation: a guide to best-practices. *WWF Conservation Technology Series 1(1)*. WWF-UK, Woking, United Kingdom.

Chapter 3

Using the Acoustic Complexity Index to quantify soundscapes across spatial-temporal scales in Temburong’s tropical rainforests

3.1 Abstract

Sound is omnipresent throughout the natural world and is a useful indicator of healthy ecosystem functioning. However, anthropogenic changes, such as infrastructure expansion, are resulting in a shift in soundscapes. New remote surveying technologies, like Autonomous Recording Units (ARUs), and approaches to synthesise acoustic data, such as acoustic indices, can be used to inform biodiversity assessments – despite a lack of consensus surrounding acoustic indices’ ecological accuracy. Using ARUs, we collected audio data at 69 sites across a gradient of tropical rainforests in Temburong, Brunei, which ranged from pristine and remote forest to secondary forests close to human infrastructure. We computed Acoustic Complexity Indices (ACI) across recordings and compared results between *Infrastructure Pressure Zones*. In addition, we assessed the relationship between ACI and time of day, season, woody biomass, and distance to roads/buildings. As ACI has been shown elsewhere to correlate with bird abundance and diversity, we hypothesised scores to be higher in less disturbed areas and during dawn and, to a lesser extent, dusk, when birds are most vocal. Results showed significantly lower ACI scores in the low infrastructure pressure zone, with highest scores found in zones of intermediate infrastructure pressure. ACI declined significantly from midnight to midday and then increased again thereafter. ACI also declined significantly as distance to road increased and as the season progressed. Hence, many of our results were in the opposite direction to what we had initially hypothesised. We did, however, observe a marked diurnal pattern in ACI across all sites, with highest ACI variability at dawn. Higher ACI scores near roads could indicate dominance of highly vocal edge-dwelling species and/or an ecotone effect, whereby soundscapes are more complex due to a combination of vocalisations from both forest and non-forest species. It could also be that species are increasing their vocalisations to compensate against anthropogenic noise pollution to avoid masking, but this is unlikely given the low traffic volumes at most sites. This preliminary acoustic evaluation provides useful baseline information regarding the soundscapes on Bruneian forests.

3.2 Introduction

The natural world is full of sights and sounds of particular importance to the organisms that live within it. As a visually dominant species, humans often underestimate the magnitude of the role sound plays in many ecosystems. From guiding fry towards coral reefs in tropical oceans (Arvedlund & Kavanagh, 2009) and echolocation helping mammals navigate (Thomas *et al.*, 2004), to defending territories (Amorim & Neves, 2008; Pröhl, 2005; Wheeldon *et al.*, 2021) and attracting mates (Lindström & Lugli, 2000; Thomson & Bertram, 2014; Weisman & Ratcliffe, 2004), the presence of sound in nature is vital to maintain healthy ecosystem functioning. Pristine, intact habitats are often associated with more complex ecological communities, comprising both soniferous (sound producing) and non-soniferous organisms, than disturbed environments (Farina *et al.*, 2021; Watson *et al.*, 2018). Anthropogenic impacts on wildlife and their habitats are far-reaching and pervasive, with fast-paced development being entrenched in modern society. Humans are indirectly causing a global shift in the biophony (sounds produced by non-human living organisms) either by forcing species to radically change their acoustic signals (Brumm & Slabbekoorn, 2005; Dooling & Popper, 2016; Potvin *et al.*, 2011; Slabbekoorn & Peet, 2003), silencing them (Carson, 1962), or by driving them to extinction. One of the major factors inducing these negative changes is urbanisation and infrastructure expansion. Urban areas typically have less diverse habitats than non-disturbed areas, leading to habitat homogenisation (Andersson, 2006). Furthermore, urbanisation and infrastructure expansion frequently result in habitat fragmentation, further isolating ecosystems and reducing their resilience (Theodorou, 2022). Some species find such conditions inhospitable and struggle to adapt or are prone to human disturbance and hence avoid such areas, even if suitable habitat exists (Suraci *et al.*, 2021). Considering the pace of global urbanisation and the already-vulnerable status of wildlife worldwide, it is crucial to develop rapid monitoring strategies.

The very attribute of nature we are altering – biophony – can be used to study it, and ultimately aid in conservation decision-making. Eco-acoustics, the study of sound from a biological and ecosystem perspective, is a rapidly developing field of ecology in which audio recordings are used to answer ecological questions (Sueur & Farina, 2015). Audio recordings are typically acquired using Autonomous Recording Units (ARUs) which can be deployed for long periods of time in the field and record their surroundings. Thus, the audio data does not consist exclusively of the biophony, but rather is representative of the soundscape of that particular environment. A soundscape is the whole acoustic environment of a site – much like the landscape is the physical environment of a site – and consists of the biophony as well as the geophony (sounds produced by abiotic factors) and the anthrophony (sounds produced by human activities) (Pijanowski *et al.*, 2011). By analysing the soundscape, it can be possible to assess the state of biodiversity at a given location, as high acoustic activity has been correlated with high ecosystem structural complexity (Mammides *et al*., 2017). However, this is an indirect measurement as not all organisms produce acoustic signals and therefore some are acoustically indetectable. The use of eco-acoustics for biodiversity assessment uses soniferous species as bioindicators, as their presence is often dependant on that of other organisms (Farina *et al*., 2021). Various analytical tools can be used to extract information of interest from large audio datasets, with acoustic indices being a commonly applied approach to summarise the soundscape.

Acoustic indices are powerful yet simple metrics which describe the ‘acoustic energy’ in an audio recording through reducing the complexity of an audio clip to a single score (Sueur *et al*., 2014), simplifying comparison among audio files. Over 60 acoustic indices have been developed in recent decades, each measuring slightly different aspects of the audio file, and correlating with slightly different aspects (Bradfer-Lawrence *et al*., 2019). Most focus on extracting ecologically relevant parameters of the soundscape, providing a means to rapidly analyse large audio datasets, with the potential to inform about biodiversity at sites. The use of acoustic indices in biodiversity assessments assumes that ecosystems with a greater number of soniferous species will also have greater acoustic diversity, thus indicating higher biodiversity levels. Additionally, changes in soundscapes often reflect changes in ecosystem health (Tucker *et al*., 2014). Hence, monitoring soundscapes could provide information for proactive conservation strategies. The use of acoustic indices to quantify biodiversity or biodiversity change is still in its infancy and many studies using such indices have proven inconclusive or inconsistent (Alcocer *et al*., 2022). This may be due a lack of consistent guidelines being applied (Bradfer-Lawrence *et al*., 2019) but may also indicate that there is not always a correlation between acoustic and biological diversity (Alcocer *et al*., 2022). Nevertheless, acoustic indices have a lot of potential in biodiversity monitoring.

Although tropical rainforests soundscapes have been subject to several studies over the past decade, there remains a gap in the literature surrounding this ecosystem’s acoustic communities due to the relative novelty of the field of bioacoustics. Nevertheless, ARU technology has helped piece together and study in more detail than ever before the different elements which contribute to the soundscape: from biotic – birds (de Camargo *et al*., 2019; Goyette *et al*., 2011), mammals (de Oliveira *et al*., 2015; Heinicke *et al*., 2015; Kalan *et al*., 2015), anurans (Anunciação *et al*., 2022; Lapp *et al*., 2021), and insects (Symes *et al*., 2022) – and abiotic – namely rain (Kumagai & Kume, 2012; Metcalf *et al*., 2020) – elements, to anthropogenic noises caused by proximate human activity – such as poaching (Katsis *et al*., 2022). Temporal patterns have been explored in tropical rainforest soundscapes, but results vary greatly geographically and are sensitive to changes in habitat (Burivalova *et al.*, 2019, 2022; Retamosa Izaguirre *et al.*, 2021).

One of the most used acoustic indices is the Acoustic Complexity Index (ACI), which was initially developed by Farina and Morri (2008) and further tested by Pieretti *et al.* (2011). The ACI was created to “produce a direct and quick quantification of bird vocalizations by processing the intensities registered in audio-files” (Pieretti *et al.*, 2011). In other words, ACI is thought to significantly correlate with species richness for some taxa, although some studies found little to no correlation (Metcalf *et al.*, 2021). This is partly because ACI, like most other acoustic indices, is a new method for analysing bioacoustics data and therefore is still to be fully explored and the metric’s true meaning realised. Due to its focus on birds, its widespread use, and its ease of computation, we chose to use the ACI to quantitatively describe the soundscapes across our recording sites in the tropical rainforests of Temburong, Brunei. The primary aim of this chapter is to conduct a preliminary acoustic evaluation of the soundscape of these areas and to explore the environmental factors influencing the soundscapes.

We hypothesised *a priori* that the following patterns in acoustic complexity would occur in our tropical forest study systems:

(1) That acoustic complexity would be low during darkness as a result of a small number of dominant invertebrates contributing to the soundscape.
(2) That acoustic complexity would reach a maxima around dawn, with a secondary peak at dusk, when many birds and mammals vocalise, and fall to a diurnal minima at midday, associated with high temperatures and a consequent lack of activity by species.
(3) That acoustic complexity would be higher in less disturbed areas, where a more complex habitat supports a higher number of species.
(4) That relatively little variation in acoustic complexity would occur across the study period (circa 6 months), after controlling for diurnal patterns and environmental factors, due to the lack of distinct seasonality over this period.

3.3 Methods

3.3.1 Data collection

For details on the study site, sampling protocols, and general data pre-processing, see Chapter 2.

3.3.2 Acoustic Complexity Index calculation

Standardising audio file length

The inconsistency of file length used in various acoustic indices studies (ranging from 30s to 60 mins) suggests there is no consensus in the literature about the optimum duration or scheduling of audio recordings for biodiversity assessments (Bradfer-Lawrence *et al*., 2019; Buxton *et al*., 2018; Depraetere *et al*., 2012; Fairbrass *et al*., 2017; Pieretti & Farina, 2013; Towsey *et al*., 2014). A key factor however is that all recordings are of the same duration in order for their scores to be comparable. The day and night recording durations in our study were typically 7 minutes in length (Chapter 2), thus this length was chosen as it would limit data pre-processing time, as only dawn and dusk files would have to be reformatted. Dawn and dusk recordings, which were 40 mins and 20 mins in duration respectively, were subsampled into equivalent 7 min clips. Any files affected by deviations from the recording protocol (See Appendix B) were removed to ensure all audio files used were the same duration.

ACI computing

ACI assumes that, typically, the intensity of biotic sounds is intrinsically variable, compared to many anthropogenic sounds which tend to be of constant intensities (Pieretti *et al.,* 2011). ACI measures community activity by measuring the variability in sound intensities by comparing short-time averaged changes in acoustic energy across frequency and time periods (Bateman & Uzal, 2022). The ACI is calculated using a relatively simple formula based on a matrix of intensities taken from the spectrogram which is divided into temporal and frequency bins. The ACI then computes the absolute difference between two adjacent values of intensity within a frequency bin before adding up all these differences found in each temporal bin. To both reduce the effect of the distance of the birds to the recorder and get the relative intensity, the result is divided by the total sum of the intensity values in each temporal bin. Thus, ACI is obtained for each temporal and frequency bin. The ACI is then calculated for all temporal and frequency bins in the recording together (Pieretti *et al.,* 2011). A high ACI value theoretically indicates high acoustic energy whereas a low ACI value would tend to represent a quiet soundscape. We used R to compute the ACI score of each file using the *ACI*() function of the package *seewave* (Sueur *et al*., 2008). All settings for the *ACI()* function were left at their default mode.

Removing rainy files

Geophony, specifically heavy rain and dripping of water droplets, is known to bias ACI results by producing very high ACI scores for files that do not contain high biophonic acoustic diversity (Sánchez-Giraldo *et al*., 2020). Heavy rain was common in our recordings: it was usual for it to rain very heavily almost every day during the deployment period. Hence, to avoid this skewing the results, we removed the data points we deemed were biased by rain. Although research has been done to automate this process using Power Spectrum Density (amplitude) and Signal-to-Noise Ratio thresholds at certain frequency bands (Metcalf *et al*., 2020), due to software incompatibility issues we were not able to apply this method. Instead, we used a similar threshold-based method. To remove the rainy files from our ACI dataset we listened to (and viewed spectrograms of) a sample of audio files (>15 files at each score band), starting from the highest scoring file (372.9) and working our way down to the lower scores by increments of 10 until the score 200, then increments of 5 until the score 175, and then increments of 1 until rainy files appeared mainly absent, to ensure we found the most accurate cut off point. Listening to every file was not viable as there were over 4 033 files between the highest score and the rain threshold. Files containing rain were obvious visually (Figure 3.1) and confirmed auditorily. We determined a threshold ACI score of 160, where files with a score equal to or larger than this were highly likely to contain heavy to moderate rain, and files with a smaller score were unlikely to contain rain. This approach removed the majority of the rainy files which would bias the results, whilst keeping the truly high scoring files.

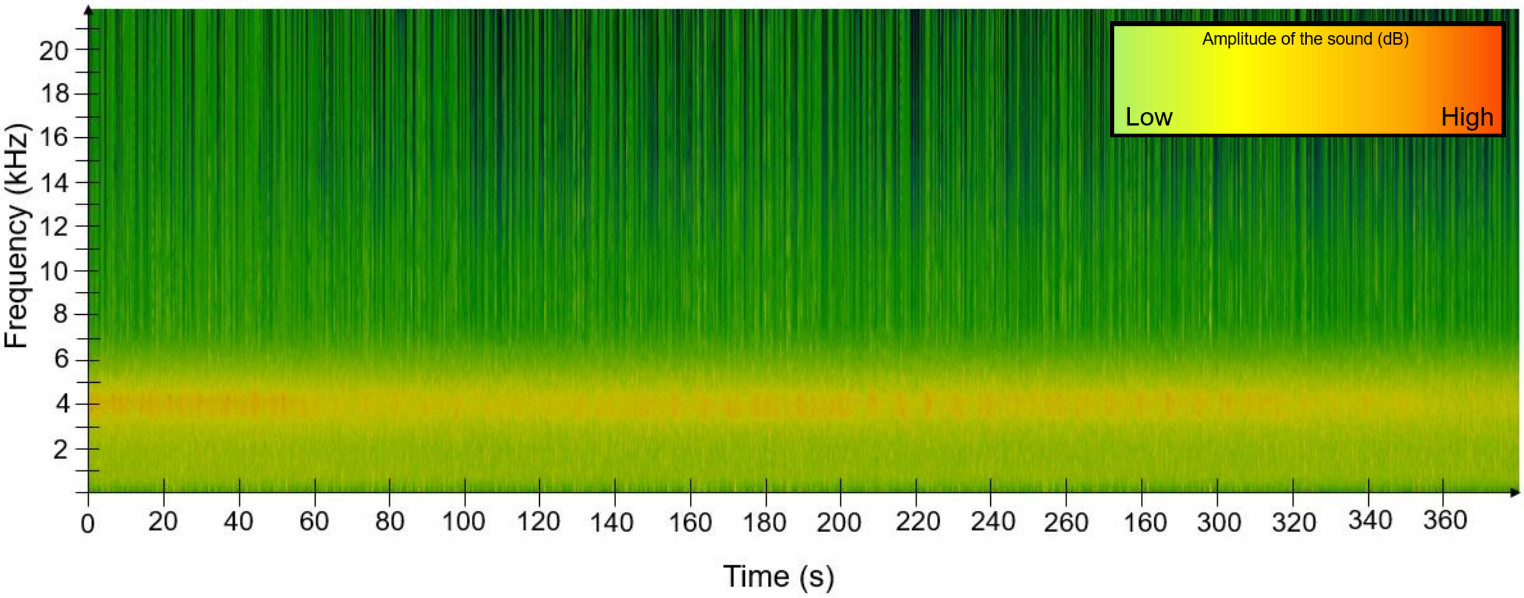


Figure 3.1 A sample spectrogram of an audio file containing heavy rain, made using Kaleidoscope Pro, the acoustic analysis software used in this study. The audio file was recorded using an Autonomous Recording Unit, more specifically a SongMeter. The vertical lines and 'busy' sonic environment present in the sonogram are typical of an audio file containing rain.

3.3.3 Habitat variables

Six habitat variables were initially measured: *Distance to Nearest Main Road, Distance to Nearest Road, Nearest Road Type, Distance to Nearest Building, Infrastructure Pressure Zone,* and *Above Ground Biomass*, which are described in more detail below.

i) *Distance to Nearest Main Road* was measured using the *Ruler (line)* function in Google Earth Pro and defined as being the shortest linear path between the site and a main road. The three main roads in the study region were Jalan Labu, Jalan Batang Duri, and the track that continued from the terminus of Jalan Batang Duri proper.

ii) The *Distance to Nearest Road* was measured using ArcMap and was defined as the shortest linear path between the site and the nearest road, no matter the size.

iii) The *Nearest Road Type* variable was assigned to each site based on the nearest main road (Jalan Labu = highway; Jalan Batang Duri = secondary main road; or track = track at the end of Jalan Batang Duri).

iv) The *Distance to Nearest Building* was also measured using ArcMaps and was defined as the shortest linear path between the site and a human built shelter.

v) Each ARU site was allocated to an *Infrastructure Pressure Zone* (High Infrastructure Pressure = HIP; Medium Infrastructure Pressure = MIP; Low Infrastructure Pressure = LIP), which was the structured component of the stratified random ARU deployment protocol (Chapter 2) and was based on what the nearest road type was (highway = HIP; secondary main road = MIP; track = LIP).

vi) Above ground woody vegetation biomass (henceforth *Biomass*) was calculated as described in Chapter 2 and was used as a proxy for habitat type and quality.

3.3.4 Habitat variable correlation

A Pearson correlation test was conducted to test the correlation between continuous variables (*Distance to Nearest Main Road, Biomass, Distance to Nearest Road,* and *Distance to Nearest Building*). Results (Appendix C: *Table 3C.1*) show that the variable *Distance to Nearest Main Road* and the variable *Distance to Nearest Road* were significantly associated. As multicollinearity is an issue in regression models, we chose to keep *Distance to Nearest Main Road* as we believed this would have a greater disturbance impact than nearest roads, which could be smaller roads or driveways used by few cars.

A Pearson's Chi-squared test was conducted to test the association between categorical variables (*Nearest Main Road Type* and *Infrastructure Pressure Zone*). The two variables were highly associated (χ^2 (4) = 131.27, $p < 2.2^{-16}$; Appendix C: *Table 3C.2*). We chose to keep *Nearest Main Road Type* as this was considered more indicative of the human disturbance at a site than *Infrastructure Pressure Zone*.

An ANOVA was conducted to test the association between the remaining continuous and categorical variables (*Distance to Nearest Main Road, Biomass,* and *Distance to Nearest Building,* and *Nearest Main Road Type*). The ANOVA showed that *Distance to Nearest Main Road* and *Nearest Main Road Type* were significantly associated ($F(2, 66) = 26.56$, $p = 3.45^{-09}$). However ANOVA also showed that *Biomass* and *Nearest Main Road Type* were not significantly associated ($F(2, 66) = 1.69$, $p = 0.19$), and also that *Distance to Nearest Building* and *Nearest Main Road Type* were not significantly associated ($F(2, 66) = 3.04$, $p = 0.05$). Nevertheless, *Nearest Main Road Type* was discarded due to its significant association with the key variable *Distance to Nearest Main Road* (Appendix C: *Figure 3C.1*).

Due to high association between many of these variables (see below), only *Distance to Nearest Main Road, Distance to Nearest Building,* and *Biomass* were retained as potential explanatory variables and used in the main model during statistical analysis. These three variables were chosen as they were deemed to be the most relevant to the research question.

3.3.5 Time variables

Two time variables were incorporated in the analyses: Time of Day and Julian Day. Time and date information were both extracted from the meta data associated with the audio files' names. The Julian day was the continuous count of days since the beginning of the study period.

3.3.6 Statistical analysis

All statistical analyses and graphics were undertaken in R version 4.1.2 (R Core Team, 2022). To investigate the impact of infrastructure expansion (measured by distances to nearest main roads, buildings, and biomass) and time (time of day and Julian day) on the ACI scores, we fitted a Linear Mixed Effects model using the *lme()* function, with *Site* as a random effect and *Distance to Nearest Main Road, Distance to Building, Biomass, Time of Day,* and *Julian Day* as dependant variables. We fitted *Site* as a random effect as we were not interested in the effect of *Site* on ACI but rather the effect of the independent environmental variables across sites, so we needed to account for that variation. Due to the non-linearity of vocalisation changes through the diurnal cycle, the *Time of Day* variable was transformed to be measured as a modular deviation from mid-day (halfway between dawn and dusk – here, 12pm). This fitted the typical observed pattern of the ACI data and allowed for easier model interpretation than using a polynomial term.

Additionally, we tested for statistical differences between the values of ACI calculated for each *Infrastructure Pressure Zones* (See Chapter 2: *Figure 2.1C*) using another linear mixed effect model (*lme()* function) with *Site* as a random factor. The effect of this variable on ACI was tested separately due to the high association between *Infrastructure Pressure Zones* and *Distance to Nearest Main Road* variables (See above). A mixed effect model was chosen instead of an ANOVA as the assumptions of an ANOVA test were not met: the data within each infrastructure pressure zone group was sub-grouped by site, and thus violated the assumption that the data are independent.

3.4 Results

Overview

ACI scores ranged from 372.9 (containing rain) to 121.6 (Figure 3.2). After the data truncation at 160, the ACI scores of 53 715 audio files were used in the analyses (LIP n = 16 349; MIP n = 13 728; HIP n = 23 638). Some example spectrograms of files with a mid-range ACI score are provided for reference (Figure 3.3 & 3.4).

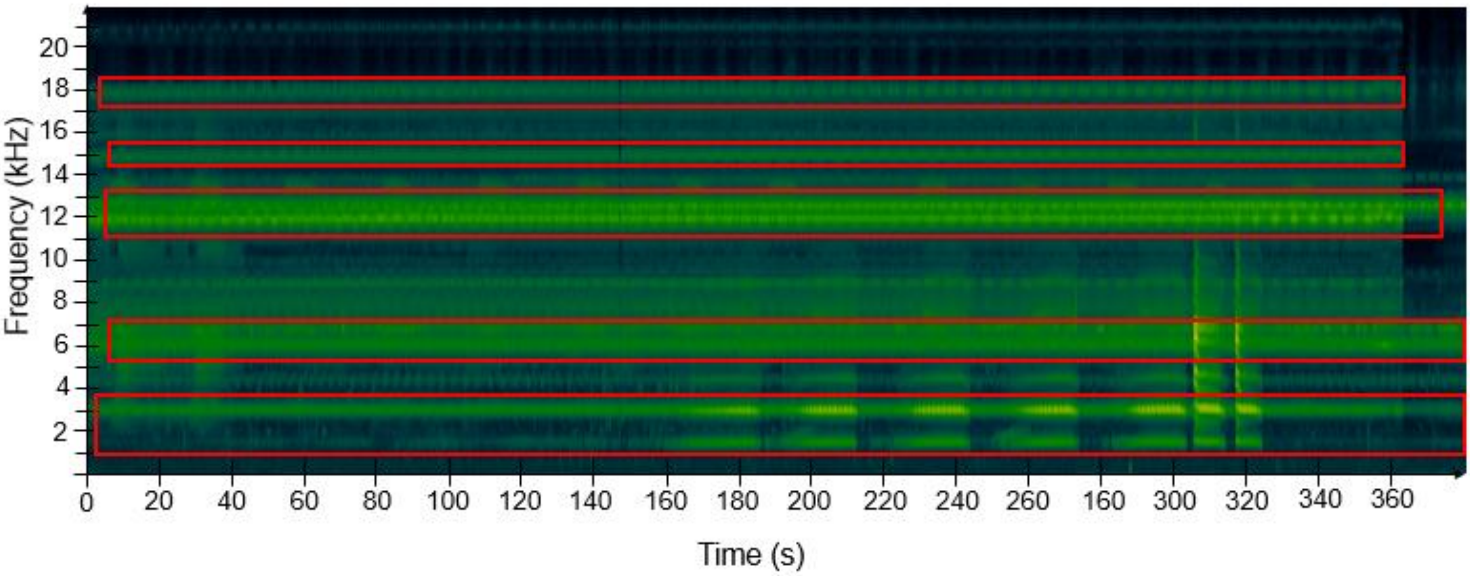


Figure 3.2 Spectrogram of the audio file with the lowest ACI score of 121.6, recorded during the daytime at a Low Infrastructure Pressure site. The spectrogram was generated using Kaleidoscope Pro, the acoustic analysis software used in this study. The constant-frequency sounds present in the recording are insect stridulations (sounds made by rubbing together special bodily structures) which can be seen at multiple frequency bands (indicated by the red boxes).

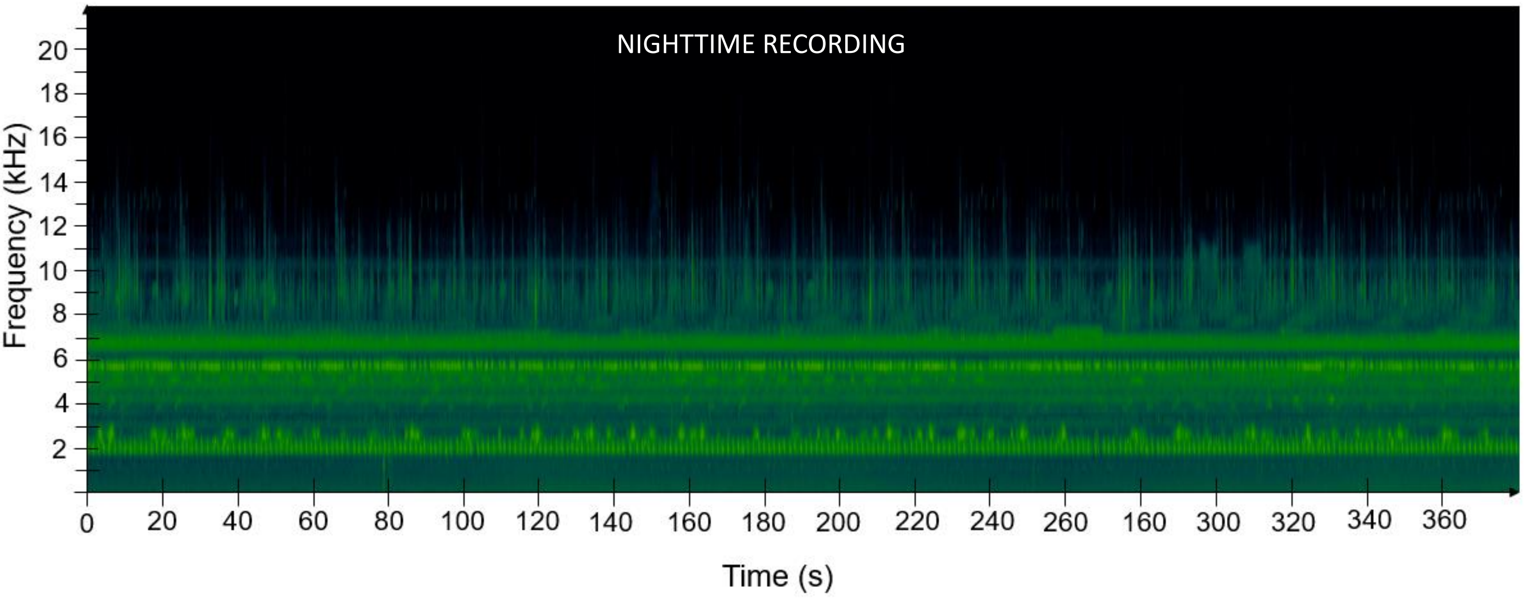


Figure 3.3 Example spectrogram of an audio file with a mid-range Acoustic Complexity Index score of 150.4, showing a typical nighttime soundscape, recorded at a Low Infrastructure Pressure site. The spectrogram was generated using Kaleidoscope Pro, the acoustic analysis software used in this study.

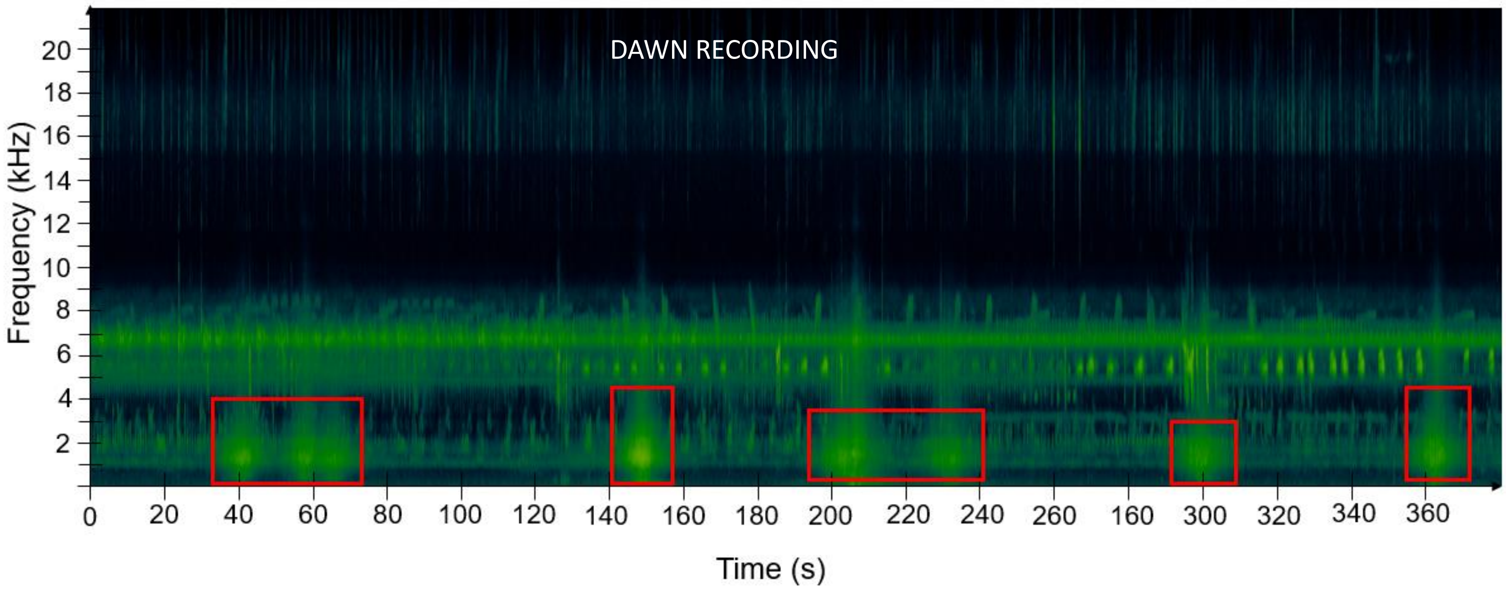


Figure 3.4 Example spectrogram of an audio file recorded at dawn at a High Infrastructure Pressure site with a mid-range Acoustic Complexity Index score of 150.4. The spectrogram was generated using Kaleidoscope Pro, the acoustic analysis software used in this study. The red boxes indicate the noise produced by the passing of a car. The constant-frequency insect stridulations (sounds made by rubbing together special bodily structures) can be seen between 6-7 kHz.

Distribution of the ACI data

Although the ACI data were slightly left-skewed (Figure 3.5A), this was likely due to the truncation of the dataset at 160 to avoid bias by rain. The distribution of all ACI scores (including those computed for rainy files) is shown in Figure 3.5B. Thus, the data were deemed normally distributed.

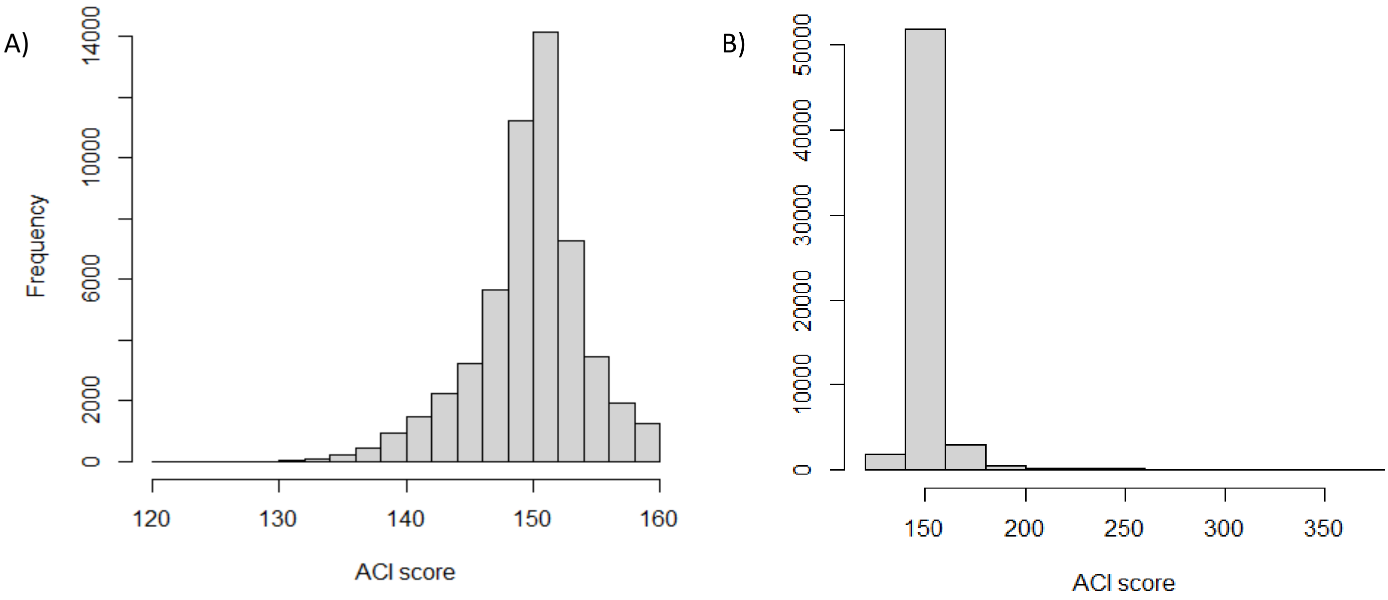


Figure 3.5 Distribution of the Acoustic Complexity Index (ACI) scores across all 69 recording sites A) truncated at 160 ACI to avoid bias by rain-dominated recordings B) including all files. Rain dominated files typically have very high ACI score as a result of the busy sonic environment created by the rain. However when using ACI to assess biodiversity levels through animal produced sounds, this can bias the results. Therefore it can be beneficial to remove rainy files from the analysis, as done in this study.

Model results

The linear mixed effect model, with S*ite* as a random effect, indicated that ACI scores were related to both *Time of Day* and *Distance to Nearest Main Road* (Table 3.1). By contrast, *Julian Day*, *Distance to Building*, and *Biomass* did not significantly impact ACI scores (Table 3.1). This model was slightly under-dispersed (dispersion statistic = 0.998).

Time of Day had a significant positive relationship with ACI, meaning that there was a significant decline in ACI from midnight to midday and a significant increase of ACI from midday to midnight (t-value = 127.17; Table 3.1; Figure 3.6), for example with ACI increasing from 100 to 103.72 over a period of 6 hours from midday to midnight and decreasing from 100 to 96.28 over a period of 6 hours from midnight to midday. Individual graphs of ACI variation were made for each key time of day (dawn, daytime, dusk, and night-time) (Figure 3.7) to enable differences between individual sites to be represented graphically and to avoid masking of trends when amalgamating all the times of day into one graph. *Distance to Nearest Main Road* had a significant but weakly negative relationship with ACI (t-value = -2.71; Table 3.1; Figure 3.8 & 3.9), for example with ACI decreasing from 100 to 99.81 for each 10-kilometre increase of distance from the nearest main road. *Julian Day* was also weakly negatively related to ACI scores (Table 3.1; Figure 3.10). Due to marked diurnal patterns and to avoid masking trends in the data, the variation of ACI scores according to *Distance to Nearest Main Road* and *Julian Day* were only shown graphically for a sub-selection of times of day (i.e. 8am and midnight for *Distance to Nearest Main Road*, and 8am for *Julian Day*). Two times of day were chosen for *Distance to Nearest Main Road* to account for possible variation in traffic through the day.

Table 3.1 Statistical results from the Linear Mixed Effect Model with *Site* as a random effect applied to the Acoustic Complexity Index (ACI) score data. ACI scores were calculated in R for each audio recording in the dataset used. AIC was 292970.2. R^2 (conditional) = 0.29. Random effect (Site): Standard Deviation: Intercept = 1.02; Residual = 3.69. Significant effects are shown in green ($p < 0.05$). Distance to building is the distance between each site and the nearest building, distance to nearest main road is the distance between each site and the nearest main road to that site, and biomass is the total above ground biomass calculated using an allometric equation previously used in tropical forests in conjunction with data collected in the field. The distance variables were measured using Google Earth Pro. The time variables (Julian day and time of day) were deducted from the metadata in the audio files.

	Estimate	**Standard Error**	**DF**	**t-value**	***p*-value**
(Intercept)	147.05	3.05^{-1}	53642	481.50	<0.0001
Distance to Building	-0.29^{-4}	1.97^{-4}	65	-1.48	0.1437
Biomass	-0.01^{-5}	1.05^{-5}	65	-0.91	0.3644
Julian Day	-3.01^{-3}	1.64^{-3}	53642	-1.83	0.0672
Distance to Nearest Main Road	-0.19^{-4}	0.07^{-3}	65	-2.71	0.0087
Time of Day	0.62	4.91^{-3}	53642	127.17	<0.0001

The linear mixed effect model, with *Site* as a random effect, for ACI scores across different *Infrastructure Pressure Zones* indicated that the ACI scores from the Low Infrastructure Pressure Zone were significantly lower than those from the Medium Infrastructure Pressure Zone (Estimate = 1.46 ± 0.32; DF = 66; t-value = 4.52; *p*-value <0.0001) and High Infrastructure Pressure Zone (Estimate = 0.95 ± 0.29; DF = 66; t-value = 3.25; *p*-value ≤ 0.0018) but that ACI scores from the Medium Infrastructure Pressure Zone were not significantly higher than those from the High Infrastructure Pressure Zone (Estimate = 0.56 ± 0.30; DF = 66; t-value = 1.7; *p*-value ≤ 0.0860). These trends can be seen in Figure 3.7.

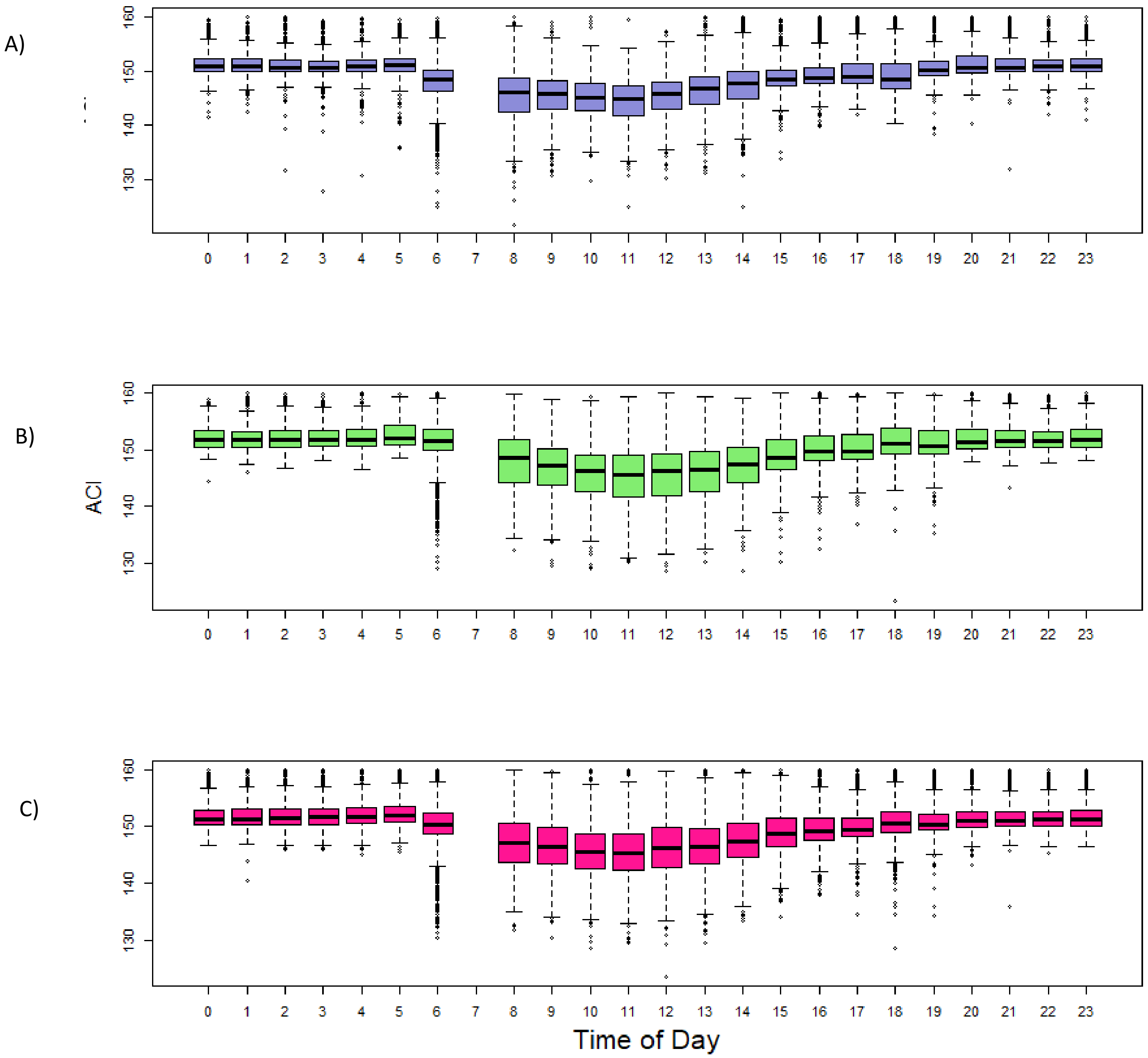
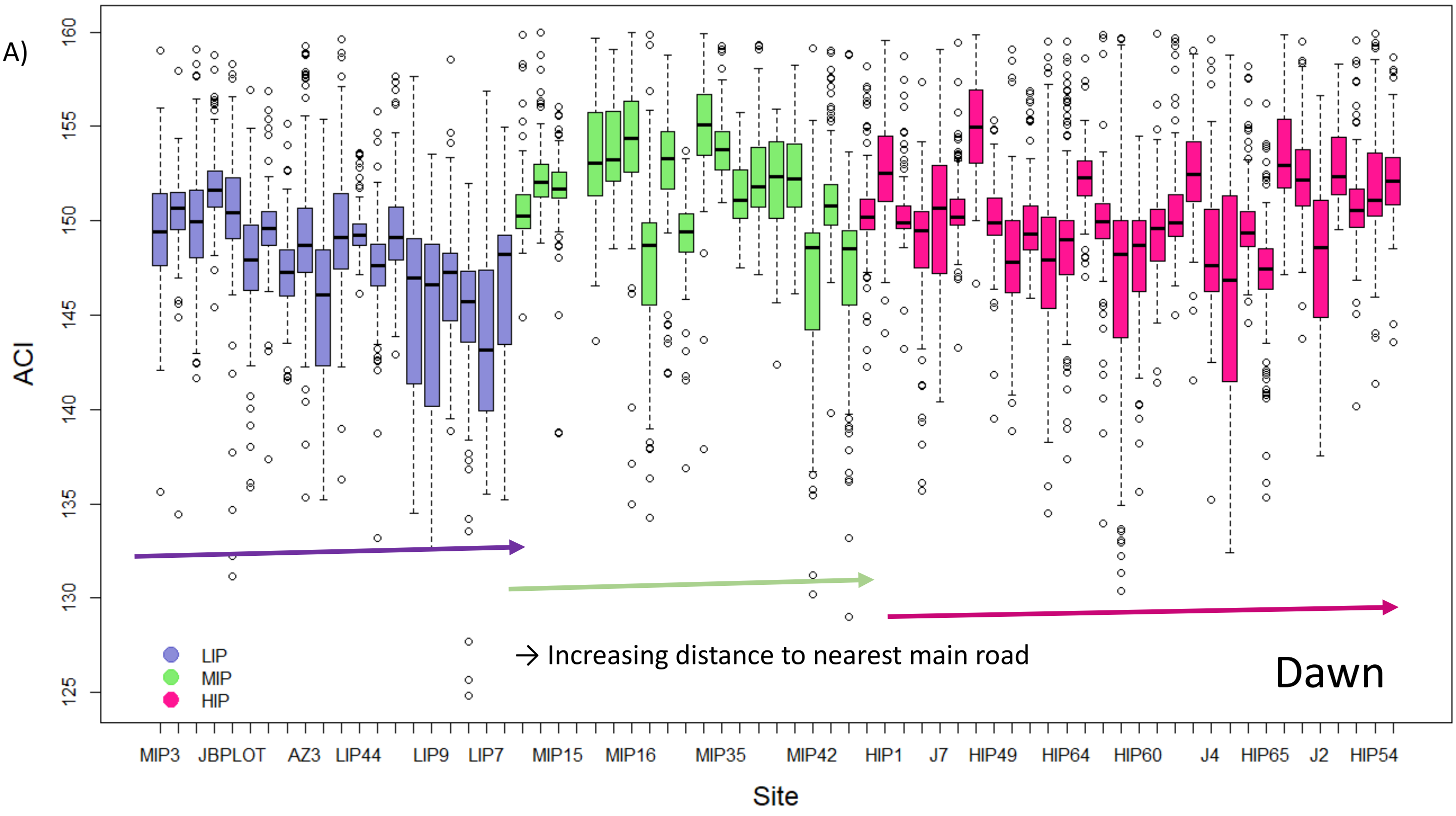
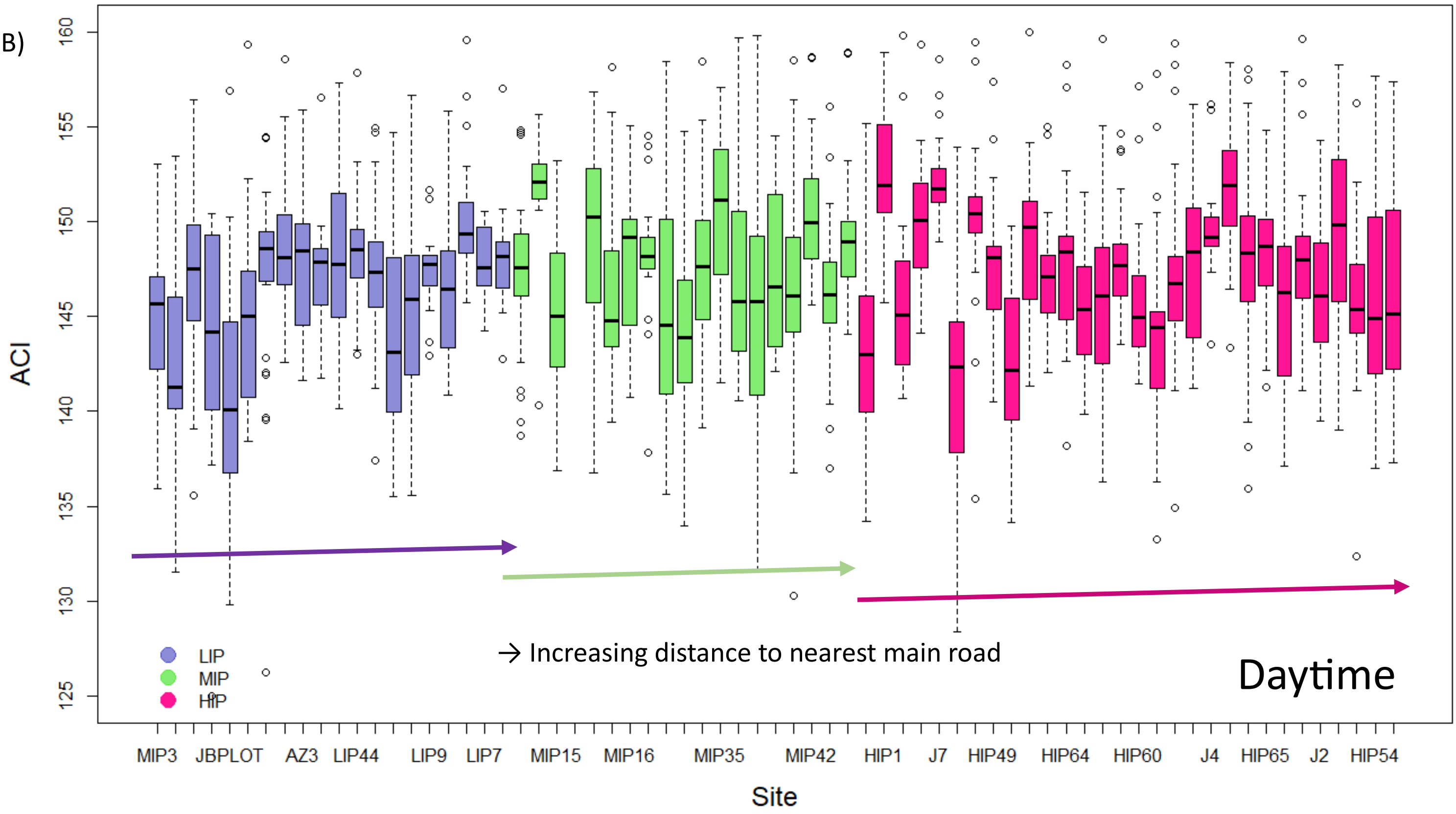


Figure 3.6 Diurnal patterns of the variation of Acoustic Complexity Index (ACI) scores over the 24h period (except 7am, as indicated by the dotted red lines, as this was not included in our recording protocol) across all 69 recording sites, grouped by *Infrastructure Pressure Zones*: A) Low Infrastructure Pressure Zone B) Medium Infrastructure Pressure Zone C) High Infrastructure Pressure Zone. Colours are the same as the ones in Figure 3.7 to facilitate comparison. ACI scores were calculated for each audio file in the dataset using R. Audio files including heavy rain were excluded from analysis to avoid bias when evaluating biodiversity acoustically, as this abiotic factor drives the ACI scores up despite the audio file not necessarily containing high levels of animal produced sounds.

A)


ACI
160
155
150
145
140
135
130
125
LIP
MIP
HIP
→ Increasing distance to nearest main road
Dawn
MIP3
JBPLOT
AZ3
LIP44
LIP9
LIP7
MIP15
MIP16
MIP35
MIP42
HIP1
J7
HIP49
HIP64
HIP60
J4
HIP65
J2
HIP54
Site

B)


ACI
160
155
150
145
140
135
130
125
LIP
MIP
HIP
→ Increasing distance to nearest main road
Daytime
MIP3
JBPLOT
AZ3
LIP44
LIP9
LIP7
MIP15
MIP16
MIP35
MIP42
HIP1
J7
HIP49
HIP64
HIP60
J4
HIP65
J2
HIP54
Site

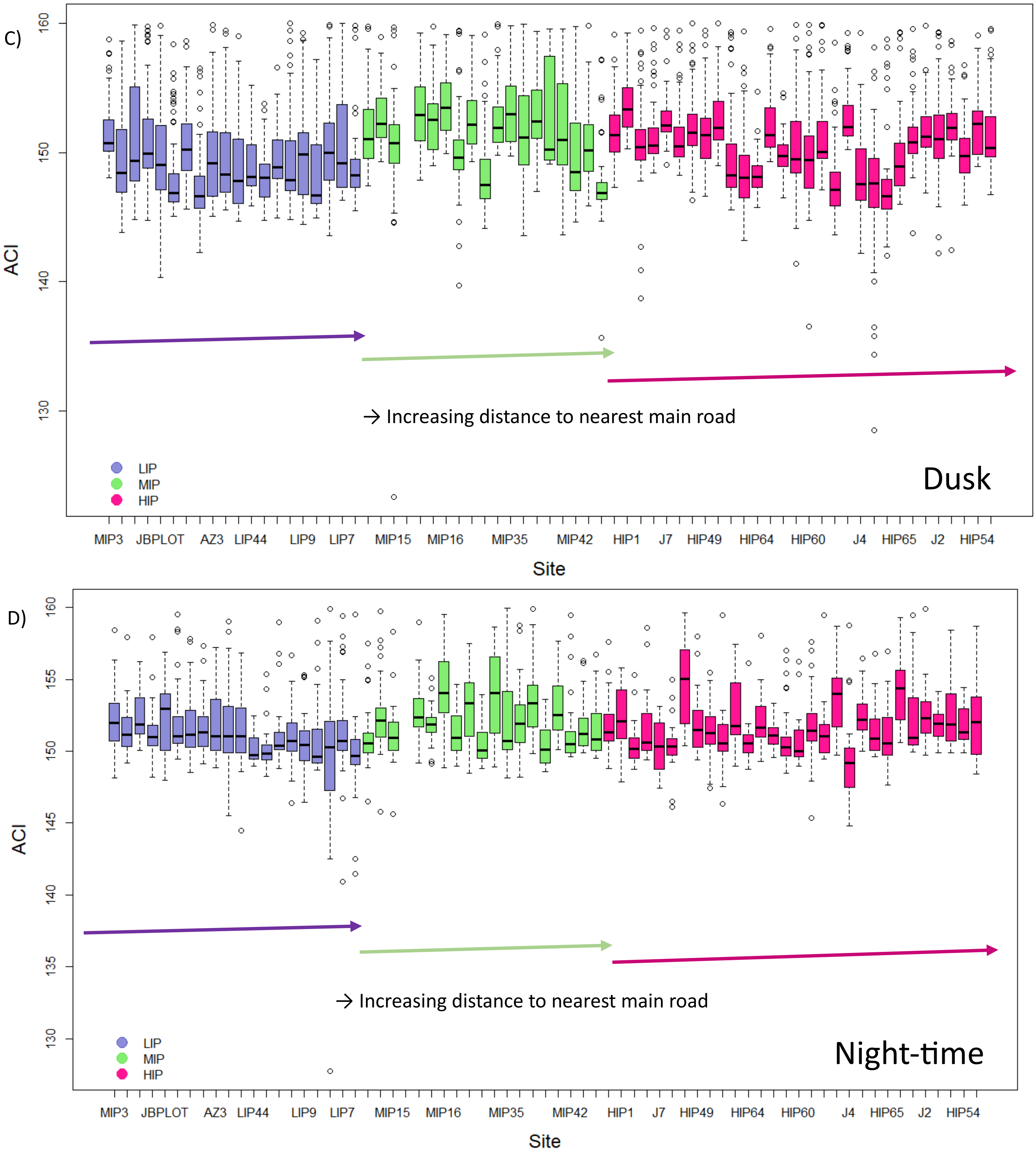


Figure 3.7 Variation of Acoustic Complexity Index (ACI) scores at A) Dawn B) Day-time C) Dusk D) Night-time at each 69 recording sites. Scores are separated according to time of day to avoid masking possible patterns. ACI scores were calculated for each audio file in the dataset using R. Sites are ordered in ascending order in relation to distance to nearest main road (i.e. sites closest to main roads are towards the left) within each Infrastructure Pressure

Zone category (indicated by colour coded arrows). Colours indicate *Infrastructure Pressure Zone Type*: LIP = Low Infrastructure Pressure; MIP = Medium Infrastructure Pressure; HIP = High Infrastructure Pressure. Due to the large number of sites, not all the site names could be displayed.

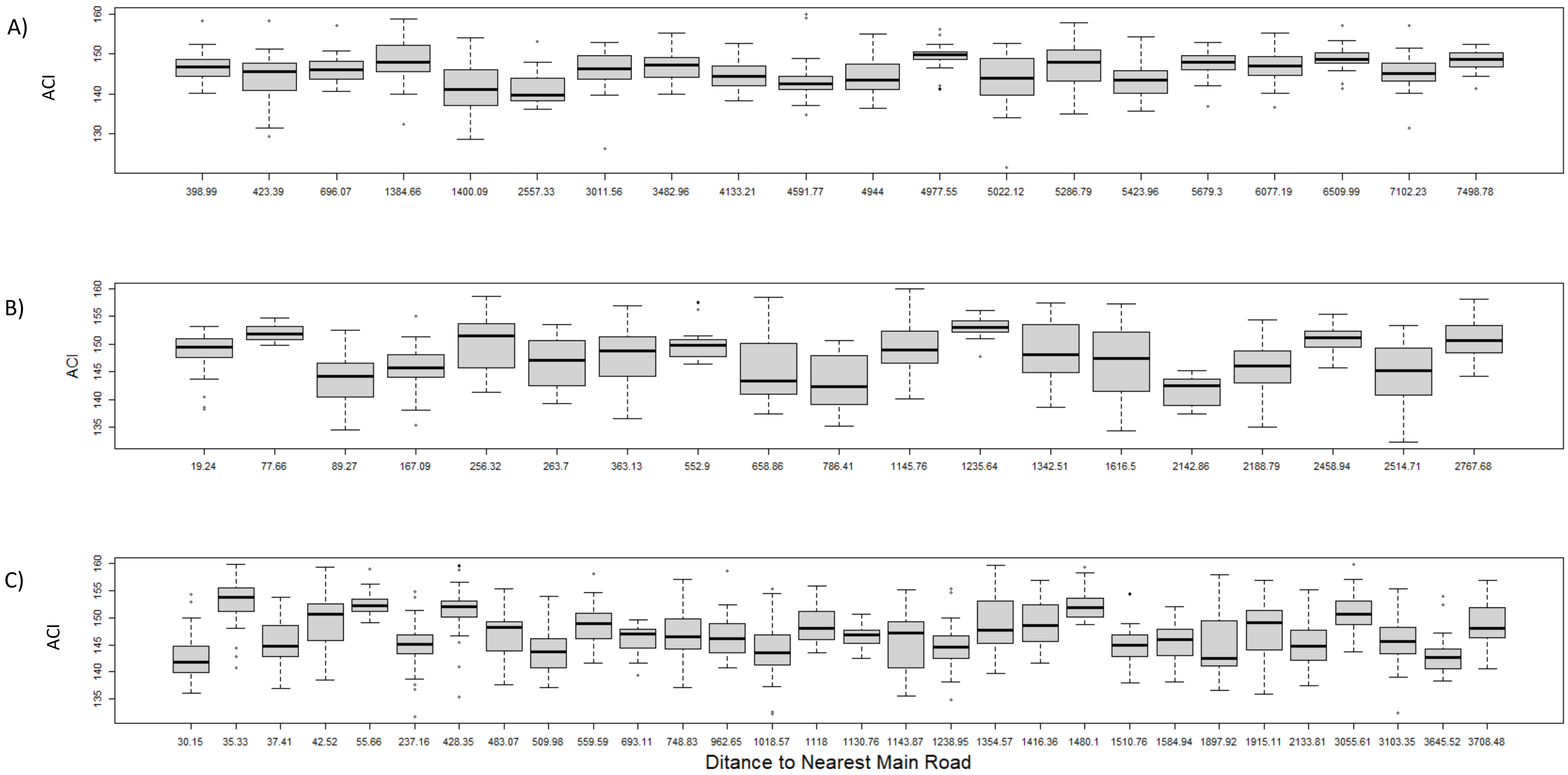


Figure 3.8 Variation of Acoustic Complexity Index (ACI) scores according to *Distance to Nearest Main Road* at 8am for the A) Low Infrastructure Pressure Zone B) Medium Infrastructure Pressure Zone C) High Infrastructure Pressure Zone. The x axes are not continuous (as sites were not distributed in a linear fashion away from the roads, thus making the *Distance to Nearest Main Road* variable a categorical variable rather than a continuous variable) but are ordered in ascending order, with the smallest distance on the left. ACI scores were calculated for each audio file in the dataset using R.

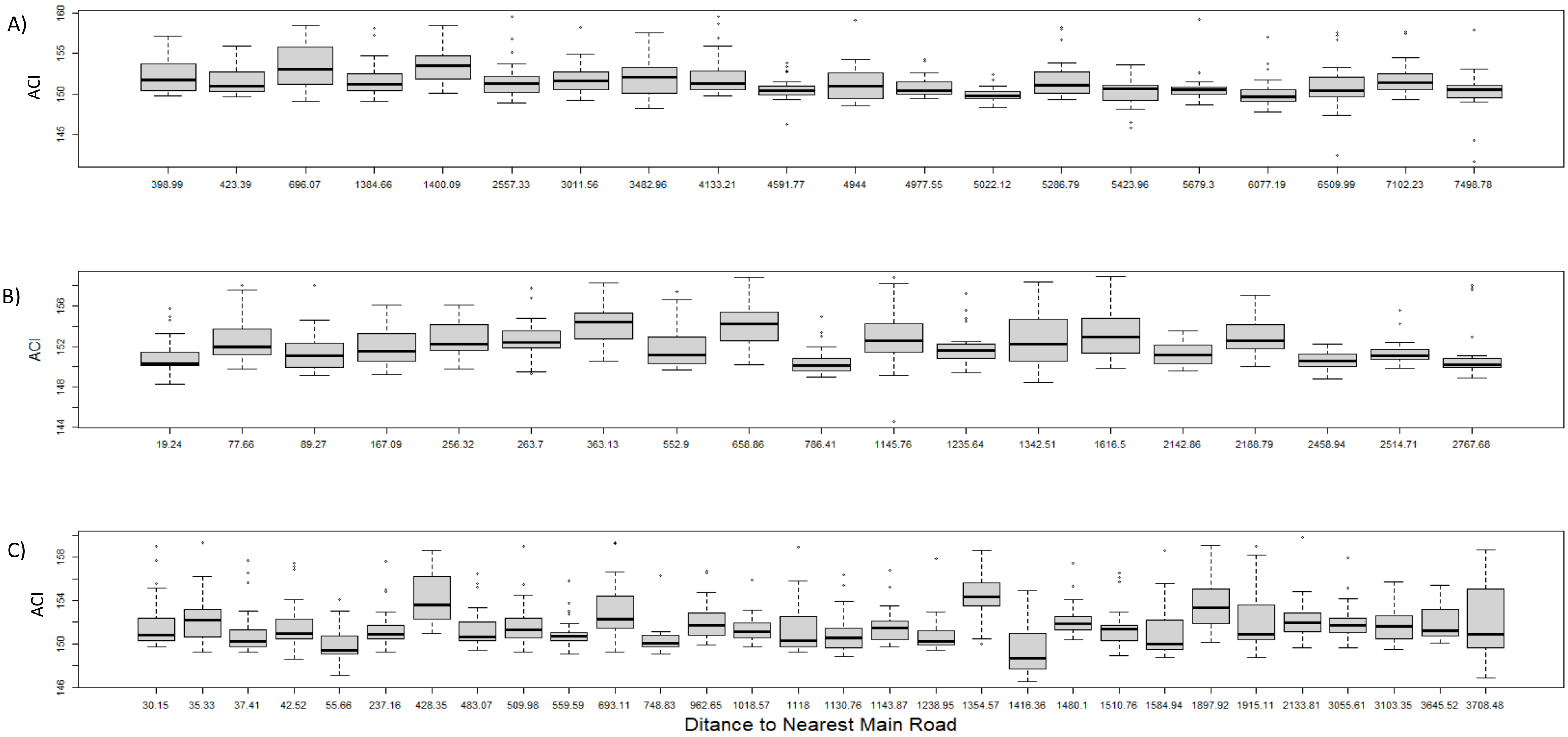


Figure 3.9 Variation of Acoustic Complexity Index (ACI) scores according to *Distance to Nearest Main Road* at midnight for the A) Low Infrastructure Pressure Zone B) Medium Infrastructure Pressure Zone C) High Infrastructure Pressure Zone. The x axes are not continuous (as sites were not distributed in a linear fashion away from the roads, thus making the *Distance to Nearest Main Road* variable a categorical variable rather than a continuous variable) but are ordered in ascending order, with the smallest distance on the left. ACI scores were calculated for each audio file in the dataset using R.

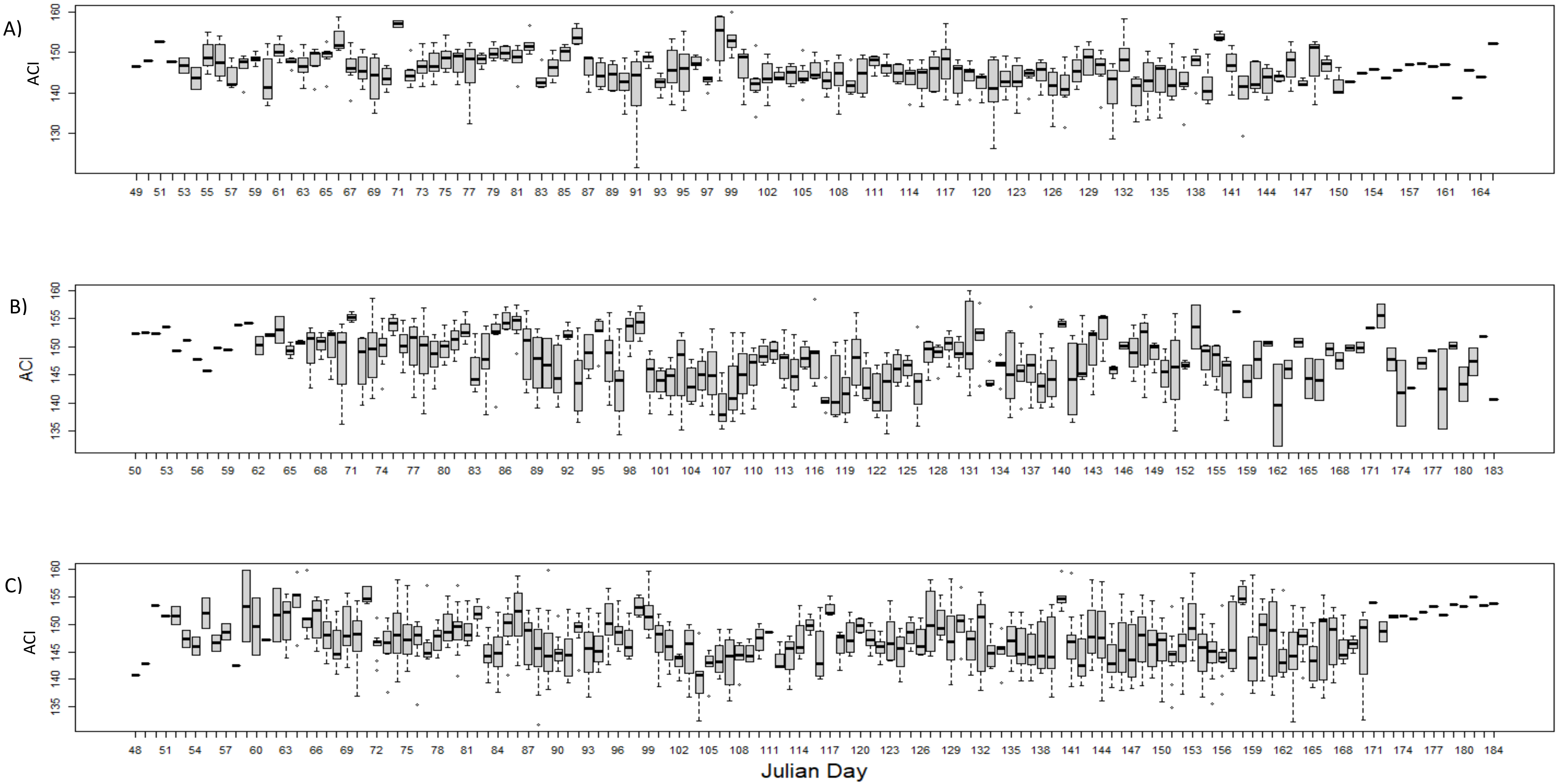


Figure 3.10 Variation of Acoustic Complexity Index (ACI) scores according to Julian day at 8am for the A) Low Infrastructure Pressure Zone B) Medium Infrastructure Pressure Zone C) High Infrastructure Pressure Zone. Julian day assigns a number to each day in the study period to allows systematic comparisons to be made. ACI scores were calculated for each audio file in the dataset using R.

3.5 Discussion

Infrastructure expansion and predictable temporal patterns can both affect biodiversity in a plethora of ways (Sparks & Menzel, 2002; Concepción *et al*., 2015; Lijun *et al*., 2019; Cassone & Kumar, 2022; Petersen *et al*., 2022; Theodorou, 2022). Using the Acoustic Complexity Index (ACI) (Pieretti *et al*., 2011), we quantitatively described the soundscape across the tropical rainforests of the Temburong district of Brunei, relating it to time of day, Julian day, level of biomass at the recording site, as well as distance to the nearest main road and building. We found that time of day had a significant impact on ACI, with scores diminishing from midnight to midday and then increasing thereafter. We also found that the distance between the site and the nearest main road had a significant negative effect on ACI, with scores diminishing as remoteness increases. The LIP zone had significantly lower ACI scores than the other two, with the MIP zone having the highest ACI scores. Similarly, Julian day had a slight negative effect on ACI, with scores diminishing throughout the study season. We did not find distance to building and biomass to have a significant effect on ACI scores.

Most organisms – and thus ecosystems – on earth follow a daily pattern, or cycle, across the 24-hour period, repeating certain activities at certain times of day, every day (Hardin & Panda, 2013). Abiotic factors – such as sunlight – repeatedly trigger certain behaviours in certain organisms, such as the dawn chorus for birds for instance (Gil & Llusia, 2020). Thus, the fact that time of day had a significant impact on ACI scores was in line with our expectations. However, as ACI has been described as an acoustic index particularly sensitive to bird vocalisations (Pieretti *et al*., 2011), we were expecting ACI to be lower at night-time, with a notable peak at dawn and a smaller one at dusk. Hence, some of our findings were the opposite of what we were expecting (aside from the minima at midday), thus our first two proposed hypotheses were not validated by our findings. Furthermore, this non-intuitive trend was seen across all *Infrastructure Pressure Zones* (Figure 3.6) and was the most significant factor in our model (Table 3.1). There was a clear distinction between day and night across all sites (Figure 3.7B and 3.7D), with night ACI scores being significantly higher. ACI trends over the 24-hour period do not seem to be consistent across studies, with some finding no trends (Bradfer-Lawrence *et al*., 2019; Dröge *et al*., 2021), and others finding the opposite patterns to here (Budka *et al*., 2023; Farina *et al*., 2021). A study found similar patterns to the ones revealed here, but the study site was a coral reef, so comparisons remain tenuous (Bertucci *et al*., 2020). One study found that as land use intensity increases in tropical ecosystems, acoustic communities lose their typical diurnal patterns (including dawn and dusk peaks) and that insects increasingly dominate the soundscape at night (Burivalova *et al*., 2022) – providing a possible explanation for the absence of dawn and dusk peaks as well as high ACI values at night in our results. However, the lowest scoring audio file seems to have many stridulating insects (Figure 3.2) and yet had a very lower ACI score (121.6), suggesting that these sounds are not driving ACI scores up. Daytime ACI scores seemed to vary more throughout the daytime (Figure 3.6) and between sites (Figure 3.7B) than at night-time, where scores seemed more consistent throughout the night and between sites (Figure 3.6 & Figure 3.7D). This might be indicative of a more homogenised nocturnal eco-acoustic community compared to daytime. Dawn saw the first drop of the day in ACI across all *Infrastructure Pressure Zones* but seemed to have the largest spread of ACI values of any time slot in the 24-hour period (Figure 3.6; Figure 3.7A). Thus, although a drop in ACI at dawn is in misalignment with our expectations, this greater variation around median dawn ACI values nevertheless portrays this hour as an important time of day for eco-acoustic communities, as expected. This counter-intuitive drop in ACI at dawn has been previously described in tropical climates but not temperate (Eldridge *et al.*, 2018). Despite these observed trends, ACI scores were relatively stable across the 24-hour period, with revealed diurnal patterns being a lot less pronounced than those depicted using other acoustic indices in other studies (Bradfer-Lawrence *et al.*, 2019; Dröge *et al.*, 2021). This suggests that ACI might not be the best predictor of diurnal patterns in soundscapes. However due to time and computing power limitations, we were not able to describe the soundscape using more than one index. Hence, further studies could undergo a similar study but use a multitude of commonly used acoustic indices (such as the Acoustic Diversity index, the Acoustic evenness index, the Normalised difference soundscape index, the Bioacoustic index, and the Acoustic entropy index) to explore which describe the diurnal patterns within the soundscapes in Temburong the best.

As with daily activity patterns, ecosystems tend to follow yearly cycles of activity, known as seasonal cycles. Most organisms rely on predictable environmental conditions to undergo many of their essential behaviours, such as reproduction (Wingfield *et al.*,1992). However, depending on the climate of the ecosystem in question, variation within the cycle can be more or less pronounced. Ecosystems nearer the equator have less environmental variance between seasons than temperate climates nearer the poles, with the major change being the level of precipitation (Trenberth, 1983). Many areas in the tropics experience a ‘wet’ (otherwise known as a monsoon) and ‘dry’ season, instead of the four seasons which take place in temperate regions. However, changes in precipitation can be very localised even within certain parts of the tropics. For instance, Borneo has two monsoons (North-East monsoon between December and March, and the South-West monsoon between June and September), yet climate varies greatly between regions of the island, with the south being significantly drier than the north (Phillips & Phillips, 2014). Thus, the fact that we observed only a weakly significant negative effect of Julian day on ACI scores was in line with our expectations – validating our 4th hypothesis –, as Brunei is a tropical ecosystem with little seasonal variation despite experiencing some shifts in precipitation levels. Our ARUs were deployed from February to July, thus monitoring the end of one monsoon, the dry period between the two, and the start of the next monsoon. Most acoustic studies are short term, and we did not find previous work exploring the seasonal variation of ACI in the tropics. Nevertheless, due to logistical limitations, we were only able to collect data for six months, leaving half the year with no data. Thus, it would be interesting to conduct a similar study in the latter half of the year to explore whether there is a greater impact of seasonality on ACI score than we have been able to describe here.

Temporal patterns are not the only factor influencing Temburong's eco-acoustic communities: the proximity of roads caused a significant, but small, increase in ACI scores. A similar trend was observed between *Infrastructure Pressure Zones*, with the LIP zone having significantly lower ACI scores than the other two *Infrastructure Pressure Zones*, followed by the HIP zone and then the MIP zone. Hence our 3rd proposed hypothesis was not validated by our findings. Indeed, this result was the opposite of what we were expecting to find, as generally there is a greater level of biodiversity in more remote areas, as roads cause detrimental effects to wildlife (Bennett, 2017; Laurance *et al*., 2009), theoretically inducing higher ACI scores. It is unlikely that the ACI scores are being directly driven up by traffic noise as it has been stated that ACI is insensitive to anthropogenic sounds (Eldridge *et al*., 2018; Pieretti *et al*., 2011). Nevertheless, another study correlating proximity of roads to ACI levels found similar trends (Pieretti & Farina, 2013), with others also finding lowest ACI scores in primary forests (Dröge *et al*., 2021). It can be suggested that higher ACI scores nearer roads could indicate a higher level of acoustic energy, but not necessarily a higher level of biodiversity. Species could be vocalising more and at greater amplitudes nearer roads to compensate for signal masking by traffic noise (Figure 3.3; Pieretti & Farina, 2013). Conversely, species in undisturbed environments may not need to vocalise as loudly or frequently to communicate the same amount of information as in a disturbed environment (Brumm, 2004; Brumm & Slabbekoorn, 2005). Additionally, the presence of roads creates a larger area of edge habitat, potentially beneficial to certain species (Ries *et al*., 2004; Ries & Sisk, 2010). All it would take is a distinct and highly vocal species, with an acoustically complex call, that prospers in edge habitats – and thus dominates areas in proximity to roads – to drive ACI scores up in such sites. Furthermore, studies have shown that ecotones – such as the MIP zone – harbour more species that other habitats as they present an overlap in habitat types, thus supporting more organisms overall (Maes *et al*., 2014). Additionally, in naturally complex environments – such as primary rainforests – different species' vocalisation boundaries may overlap, resulting in reduced acoustic intensity variation and ultimately lower ACI scores (Dröge *et al*., 2021). This might suggest that ACI is not an accurate (or at least reliable) biodiversity indicator in tropical ecosystems (Eldridge *et al*., 2018). Studies have found either positive, negative, or no correlations between species – notably bird – diversity and abundance and ACI scores (See Table 1 in Bateman & Uzal, 2022). Thus, more research must be conducted exploring the relationship between ACI scores and true biodiversity levels in order for such acoustic tools to become commonplace in rapid biodiversity assessments during conservation projects. To avoid having to undergo more fieldwork, future studies could lean on a project design used by Pieretti *et al*. (2011) where a recogniser is built to detect all bird calls and correlate findings to ACI scores and/or other acoustic indices.

Nevertheless, other environmental variables we considered proxies for infrastructure expansion (proximity to buildings and level of biomass at the sites) did not significantly impact ACI. It is somewhat surprising that proximity to buildings did not significantly influence ACI scores as the presence of buildings, and more generally the presence of people, is known to cause negative anthropogenic impacts on organisms, ecosystems, and their interactions (Morris, 2010; Prakash & Verma, 2022). This is often due to noise (Sordello *et al*., 2020) or light pollution – namely Artificial Light at Night (ALAN) (Dominoni, 2015; Falchi *et al*., 2016; Gaston *et al*., 2015; Rich & Longcore, 2013) – being most prevalent in or near urban areas. Thus, the fact that buildings did not have a significant effect on ACI in Temburong, indicates that the proximity to human settlements is not causing significant disruption to the acoustic complexity of the soundscapes here. This is a positive result as noise and light disturbance can have widespread negative impact on biodiversity, ranging from changing foraging and reproduction behaviours, as well as organisms' fitness, predation risk, and reproductive success – all of which can have cascading effects at larger ecological scales (Newport *et al*., 2014). Again, it is surprising that biomass did not impact ACI scores as we would expect a higher level of biomass to represent either greater structural complexity and/or resources present at a given site, and thus supporting more organisms (Basham *et al*., 2019; Niklaus *et al*., 2017; Pace *et al*., 1999), ultimately resulting in higher ACI scores. However, another study relating ACI to vegetation variables also found no correlation (Fuller *et al*., 2015), whilst another study found a positive correlation between the two (Farina & Pieretti, 2014) possibly suggesting that this index is not a reliable proxy to describe vegetative variations in habitats.

Overall, using the ACI to quantitatively describe the soundscapes across our study area provided a good baseline understanding of Temburong's eco-acoustic communities and how they respond to various temporal and environmental factors. Nevertheless, there remains too much uncertainty surrounding the biological meaning of the results of various acoustic indices, including that of the ACI, limiting their use in ecological research for now. Acoustic indicators are not yet clear indicators for biodiversity and ecosystem health and thus have limited power over conservation decision-making until further development. Here we describe the diurnal and seasonal patterns in soundscapes, with ACI scores decreasing from midnight to midday and increasing thereafter, as well as decreasing slightly as the year progressed. ACI scores were sensitive to the proximity of roads, showing an unexpected increase closer to roads. However, ACI scores seemed unaffected by the presence of buildings or changes in biomass levels. We would like to emphasise that the use of acoustic indices in ecological studies is a relatively new practice and results of this chapter remain preliminary. Further work must be done to fully describe Temburong soundscapes (through using multiple acoustic indices simultaneously) and consolidate the true significance of ACI scores (through correlating results with other in situ proxies of biodiversity).

3.6 References

Alcocer, I., Lima, H., Sugai, L.S.M. and Llusia, D., 2022. Acoustic indices as proxies for biodiversity: a meta-analysis. *Biological Reviews*, *97*(6), pp.2209-2236.

Amorim, M.C.P. and Neves, A.S.M., 2008. Male painted gobies (Pomatoschistus pictus) vocalise to defend territories. *Behaviour*, pp.1065-1083.

Andersson, E., 2006. Urban landscapes and sustainable cities. *Ecology and Society*, *11*(1), pp.34-40

Anunciação, P.R., Sugai, L.S.M., Martello, F., de Carvalho, L.M.T. and Ribeiro, M.C., 2022. Estimating the diversity of tropical anurans in fragmented landscapes with acoustic monitoring: lessons from a sampling sufficiency perspective. *Biodiversity and Conservation*, *31*(12), pp.3055-3074.

Arvedlund, M. and Kavanagh, K., 2009. The senses and environmental cues used by marine larvae of fish and decapod crustaceans to find tropical coastal ecosystems. *Ecological Connectivity Among Tropical Coastal Ecosystems*, pp.135-184.

Basham, E.W., Seidl, C.M., Andriamahohatra, L.R., Oliveira, B.F. and Scheffers, B.R., 2019. Distance–decay differs among vertical strata in a tropical rainforest. *Journal of Animal Ecology*, 88(1), pp.114-124.

Bateman, J. and Uzal, A., 2022. The relationship between the Acoustic Complexity Index and avian species richness and diversity: a review. *Bioacoustics*, 31(5), pp.614-627.

Bennett, V.J., 2017. Effects of road density and pattern on the conservation of species and biodiversity. *Current Landscape Ecology Reports*, 2, pp.1-11.

Bertucci, F., Guerra, A.S., Sturny, V., Blin, E., Sang, G.T. and Lecchini, D., 2020. A preliminary acoustic evaluation of three sites in the lagoon of Bora Bora, French Polynesia. *Environmental Biology of Fishes*, 103, pp.891-902.

Bradfer-Lawrence, T., Gardner, N., Bunnefeld, L., Bunnefeld, N., Willis, S.G. and Dent, D.H., 2019. Guidelines for the use of acoustic indices in environmental research. *Methods in Ecology and Evolution*, *10*(10), pp.1796-1807.

Bradfer-Lawrence, T., Bunnefeld, N., Gardner, N., Willis, S.G. and Dent, D.H., 2020. Rapid assessment of avian species richness and abundance using acoustic indices. *Ecological Indicators*, 115, p.106-400.

Brumm, H., 2004. The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology*, 73(3), pp.434-440.

Brumm, H. and Slabbekoorn, H., 2005. Acoustic communication in noise. *Advances in the Study of Behavior*, 35, pp.151-209.

Budka, M., Sokołowska, E., Muszyńska, A. and Staniewicz, A., 2023. Acoustic indices estimate breeding bird species richness with daily and seasonally variable effectiveness in lowland temperate Białowieża forest. *Ecological Indicators*, 148, p.110027.

Burivalova, Z., Wahyudi, B., Boucher, T.M., Ellis, P., Truskinger, A., Towsey, M., Roe, P., Marthinus, D., Griscom, B. and Game, E.T., 2019. Using soundscapes to investigate homogenization of tropical forest diversity in selectively logged forests. *Journal of Applied Ecology*, *56*(11), pp.2493-2504.

Burivalova, Z., Maeda, T.M., Rayadin, Y., Boucher, T., Choksi, P., Roe, P., Truskinger, A. and Game, E.T., 2022. Loss of temporal structure of tropical soundscapes with intensifying land use in Borneo. *Science of the Total Environment*, *852*, p.158268.

Buxton, R.T., McKenna, M.F., Clapp, M., Meyer, E., Stabenau, E., Angeloni, L.M., Crooks, K. and Wittemyer, G., 2018. Efficacy of extracting indices from large-scale acoustic recordings to monitor biodiversity. *Conservation Biology*, *32*(5), pp.1174-1184.

Carson, R., 1962. *Silent Spring*. London: Penguin Books.

Cassone, V.M. and Kumar, V., 2022. Circadian rhythms. In *Sturkie's Avian Physiology* (pp. 1143-1161). Academic Press.

Concepción, E.D., Moretti, M., Altermatt, F., Nobis, M.P. and Obrist, M.K., 2015. Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale. *Oikos*, 124(12), pp.1571-1582.

de Camargo, U., Roslin, T. and Ovaskainen, O., 2019. Spatio-temporal scaling of biodiversity in acoustic tropical bird communities. *Ecography*, *42*(11), pp.1936-1947.

de Oliveira, L.Q., Marciente, R., Magnusson, W.E. and Bobrowiec, P.E.D., 2015. Activity of the insectivorous bat Pteronotus parnellii relative to insect resources and vegetation structure. *Journal of Mammalogy*, *96*(5), pp.1036-1044.

Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S. and Sueur, J., 2012. Monitoring animal diversity using acoustic indices: implementation in a temperate woodland. *Ecological Indicators*, *13*(1), pp.46-54.

Dominoni, D.M., 2015. The effects of light pollution on biological rhythms of birds: an integrated, mechanistic perspective. *Journal of Ornithology*, *156*(Suppl 1), pp.409-418.

Dooling, R.J. and Popper, A.N., 2016, July. Some lessons from the effects of highway noise on birds. In *Proceedings of Meetings on Acoustics 4ENAL* (Vol. 27, No. 1, p. 010004). Acoustical Society of America.

Dröge, S., Martin, D.A., Andriafanomezantsoa, R., Burivalova, Z., Fulgence, T.R., Osen, K., Rakotomalala, E., Schwab, D., Wurz, A., Richter, T. and Kreft, H., 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*, 120, p.106929.

Eldridge, A., Guyot, P., Moscoso, P., Johnston, A., Eyre-Walker, Y. and Peck, M., 2018. Sounding out ecoacoustic metrics: Avian species richness is predicted by acoustic indices in temperate but not tropical habitats. *Ecological Indicators*, 95, pp.939-952.

Fairbrass, A.J., Rennert, P., Williams, C., Titheridge, H. and Jones, K.E., 2017. Biases of acoustic indices measuring biodiversity in urban areas. *Ecological Indicators*, *83*, pp.169-177.

Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C.C., Elvidge, C.D., Baugh, K., Portnov, B.A., Rybnikova, N.A. and Furgoni, R., 2016. The new world atlas of artificial night sky brightness. *Science Advances*, 2(6), p.e1600377.

Farina, A. and Morri, D., 2008. Source-sink & ecofield: Ipotesi ed evidenze sperimentali. Proceedings SIEP-IALE Bari. In *Ecologia e Governance del Paesaggio* (pp. 365-372). ITA.

Farina, A. and Pieretti, N., 2014. Sonic environment and vegetation structure: a methodological approach for a soundscape analysis of a Mediterranean maqui. *Ecological Informatics*, *21*, pp.120-132.

Farina, A., Righini, R., Fuller, S., Li, P. and Pavan, G., 2021. Acoustic complexity indices reveal the acoustic communities of the old-growth Mediterranean forest of Sasso Fratino Integral Natural Reserve (Central Italy). *Ecological Indicators*, 120, p.106927.

Fuller, S., Axel, A.C., Tucker, D. and Gage, S.H., 2015. Connecting soundscape to landscape: Which acoustic index best describes landscape configuration? *Ecological Indicators*, *58*, pp.207-215.

Gaston, K.J., Visser, M.E. and Hölker, F., 2015. The biological impacts of artificial light at night: the research challenge. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1667), p.20140133.

Gil, D. and Llusia, D., 2020. The bird dawn chorus revisited. *Coding Strategies in Vertebrate Acoustic Communication*, 7, pp.45-90.

Goyette, J.L., Howe, R.W., Wolf, A.T. and Robinson, W.D., 2011. Detecting tropical nocturnal birds using automated audio recordings. *Journal of Field Ornithology*, *82*(3), pp.279-287.

Hardin, P.E. and Panda, S., 2013. Circadian timekeeping and output mechanisms in animals. *Current Opinion in Neurobiology*, 23(5), pp.724-731.

Heinicke, S., Kalan, A.K., Wagner, O.J., Mundry, R., Lukashevich, H. and Kühl, H.S., 2015. Assessing the performance of a semi-automated acoustic monitoring system for primates. *Methods in Ecology and Evolution*, *6*(7), pp.753-763.

Jorge, F.C., Machado, C.G., da Cunha Nogueira, S.S. and Nogueira-Filho, S.L.G., 2018. The effectiveness of acoustic indices for forest monitoring in Atlantic rainforest fragments. *Ecological Indicators*, 91, pp.71-76.

Kalan, A.K., Mundry, R., Wagner, O.J., Heinicke, S., Boesch, C. and Kühl, H.S., 2015. Towards the automated detection and occupancy estimation of primates using passive acoustic monitoring. *Ecological Indicators*, *54*, pp.217-226.

Katsis, L.K., Hill, A.P., Pina-Covarrubias, E., Prince, P., Rogers, A., Doncaster, C.P. and Snaddon, J.L., 2022. Automated detection of gunshots in tropical forests using convolutional neural networks. *Ecological Indicators*, *141*, p.109128.

Kumagai, T.O. and Kume, T., 2012. Influences of diurnal rainfall cycle on CO2 exchange over Bornean tropical rainforests. *Ecological Modelling*, *246*, pp.91-98.

Lapp, S., Wu, T., Richards-Zawacki, C., Voyles, J., Rodriguez, K.M., Shamon, H. and Kitzes, J., 2021. Automated detection of frog calls and choruses by pulse repetition rate. *Conservation Biology*, *35*(5), pp.1659-1668.

Laurance, W.F., Goosem, M. and Laurance, S.G., 2009. Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution*, 24(12), pp.659-669.

Lijun, C., Zufei, S. and Zhishu, X., 2019. Application of camera-trapping data to study daily activity patterns of Galliformes in Guangdong Chebaling National Nature Reserve. *Biodiversity Science*, 27(3), p.266.

Lindström, K. and Lugli, M., 2000. A quantitative analysis of the courtship acoustic behaviour and sound patterning in male sand goby, Pomatoschistus minutus. *Environmental Biology of Fishes*, *58*, pp.411-424.

Maes, D., Jacobs, I., Segers, N., Vanreusel, W., Van Daele, T., Laurijssens, G. and Van Dyck, H., 2014. A resource-based conservation approach for an endangered ecotone species: the Ilex Hairstreak (Satyrium ilicis) in Flanders (north Belgium). *Journal of Insect Conservation*, *18*, pp.939-950.

Mammides, C., Goodale, E., Dayananda, S.K., Kang, L. and Chen, J., 2017. Do acoustic indices correlate with bird diversity? Insights from two biodiverse regions in Yunnan Province, south China. *Ecological Indicators*, 82, pp.470-477.

McGrann, M.C., Wagner, B., Klauer, M., Kaphan, K., Meyer, E. and Furnas, B.J., 2022. Using an acoustic complexity index to help monitor climate change effects on avian diversity. *Ecological Indicators*, 142, p.109271.

Metcalf, O.C., Lees, A.C., Barlow, J., Marsden, S.J. and Devenish, C., 2020. hardRain: An R package for quick, automated rainfall detection in ecoacoustic datasets using a threshold-based approach. *Ecological Indicators*, *109*, p.105793.

Metcalf, O.C., Barlow, J., Devenish, C., Marsden, S., Berenguer, E. and Lees, A.C., 2021. Acoustic indices perform better when applied at ecologically meaningful time and frequency scales. *Methods in Ecology and Evolution*, *12*(3), pp.421-431.

Morris, R.J., 2010. Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1558), pp.3709-3718.

Newport, J., Shorthouse, D.J. and Manning, A.D., 2014. The effects of light and noise from urban development on biodiversity: Implications for protected areas in Australia. *Ecological Management & Restoration*, 15(3), pp.204-214.

Niklaus, P.A., Baruffol, M., He, J.S., Ma, K. and Schmid, B., 2017. Can niche plasticity promote biodiversity–productivity relationships through increased complementarity? *Ecology, 98*(4), pp.1104-1116.

Pace, M.L., Cole, J.J., Carpenter, S.R. and Kitchell, J.F., 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution, 14*(12), pp.483-488.

Petersen, T.K., Speed, J.D., Grøtan, V., Frøyen, Y.K. and Austrheim, G., 2022. Urbanisation and land-cover change affect functional, but not compositional turnover of bird communities. *Urban Ecosystems*, pp.1-20.

Phillipps, Q. and Phillipps, K. (2014). *Phillipps' field guide to the birds of Borneo: Sabah, Sarawak, Brunei and Kalimantan*. Oxford, England: John Beaufoy Publishing.

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*, 11(3), pp.868-873.

Pieretti, N. and Farina, A., 2013. Application of a recently introduced index for acoustic complexity to an avian soundscape with traffic noise. *The Journal of the Acoustical Society of America*, *134*(1), pp.891-900.

Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H. and Pieretti, N., 2011. Soundscape ecology: the science of sound in the landscape. *BioScience*, *61*(3), pp.203-216.

Potvin, D.A., Parris, K.M. and Mulder, R.A., 2011. Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in silvereyes (Zosterops lateralis). *Proceedings of the Royal Society B: Biological Sciences*, *278*(1717), pp.2464-2469.

Prakash, S. and Verma, A.K., 2022. Anthropogenic activities and Biodiversity threats. *International Journal of Biological Innovations*, IJBI, 4(1), pp.94-103.

Pröhl, H., 2005. Territorial behavior in dendrobatid frogs. *Journal of herpetology*, *39*(3), pp.354-365.

R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rich, C. and Longcore, T. eds., 2013. *Ecological Consequences of Artificial Night Lighting*. Island Press. Washington D.C.

Retamosa Izaguirre, M.I., Segura Sequeira, D., Barrantes-Madrigal, J., Spínola Parallada, M. and Ramírez-Alán, Ó., 2021. Vegetation, bird and soundscape characterization: a case study in Braulio Carrillo National Park, Costa Rica. *Biota Colombiana*, *22*(1), pp.57-73.

Ries, L., Fletcher Jr, R.J., Battin, J. and Sisk, T.D., 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annu. Rev. Ecol. Evol. Syst.*, 35, pp.491-522.

Ries, L. and Sisk, T.D., 2010. What is an edge species? The implications of sensitivity to habitat edges. *Oikos*, 119(10), pp.1636-1642.

Sánchez-Giraldo, C., Bedoya, C.L., Morán-Vásquez, R.A., Isaza, C.V. and Daza, J.M., 2020. Ecoacoustics in the rain: understanding acoustic indices under the most common geophonic source in tropical rainforests. *Remote Sensing in Ecology and Conservation*, *6*(3), pp.248-261.

Slabbekoorn, H. and Peet, M., 2003. Birds sing at a higher pitch in urban noise. *Nature*, *424*(6946), pp.267-267.

Sordello, R., Ratel, O., Flamerie De Lachapelle, F., Leger, C., Dambry, A. and Vanpeene, S., 2020. Evidence of the impact of noise pollution on biodiversity: A systematic map. *Environmental Evidence*, 9, pp.1-27.

Sparks, T.H. and Menzel, A., 2002. Observed changes in seasons: an overview. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, 22(14), pp.1715-1725.

Sueur, J., Aubin, T. and Simonis, C., 2008. Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics*, *18*(2), pp.213-226.

Sueur, J., Farina, A., Gasc, A., Pieretti, N. and Pavoine, S., 2014. Acoustic indices for biodiversity assessment and landscape investigation. *Acta Acustica united with Acustica*, *100*(4), pp.772-781.

Sueur, J. and Farina, A., 2015. Ecoacoustics: the ecological investigation and interpretation of environmental sound. *Biosemiotics*, 8, pp.493-502.

Suraci, J.P., Gaynor, K.M., Allen, M.L., Alexander, P., Brashares, J.S., Cendejas-Zarelli, S., Crooks, K., Elbroch, L.M., Forrester, T., Green, A.M. and Haight, J., 2021. Disturbance type and species life history predict mammal responses to humans. *Global Change Biology*, *27*(16), pp.3718-3731.

Symes, L.B., Madhusudhana, S., Martinson, S.J., Kernan, C.E., Hodge, K.B., Salisbury, D.P., Klinck, H. and ter Hofstede, H., 2022. Estimation of katydid calling activity from soundscape recordings. *Journal of Orthoptera Research*, *31*(2), pp.173-180.

Theodorou, P., 2022. The effects of urbanisation on ecological interactions. *Current Opinion in Insect Science*, p.100922.

Thomas, J.A., Moss, C.F. and Vater, M. eds., 2004. *Echolocation in Bats and Dolphins*. University of Chicago press. Chicago.

Thomson, I.R. and Bertram, S.M., 2014. Spring field crickets (Gryllus veletis) use two different pulse types when signalling to attract mates. *Journal of Insect Behavior*, *27*, pp.217-227.

Towsey, M., Wimmer, J., Williamson, I. and Roe, P., 2014. The use of acoustic indices to determine avian species richness in audio-recordings of the environment. *Ecological Informatics*, *21*, pp.110-119.

Trenberth, K.E., 1983. What are the seasons? *Bulletin of the American Meteorological Society*, 64(11), pp.1276-1282.

Tucker, D., Gage, S.H., Williamson, I. and Fuller, S., 2014. Linking ecological condition and the soundscape in fragmented Australian forests. *Landscape Ecology*, *29*, pp.745-758.

Watson, J.E., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J.C., Murray, K., Salazar, A. and McAlpine, C., 2018. The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution*, *2*(4), pp.599-610.

Weisman, R.G. and Ratcliffe, L., 2004. Relative pitch and the song of black-capped chickadees: chickadees, like people, have a strong sense of relative pitch. These birds use skillful, precise pitch changes to advertise their quality and attract mates. *American Scientist*, *92*(6), pp.532-539.

Wheeldon, A., Szymański, P. and Osiejuk, T.S., 2021. Yellow-breasted Boubous (Laniarius atroflavus) jointly defend territories with male-led duets against stranger pairs, males and females. *Ethology*, *127*(2), pp.176-186.

Wingfield, J.C., Hahn, T.P., Levin, R. and Honey, P., 1992. Environmental predictability and control of gonadal cycles in birds. *Journal of Experimental Zoology*, 261(2), pp.214-231.

Chapter 4

Comparing the performance of Helmeted Hornbill acoustic recognisers built using Kaleidoscope Pro

4.1 Abstract

Auditory signalling provides a means for key social communication in many species, with birds being amongst the most vocal taxa. Such vocalisations also provide a useful way for humans to detect and monitor vocal species. Autonomous Recording Units (ARUs) have revolutionised the field of surveying vocalising species, by providing a non-intrusive remote-sensing technology capable of being deployed in the field for long periods of time, providing many benefits over traditional surveying methods. Nevertheless, extracting key information from large audio datasets in a reliable but time-efficient manner remains a challenge. Here, we build and trial six recognisers (algorithms to detect and extract target calls from audio data) to detect the call of Helmeted Hornbills (*Rhinoplax vigil*) using the software Kaleidoscope Pro. The recognisers varied in the type of training data provided and in the labelling of training calls. We tested all six recognisers on a subset of field data and compared their performance. We found that the recogniser trained using a sample of Helmeted Hornbill calls of varying quality, and where the calls were collected from within the study region, performed best overall. By contrast, recognisers trained using sample calls from across the species range (from an online audio repository) performed less well. Providing recognisers with training calls of varying perceived quality enables them to detect more target calls than those built on high-quality calls only, though at the expense of more false positives. The results suggested that recognisers are sensitive to the background noise in the training data as well as to the provenance of the training calls. Our findings that the use, in recogniser training, of generic calls from across a species range were less capable of detecting vocalisations than local recordings, leads us to recommend that, where possible, recogniser training data should be locally sourced – at least in situations where the algorithm is only to be applied locally.

4.2 Introduction

Animal communication is a focus of social interaction in many species. Interactions are mediated via specific sensory domains and can be conveyed using cues such as displays (both through ritualistic movements and architectural structures), physical touch, scent production, and auditory signalling. Some even rely on multi-component signalling (Bro-Jørgensen, 2010; Ruxton & Schaefer, 2013) making them vulnerable to environmental change. Auditory signalling is a frequently used mode of communication for invertebrates and vertebrates alike. Birds are amongst the most vocal taxa on earth (Gill & Bierema, 2013), producing alarm, mating, contact, and flight calls, as well as songs for some species. Some are capable of vocal learning and even compositional syntax, allowing them to express almost limitless meanings with a finite set of calls (Suzuki *et al*., 2016). Nevertheless, the study of complex animal communications remains in its infancy (Hebets, 2011; Higham & Hebets, 2013).

The research community is developing new ways to record and analyse sounds created by biological organisms, otherwise known as biophony (Pijanowski *et al.*, 2011). Efforts have mainly been concentrated on the study of wild animals, where biophony is placed in its ecological context, alongside geophony (sounds from non-biological origin) and anthrophony (sounds created by human activities). A breakthrough in terms of recording acoustic data was the use of Autonomous Recording Units (ARUs). By collaborating with engineers and computer scientists, biologists have created technology capable of remotely recording sounds in the field in an automated way. ARUs allow users to non-invasively survey animals to gain further understanding about their social interactions and monitor effects of variables of interest on phenology and wider biodiversity (Blumstein *et al*., 2011). ARUs offer a multitude of benefits over traditional survey methods, such as: removal of observer bias, digital datasets, higher repeatability and accuracy of data collection, increased sampling efforts for significantly lower costs, accessibility to remote locations, and ability to sample species that vocalise at anti-social times or too irregularly to monitor using traditional site-visit methods (Zwart *et al*., 2014). Although originally used principally for marine mammal research (Sousa-Lima *et al*., 2013), ARUs are increasingly used in terrestrial habitat surveys, particularly for avian studies (Shonfield & Bayne, 2017) because many members of this taxon are highly vocal. Additionally, ARUs allow collection of digital ‘big data’, often spanning large distances and/or time periods.

Large scale acoustic recording projects which collect vast amounts of audio data are thought to be critical to future conservation monitoring for many vocalising species (Brandes, 2008). Nevertheless, extracting information of interest from the immense quantity of audio recordings typically acquired remains problematic. Different elements can be drawn out from audio data depending on the research question. The data can be processed using a 'big picture' approach whereby the soundscape is analysed, often by summarising the acoustic structure of the data with acoustic indices (Chapter 3; Alcocer *et al.,* 2022; Bradfer-Lawrence *et al*., 2019; Sueur *et al*., 2014). Alternatively, the vocalisations of focal species can be detected, extracted, and their frequency compared to variables of interest and/or abundance estimated (Rycyk *et al*., 2022; Pérez-Granados & Schuchmann, 2021; Enari *et al*., 2019). However, finding a method that allows efficient and reliable extraction of information of interest from audio datasets can be challenging, a difficulty encountered with other automated data collection methods such as camera traps (Norouzzadeh *et al*., 2018). For example, the goal in this study is to detect the calls of a single bird species – the Helmeted Hornbill (*Rhinoplax vigil*) – to later assess the impact of land-use on this Critically Endangered species (BirdLife International, 2020; Chapter 5). We collected 7 141 hours of audio recording in total. Thus, assuming we worked 5 days per week for 8 hours per day, it would take 3.5 years just to listen to the audio data. Documenting detections and non-detections would further add to the workload. Given the relatively small scale of this recording project, compared to larger scale and duration ARU projects, the critical need for automated processing and identification becomes clear (Blumstein *et al*., 2011).

There are several software packages – both commercial and open source – available to automate the analysis of audio datasets, namely using recognisers: algorithms capable of automatically detecting and extracting target calls from audio data. These packages vary in terms of the different types of processing and classification algorithms they use, which are sometimes tailored to research aims as well as to the structure of the audio files and target sounds (Knight *et al*., 2017; Brooker *et al*., 2020). For instance, Brandes (2008) suggests there are at least five types of discrete sound unit shapes that make up bird sounds and a plethora of classification models that best suit each. Kaleidoscope Pro is one of the commercially available software packages (US$300 annual license, Wildlife Acoustics, USA) which aids in acoustic data processing by providing a ready-to-use algorithm to detect and classify acoustic sounds through Hidden Markov Models (HMM). Kaleidoscope allows users to build species-specific recognisers using this algorithm. Although it has been suggested that Kaleidoscope Pro is not the most reliable software and is often outperformed by other software packages (Wilhite *et al*., 2020; Brooker *et al*., 2020), it presents a user-friendly interface suitable for use by non-specialists.

It has also been suggested that recogniser performance can vary according to the methods adopted during its building phase (Brooker *et al*., 2020). Here, we explore this suggestion by building a series of recognisers to detected Helmeted Hornbill calls using Kaleidoscope Pro but employing different construction methods for each recogniser, (1) by varying the training datasets and (2) by adjusting the labelling of training calls. The individual recogniser performances are measured and compared, and the advantages and disadvantages of each are discussed. The aim being to identify a recogniser construction method that yields the best performing recogniser, specifically to detect Helmeted Hornbill calls in the audio dataset collected in the tropical forests of Temburong, Brunei.

4.3 Methods

4.3.1 Data collection

For details on the study site, sampling protocols, and data pre-processing, see Chapter 2.

4.3.2 Building recognisers

Signal Parameters

To locate target calls (in this case Helmeted Hornbill calls) in the data, recognisers (referred to as advanced classifiers in Kaleidoscope Pro) were made using Kaleidoscope Pro 5.4.8 (Wildlife Acoustics Inc., Maynard, MA, USA), an automatic signal recognition software to aid in audio data analysis. To make the data processing more efficient, signal parameters of the Helmeted Hornbill call (frequency band of call, length of call, and time between calls) are entered into Kaleidoscope Pro before the scanning process begins, thus limiting the output detections to sounds that fit those criteria. The signal parameters used to help locate Helmeted Hornbill calls were acquired using example calls from Xeno-Canto (an online audio repository: www.xeno-canto.org), viewed using the Kaleidoscope Pro viewer window, which produces a real time spectrogram of audio recordings (See Figure 4.1). As the availability of Helmeted Hornbill calls on Xeno-Canto are restricted (to protect the species from trapping using audio playback), a special access agreement was obtained by directly contacting the website and explaining the goals of the research project. The signal parameters used to help detect Helmeted Hornbill calls were as follows: 250 Hz minimum frequency, 750 Hz maximum frequency, 10s minimum detection length, 25s maximum detection length, and 2.8s maximum inter-syllable gap. The maximum inter-syllable gap is the length of time after a call syllable which, when exceeded without detection of another syllable, classes the next call syllable detected as a separate call. A 21.33ms Fast Fourier Transform (FFT) window was used as this was the recommended setting by Wildlife Acoustics, Inc. for low frequency sounds as it provides higher resolution of frequency. Due to the Helmeted Hornbill call being so low frequency, it is acoustically partitioned from most other bird calls thus making it easier to detect amongst the bulk of higher frequency noise in the audio data.

Training data

To explore which construction approach yields the best recogniser in Kaleidoscope Pro, six different recognisers were built, and their performance compared. Some were built using only the data collected at the study sites as part of this research programme, whilst others were built on the same set of collected data in addition to downloaded Helmeted Hornbill calls from Xeno-Canto. In some recognisers, only high-quality calls were retained. A poor-quality call was defined as a masked or very faint Helmeted Hornbill call. The details on how each recogniser was built are provided in Table 4.1. The set of collected data used as training data across all recognisers was a subset of the total audio dataset collected at the study site. The training data were obtained from five ARUs. The localities of these five sites, all of which included some Helmeted Hornbill vocalisations, are not specified here to avoid informing future persecution. The training sites tended, from preliminary data exploration, to have more frequent calls. Although the selected sites were grouped, they were nonetheless selected as training data following the recommendation of Enari *et al*. (2019), as typically the more calls that are used to build a recogniser, the better it performs.

Recogniser construction workflows

The workflow used to build a recogniser in Kaleidoscope Pro is a three-tier process.

i) Firstly, the software detects all the sounds in the training data provided that fit the *a priori* signal parameters given. Kaleidoscope Pro then automatically groups all the detections into clusters of similar sounds using the cluster analysis function. This process is based on statistical density (explained below), and results in the creation of a csv output file. As explained by Pérez-Granados & Schuchmann (2021), Kaleidoscope Pro estimates the ‘discrete cosine transform coefficients of the spectrum of the detections’ and fits a Hidden Markov Model based on the vector of these. This statistical-state machine model has been used in multiple software packages dealing with sound recognition due to their “robustness and flexibility for eco-acoustic signal classification across a variety of species” (Enari *et al.*, 2019). K-means clustering (Pérez-Granados & Schuchmann, 2021) is then used to groups the vectors into clusters. Clusters are formed by grouping detections together based on minimising distances of each detection from ‘cluster centres’. The ‘maximum distance to cluster centre for building clusters’ was set to 0.5 for all six Recognisers, which is the recommended setting for this parameter. A smaller value for maximum cluster distance results in the creation of more clusters, with the sounds in each cluster being more similar. Within each cluster, the detections are ordered from ‘closest-to’ to ‘furthest-from’ the ‘cluster centre’, thus detections become less representative of the cluster as the list progresses. Kaleidoscope Pro also requires a ‘maximum distance from cluster centre to include outputs in the cluster’. In this case, the maximum value of 2 was inputted in the aims of maximising the target calls included in the output, despite the risk of increasing the number of false positives being falsely classified as target calls. Maximum number of states (target size of the HMM classification model) was set to 15, which is higher than the default setting. This higher value is recommended in the Kaleidoscope Pro documentation (https://www.wildlifeacoustics.com/resources/user-guides) for environments with a more diverse acoustic structure, as this can help tease apart subtle differences between similar sounds. As the study site was a biodiverse tropical rainforest, and given the results in Chapter 3, the audio data collected was deemed to have a ‘diverse acoustic structure’.

ii) Secondly, the user verifies all the detections in order to sort the target sounds from the other detections that also fit the signal parameters. This is done by manually labelling target sounds in the csv file, leaving non-target detections with their original cluster label. This will train the algorithm to further differentiate target and non-target calls in future datasets. Detections which the user wishes to remove from the learning process altogether (e.g. heavily masked target calls) can be blank labelled.

iii) Lastly, the same training dataset needs then to be re-scanned alongside the edited csv file to create a ksc file. The ksc file is a special file which can only be used by Kaleidoscope Pro and contains the mathematical models of the clusters that were made during the original cluster analysis process. The ksc file is the recogniser and it is scanned against new audio data to automatically detect target calls.

Table 4.1 Details on how each of the six recognisers (algorithms to detect and extract target calls from audio data) to detect Helmeted Hornbill calls were built in Kaleidoscope Pro 5.4.8 (acoustic analysis software used in this study which groups calls based on similarity levels). *Site* calls refer to the ones collected in the field study area whilst *Off-site* calls are ones acquired through an audio repository. The audio repository used was Xeno-Canto, a free online audio file database. A poor-quality call was defined as a masked or very faint Helmeted Hornbill call. All other calls were considered high-quality. The calls were manually labelled by the user when processing the data. A blank labelled call is then removed from the recogniser training process.

Recogniser	**Building method**	**Number of calls labelled**
A - Site-only (all calls)	Recogniser with prior labelling of a sample of Helmeted Hornbill calls of varying quality within the data collected in the study region.	224
B - Site-only (high quality)	Recogniser with prior labelling of a sample of high-quality Helmeted Hornbill calls within the data collected in the study region. Poor-quality Helmeted Hornbill calls were blank labelled.	147 (77 blank labelled)
C - Site (all calls) + off-site (high quality)	Recogniser with prior labelling of a sample of Helmeted Hornbill calls of varying quality from within the study region, augmented with a sample of high-quality calls from an audio repository, the latter collected from across the species range.	345 (224 from the study region and 121 from audio repository)
D - Site (high quality) + off-site (high quality)	Recogniser with prior labelling of a sample of high-quality Helmeted Hornbill calls from within the study region, augmented with a sample of high-quality calls from an audio repository, the latter collected from across the species range. Poor-quality Helmeted Hornbill calls were blank labelled.	268 (147 from the study region and 121 from audio repository and 77 blank labelled)
E- Off-site only (high quality)	Recogniser with prior labelling of calls from across the species range from an audio repository, with all detected on-site Helmeted Hornbill calls blank labelled.	121 (224 blank labelled)
F - Off-site (high quality) + on-site (unlabelled)	Recogniser with prior labelling of Helmeted Hornbill calls from an audio repository containing calls from across the species range, with all detected Helmeted Hornbill calls from study site data left in original cluster.	121

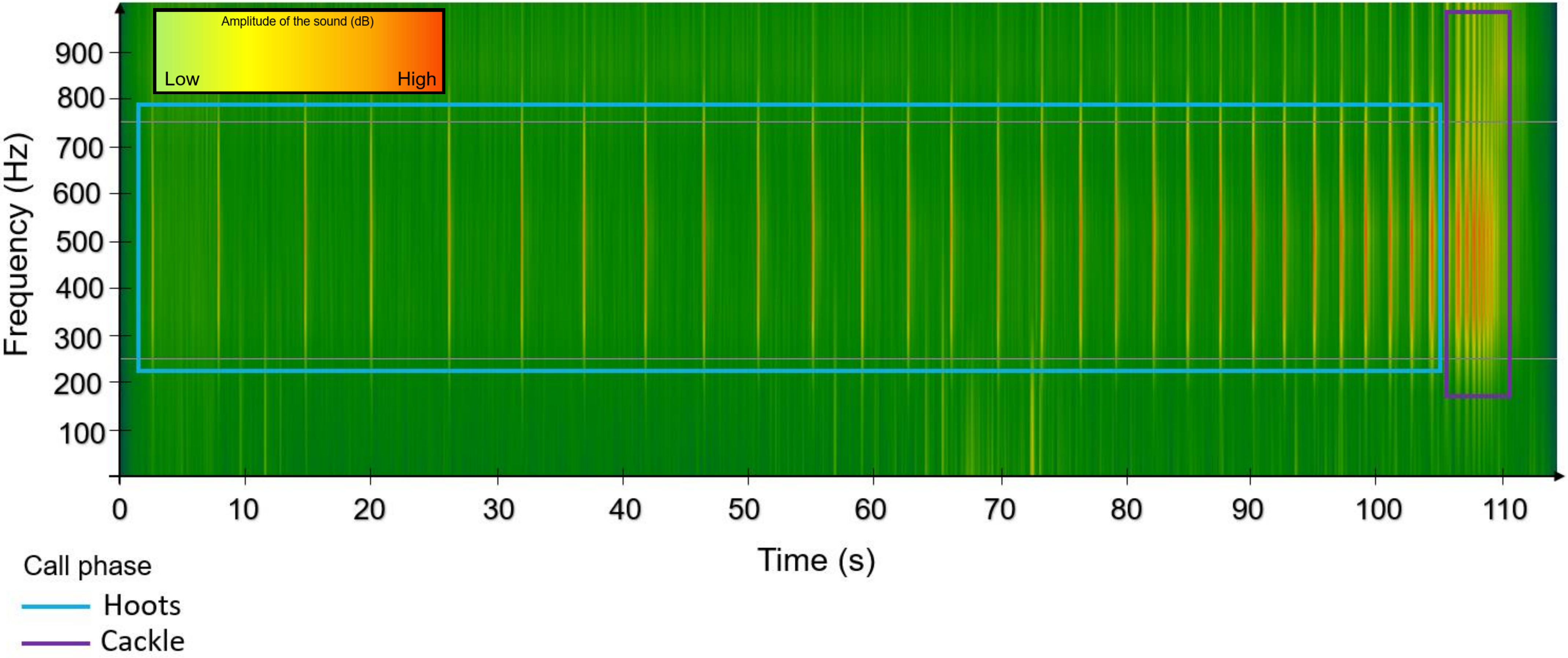


Figure 4.1 Sound spectrogram of a Helmeted Hornbill call acquired using Kaleidoscope Pro 5.4.8 software (the acoustic analysis software used in this study). The two horizontal lines indicate the frequency range (250 - 750 kHz) used in the construction of the Helmeted Hornbill recogniser (algorithm to detect and extract target calls from audio data) used for the detection of the target calls during analysis. The two coloured boxes indicated the two phases of the call (hoot and cackle).

4.3.3 Evaluating recogniser performance

Test data subset

To assess recogniser performance, all six recognisers were tested against the same subset of non-training data and the results compared. To create a test data subset, 69 audio samples (one per sampling site) were extracted, with the file from each site being randomly selected. Additionally, 35 further samples containing at least one Helmeted Hornbill call were included, with these 35 samples being evenly distributed across all sites known to have at least one audio file containing at least one Helmeted Hornbill call. The 35 samples were added due to the sparsity of Helmeted Hornbill calls, to ensure a minimum number of files in the test data subset contained Helmeted Hornbill calls. Samples consisting of recordings made at dawn or dusk were excluded from the subset and replaced with a new randomly selected file to ensure all audio files in the test data subset were the same length (7 minutes), thus ensuring balanced stratified random sampling across sites. Therefore, in total, the test data subset was made up of 728 mins of acoustic survey ((69 + 35 sites) x 7 mins recording per site).

Manual call detection

Using the Kaleidoscope Pro viewer window, we manually scanned through spectrograms of the test data subset, whilst simultaneously listening to the audio. This allowed us to record all the Helmeted Hornbill calls present in the selected files as well as any other non-target calls. A Helmeted Hornbill call was defined as an individual making at least part of the whole Helmeted Hornbill call. Typically, Helmeted Hornbills tend to produce very long calls which can be sorted into two distinct phases: the hoots and the cackle (Figure 4.1). The hoot phase comes first and consists of a long series of low-pitched hoots which start off very widespread and accelerate in frequency over time until they reach a climax, otherwise known as the cackle phase (Haimoff, 1987). The recognisers were built to detect the hoot phase as it is lower in frequency and longer than the cackle phase. These factors make this phase of the call easier to detect as, in this environment, fewer animals vocalised at lower frequencies and the longer duration of the call increases the likelihood that the recognisers will detect it. The start and end time of each hoot phase was recorded manually. If a call could not be classified as a Helmeted Hornbill with confidence (due to masking or faintness), it was discarded from the analysis.

Calculating performance metrics

To determine the ability of each recogniser to correctly identify Helmeted Hornbill calls, a series of eight performance metrics were calculated (Table 4.2) based on a confusion matrix used to evaluate machine learning outcomes (Table 4.3). The manually detected start and stop times were compared to each of the calls identified by all six recognisers: detection overlap between the two sets of start and stop times were taken on a second-by-second basis for all six recognisers. All metrics were then calculated for a 1000 randomly selected points as the data points were not independent of each other. This sampling process was repeated 1000 times to account for any possible sampling bias, with reported metrics calculated as the mean and standard deviation across all samples. The metrics were calculated in R version 4.1.2 (R Core Team, 2022) using the package *pROC* (Robin *et al*., 2011). The area under the receiver operating characteristic curves (AUC - ROC) was used to assess the trade-off between the false positive rate and sensitivity (Table 4.2) and all performance metrics were used to assess which of the six recognisers performed best overall. The Area Under the Curve (AUC) can vary between 0 and 1. When AUC is 0, the recogniser is perfectly incorrect, whereas an AUC value of 1 signifies perfect discrimination. A value of 0.5 suggests a recogniser is performing no better than random. Hence AUC scores approaching 1 signify better discrimination in terms of predicting true positives and true negatives.

Table 4.2 Metrics used to calculate and compare performance of the six Helmeted Hornbill recognisers (algorithms to detect and extract target calls from audio data). For all metrics, the scores are a value between 0 and 1 (except for TSS where values range from -1 to 1), with 1 being a perfect performing recogniser. All metrics are defined in detail and their mathematical formula given. FP = False Positive; TN = True Negative; TP = True Positive; FN = False Negative; N = TP+FP+FN+TN.

Metric & meaning	Formula
False Positive Rate (FPR) • A measure of the percentage of FP against all negatives	$\frac{FP}{FP + TN}$

Area Under the Curve (AUC) - Refers to the area under the receiver operating characteristic curve (AUC – ROC) which plots sensitivity against (1-specificity) for all possible values of threshold probability (Metz, 1978) - AUC is the compromise between False Positive Rate and sensitivity	$$\frac{FPR}{Sensitivity}$$
Sensitivity - The proportion of TP correctly predicted - Equivalent to True Positive Rate or Recall If score < 1, recogniser is missing TP and thus has a higher False Negative Rate	$$\frac{TP}{TP + FN}$$
Accuracy - The proportion of predictions the recognisers correctly assigned	$$\frac{TP + TN}{N}$$
Precision - The proportion of positive detections that are TP	$$\frac{TP}{TP + FP}$$
Specificity - The proportion of TN correctly predicted - Equivalent to True Negative Rate	$$\frac{TN}{FP + TN}$$

(Cohen's) Kappa (*κ*) • The proportion of chance-expected disagreements which do not occur (Cohen,1960) • Criticized for being dependent on prevalence	$\frac{\left(\frac{\mathrm{TP}+\mathrm{TN}}{\mathrm{N}}\right) - \frac{(\mathrm{TP}+\mathrm{FP}) * (\mathrm{TP}+\mathrm{FN}) + (\mathrm{FN}+\mathrm{TN}) * (\mathrm{TN}+\mathrm{FP})}{\mathrm{N}^2}}{1-\frac{(\mathrm{TP}+\mathrm{FP}) * (\mathrm{TP}+\mathrm{FN}) + (\mathrm{FN}+\mathrm{TN}) * (\mathrm{TN}+\mathrm{FP})}{\mathrm{N}^2}}$
True Skill Statistic (TSS) • Alternative to Kappa but accounts for prevalence in the data	$(Sensitivity + Specificity) - 1$

Table 4.3 Confusion matrix used in the performance evaluation of the six Helmeted Hornbill recognisers (algorithms to detect and extract target calls from audio data). FP = False Positive; TN = True Negative; TP = True Positive; FN = False Negative. Green cells show a correct result and red cells show an incorrect result. The best performing recogniser maximises the number of True Positives and True Negatives (correct results) whilst minimising the number of False Positives and False Negatives (incorrect results). Actual values refer to whether a call is a Helmeted Hornbill call or not and Predicted values refer to whether the recogniser in question states that a call is Helmeted Hornbill call or not.

		Actual values	
		Positive	Negative
Predicted values	Positive	TP	FP
	Negative	FN	TN

4.3.4 Statistical analysis of performance

We tested for statistical differences between the values of AUC, Kappa, and TSS calculated for each recogniser using an ANOVA test for each metric respectively. We then performed a Tukey post-hoc pairwise tests to see where the significant differences laid.

4.4 Results

Recogniser A (built with prior labelling of a sample of Helmeted Hornbill calls of varying quality calls within the data collected in the study region and with no augmentation from the sample of high-quality calls from the audio repository (Table 4.1)) had the highest performance metric values overall (Table 4.4; Figure 4.2 & 4.3), though recognisers D and E were equally as good in terms of Precision and recognisers D, E, and F were equally as good in terms of Specificity (Table 4.4). Moreover, the three summary metrics (AUC, TSS, Kappa) were all in agreement regarding the ordering of model performance (Figure 4.2 & 4.3). Thus, no single recogniser performed best in all aspects measured, but the best scoring one overall was recogniser A.

The ANOVAs showed a significant difference between performance metric values of the recognisers' AUC (F (5) = 13 588, $p < 2^{-16}$), Kappa (F (5) = 15 867, $p < 2^{-16}$), and TSS values (F (5) = 13 588, $p < 2^{-16}$). The Tukey post-hoc tests for multiple comparisons showed that there was a statistically significant difference between the performances of all six recognisers for all three summary metrics. Thus, recogniser A performed significantly better than all the other recognisers in all three statistically tested metrics.

Table 4.4 Mean values of the six Helmeted Hornbill recognisers' (algorithms to detect and extract target calls from audio data) performance metrics, along with their standard deviation, shaded according to the metric values in individual columns. Red signifies low values, through brown and pastel orange, to pastel blue and blue indicating higher values within a column. Higher values are optimal as they suggest greater recogniser performance. Full names of shortened Performance Metrics names are as follows: AUC = Area Under the Curve; Kappa = Cohen's Kappa; TSS = True Skill Statistic.

	Performance Metric						
Recogniser	**AUC**	**Accuracy**	**Precision**	**Sensitivity**	**Specificity**	**Kappa**	**TSS**
A	0.788 (±0.023)	0.950 (±0.007)	0.968 (±0.021)	0.578 (±0.047)	0.998 (±0.002)	0.697 (±0.040)	0.576 (±0.047)
B	0.697 (±0.021)	0.917 (±0.009)	0.952 (±0.030)	0.398 (±0.042)	0.997 (±0.002)	0.523 (±0.044)	0.395 (±0.042)
C	0.719 (±0.021)	0.923 (±0.008)	0.948 (±0.029)	0.441 (±0.042)	0.996 (±0.002)	0.565 (±0.042)	0.437 (±0.042)
D	0.708 (±0.022)	0.924 (±0.009)	0.968 (±0.024)	0.419 (±0.044)	0.998 (±0.002)	0.549 (±0.045)	0.417 (±0.044)
E	0.633 (±0.019)	0.894 (±0.010)	0.963 (±0.031)	0.268 (±0.037)	0.998 (±0.001)	0.380 (±0.045)	0.266 (±0.037)
F	0.572 (±0.013)	0.845 (±0.011)	0.947 (±0.042)	0.147 (±0.026)	0.998 (±0.001)	0.215 (±0.035)	0.145 (±0.026)

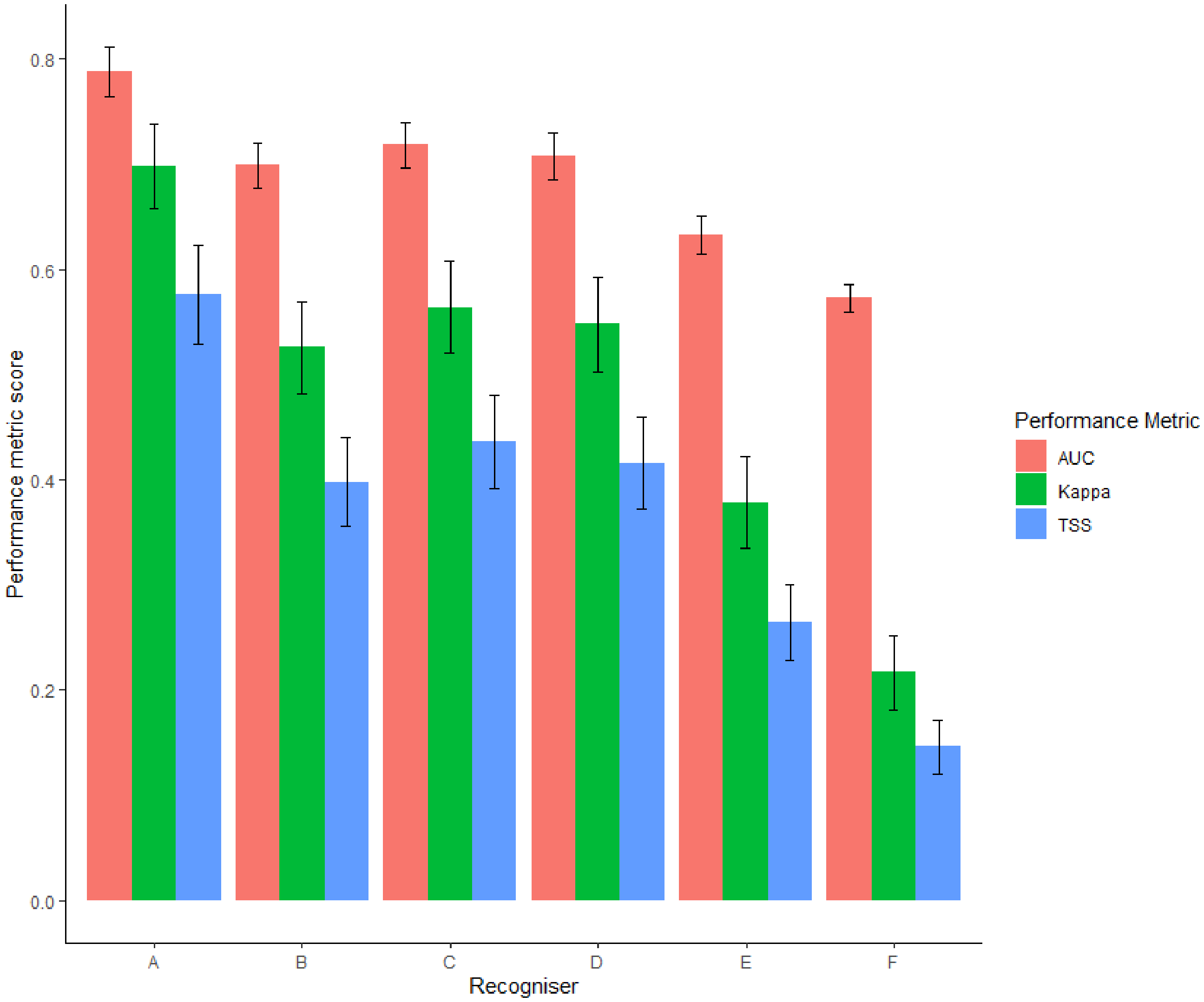


Figure 4.2 Mean performance metric scores, with their respective standard deviations (represented by the error bars), of the three summary metrics (AUC = Area Under the Curve; Kappa = Cohen’s Kappa; TSS = True Skill Statistic) used to compare performance of all six Helmeted Hornbill recognisers (algorithms to detect and extract target calls from audio data). The recogniser with the highest mean performance metric scores is the best performing recogniser, successfully differentiating True Positives from False Positives and True Negatives from False Negatives.

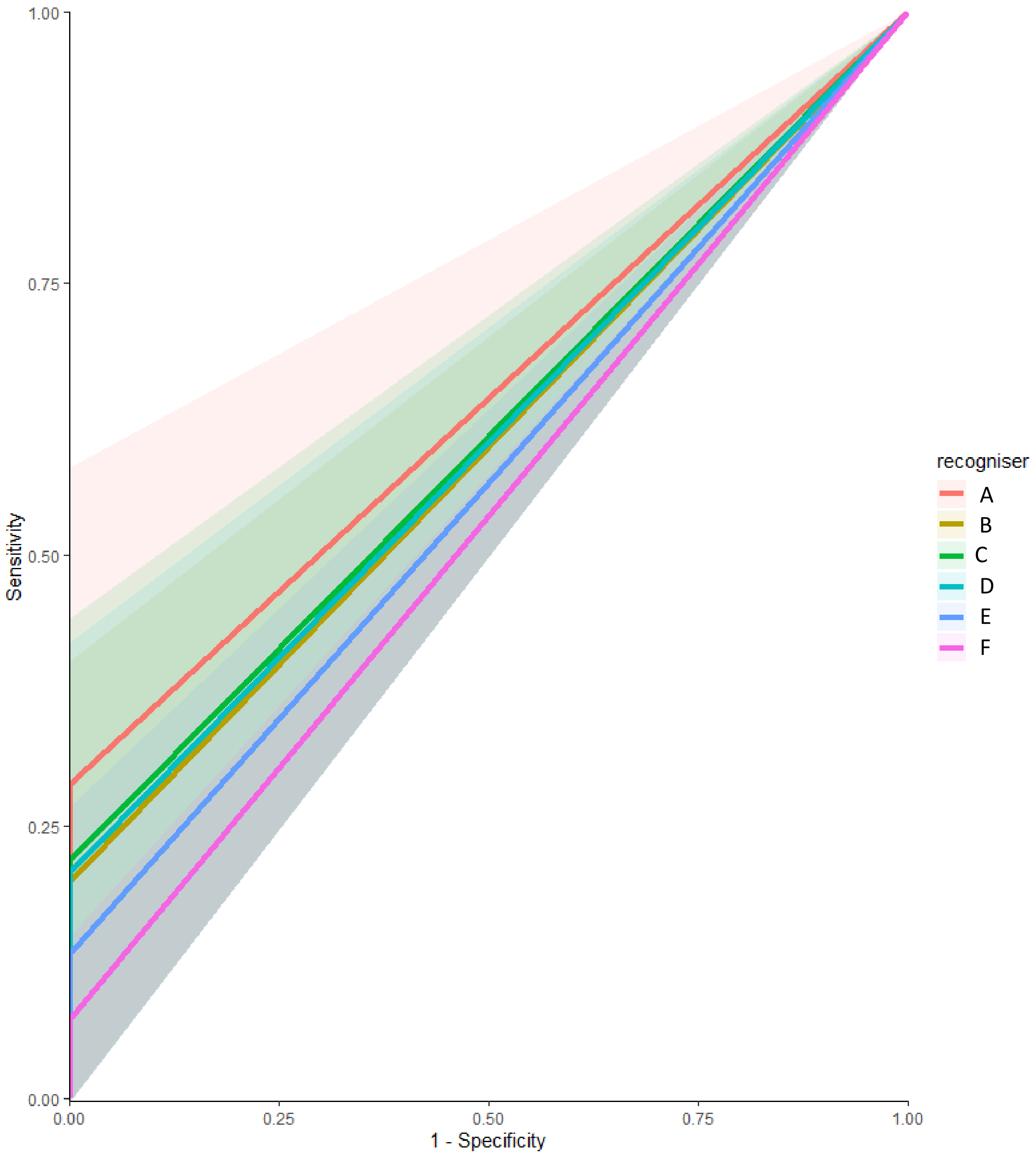


Figure 4.3 The performance of the six recognisers (algorithms to detect and extract target calls from audio data) when detecting and classifying the call of Helmeted Hornbill within acoustic surveys made through the 24-hour period. The greater the Area Under the Curve (AUC), the better performing the recogniser. When AUC is 0, the recogniser is perfectly incorrect, whereas an AUC value of 1 signifies perfect discrimination. A value of 0.5 suggests a recogniser is performing no better than random. AUC scores approaching 1 (or the greater the coverage under the curve) signify better discrimination in terms of predicting True Positives and True Negatives, and thus indicate a better performing recogniser.

4.5 Discussion

This study explored the suggestion that recogniser performance can vary according to the methods adopted during its building phase (Brooker *et al*., 2020) and provides guidance for potential users of such classification software. To do this, we developed six recognisers in Kaleidoscope Pro to automatically detect our target species (Helmeted Hornbill), using an array of different construction methods (Table 4.1) and compared their performance. We found significant differences in the performance of all six recognisers. Overall, the best performing recogniser (recogniser A) was built with prior labelling of a sample of Helmeted Hornbill calls of varying quality within the data collected in the study region. This recogniser had significantly higher AUC, TSS, and Kappa scores (Figure 4.2 & 4.3; Table 4.4) as well as higher/equal accuracy, precision, sensitivity, and specificity scores than any of the other five recognisers (Table 4.4). The only performance metrics recogniser A did not outperform all other recognisers in are precision and specificity: recognisers D and E had similar scores of precision, and recognisers D, E, and F had equal scores of specificity.

This result suggests the best method for building the most effective Helmeted Hornbill recogniser overall in Kaleidoscope Pro is to use data from the study site, as opposed to across the species range, in the training phase. Although minimal research has been done to investigate the spatial variation of soundscapes (Pijanowski *et al*., 2011; Job *et al*., 2016; Mullet *et al*., 2016), the fact that recognisers built using training data from across the species range do not perform as well when applied to our dataset suggests variation between the soundscape of other areas within the species range and the soundscape in the study area (Rodriguez *et al*., 2014). The soundscape is defined as “the entire sonic energy produced by a landscape and is the result of the overlap of three distinct sonic sources: geophony, biophony, and anthrophony” (Farina, 2013). Soundscapes are created by the organisms of a particular biome and their surroundings and thus vary with location. The soundscape therefore contains all the ‘background’ and non-target sounds recognisers must separate from target sounds. The fact that the best performing recogniser used vocalisation records collected only within the local study region as training data, suggests this recogniser is more fine-tuned to discriminate the target sounds from non-target sounds within Temburong’s soundscape specifically. However, further research needs to be done to compare the performance of these recognisers in other locations: we hypothesise that recogniser A might not perform better than recognisers built using data from across the species range when applied to data collected outside of Temburong. This was not conducted in this study due to time constraints and lack of access to a similar audio dataset from a different location. Recognisers built using data from across the species range, although less efficient than recogniser A in Temburong, might be more adapted to use on data from across the species range and thus have a more generalised usage than the latter. However, this discrepancy in recogniser performance between those trained with Xeno-Canto recordings versus on-site recordings might also be due to variation in recording devices or sound quality. Indeed, all the recordings in this study were made systematically and with the same recording devices whereas the recording methods for Xeno-Canto data vary and are ad hoc, potentially resulting in non-representative variability between calls and soundscapes present in these recordings.

In general, studies using recognisers to detect focal species tend to use data collected within the study region to build recognisers (Rycyk *et al.,* 2022; Pérez-Granados & Schuchmann, 2021; Enari *et al*., 2019). The lower performance observed when using data from across the species range may also be due to geographic variation of the call across the species' range. Although not yet studied in Helmeted Hornbills, animal vocalizations are known to differ not only within and between individuals but also between regions (Krebs & Kroodsma, 1980; Towsey *et al*., 2018; Helenbrook *et al*., 2019). Evaluating the utility of recognisers built on freely available data - such as are accessible on, for example, open-source audio databases – could be vital in more widespread adoption of recognisers in avian monitoring, as this could eliminate the time-consuming step of collecting training data in the field.

Additionally, we found that the most effective Helmeted Hornbill recogniser was one that used sample calls irrespective of their perceived quality, outperforming recognisers built on only (perceived) higher quality recordings. Including lower quality calls modified the recognisers performance in several ways. By including such calls in the *positive training* data of a recogniser, the algorithm learns a broader array of target call examples and can thus correctly categorise some less distinctive calls within a dataset. Nevertheless, as indicated by recogniser A's specificity score being equal to that of three other recognisers, this method represents a trade-off: despite detecting more target calls, this method also results in a higher false positive rate. This trade-off has been highlighted in other studies using Kaleidoscope Pro (Knight *et al.*, 2017). Thus, although labelling all quality call types ensures higher precision, it concomitantly lowers specificity, in turn lowering the proportion of true negatives correctly predicted. Thus, these trade-offs should be considered alongside the research aims and objectives of a particular project. In this project, the aim was to detect the maximum number of Helmeted Hornbill calls in the data, even if this meant spending more time manually checking for false positives. In contrast to the findings here, a previous study suggested that training recognisers with only high-quality calls improves the overall performance of the recognisers and did not change the number of true positives detected (Knight & Bayne, 2019), suggesting that the importance of call quality in recogniser creation may not be consistent. There is clear scope for a more extensive study to better understand the importance of call quality in recognisers.

Despite recogniser A proving to be the best recogniser for Helmeted Hornbill calls made in Kaleidoscope Pro, this does not necessarily make it the best potential recogniser for Helmeted Hornbill calls overall. Kaleidoscope Pro is one of many acoustic analysis software programs available; others include Raven Pro, monitoR, SongScope, and deep machine learning algorithms such as convolutional neural networks. Acoustic analysis software programs differ in their strengths and weaknesses depending on their signal detection methods, preferred frequency ranges, and robustness to noise (Brandes, 2008), which need to be considered alongside research aims. Although this varies by species and soundscape, comparative studies have found that Kaleidoscope Pro is not the best performing of these software programs (Brooker *et al*., 2020). This is depicted here in the low sensitivity score. Although recogniser A is the best performing recogniser out of the six made here in terms of sensitivity, 0.578 nevertheless remains a considerably lower score compared to other performance metrics. This suggests that there are true positives being misclassified as negatives and thus overlooked (as it was too time-costly to look through all the negative outputs to check for false negatives). Convolutional neural networks recognisers have repeatedly been found to work well as recognisers (Nolan *et al*., 2022; Zhong *et al*., 2021; Knight *et al.*, 2017) but present a greater computational/coding challenge during construction for non-experts. Ease of use is also a parameter to be considered when building recognisers: there is a need for user-friendly software programs to be available to ecologists and conservationists. Kaleidoscope Pro provides this, whilst maintaining an adequate performance level. Nevertheless, although presenting a challenge in terms of knowledge of multiple software programs, the preferable alternative to convolutional neural networks recognisers is constructing several recognisers using an array of different acoustic software (Brooker *et al*., 2020).

Regardless of the software used to extract desired elements from audio datasets, ARUs remain powerful tools for scientific research, particularly in light of the current biodiversity decline crisis (Ceballos *et al*., 2017). This surveying method is particularly useful for cryptic and rare species but also provides a cheaper, less intrusive, and more efficient way of monitoring wildlife. Here, we present a comparison of building methods for constructing recognisers in Kaleidoscope Pro for studying Helmeted Hornbills in Temburong’s tropical rainforests. Our highest performing recogniser offers the potential to easily extract Helmeted Hornbill calls from a set of audio data, despite not achieving high sensitivity scores, and is best suited to be used in areas with a similar soundscape to Temburong. Further testing needs to be conducted to see how this recogniser performs in other geographical regions compared to recognisers which have a poorer performance in our study area but might have a higher transferability to datasets with broader soundscapes. It is of utmost importance however to take care when handling data and tools which concern Critically Endangered species such as the Helmeted Hornbill, as these could ultimately worsen the problem if shared to poachers or illegal wildlife traders. Despite recent progress in automated processing and identification in audio data, there nonetheless remains great challenges when it comes to extracting data of interest out of the mass of acoustic data collected. Although this technology already exists for bats (Smith *et al*., 2020), active acoustic monitoring could present a solution to this by only recording when the target sound is detected. By implementing the filtering step earlier in the acoustic workflow, ARUs with inbuilt recognisers could be the future of biological acoustic research through essentially being in situ detectors as well as recorders. However, applying this to birds presents greater challenges as their vocalisation frequency band is lower and thus more acoustically busy than that of bats, this process could save a lot of time in downstream data processing.

4.6 References

Alcocer, I., Lima, H., Sugai, L.S.M. and Llusia, D., 2022. Acoustic indices as proxies for biodiversity: a meta-analysis. *Biological Reviews*, *97*(6), pp.2209-2236.

BirdLife International. 2020. Rhinoplax vigil. The IUCN Red List of Threatened Species 2020: e.T22682464A184587039. https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22682464A184587039.en. Accessed on 29 December 2022.

Blumstein, D.T., Mennill, D.J., Clemins, P., Girod, L., Yao, K., Patricelli, G., Deppe, J.L., Krakauer, A.H., Clark, C., Cortopassi, K.A. and Hanser, S.F., 2011. Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. *Journal of Applied Ecology*, *48*(3), pp.758-767.

Bradfer-Lawrence, T., Gardner, N., Bunnefeld, L., Bunnefeld, N., Willis, S.G. and Dent, D.H., 2019. Guidelines for the use of acoustic indices in environmental research. *Methods in Ecology and Evolution*, *10*(10), pp.1796-1807.

Brandes, T.S., 2008. Automated sound recording and analysis techniques for bird surveys and conservation. *Bird Conservation International*, *18*(S1), pp.S163-S173.

Bro-Jørgensen, J., 2010. Dynamics of multiple signalling systems: animal communication in a world in flux. *Trends in Ecology & Evolution*, *25*(5), pp.292-300.

Brooker, S.A., Stephens, P.A., Whittingham, M.J. and Willis, S.G., 2020. Automated detection and classification of birdsong: An ensemble approach. *Ecological Indicators*, *117*, p.106-609.

Ceballos, G., Ehrlich, P.R. and Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signalled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, *114*(30), pp.E6089-E6096.

Cohen, J., 1960. A coefficient of agreement for nominal scales. *Educational and Psychological Measurement*, *20*(1), pp.37-46.

Enari, H., Enari, H.S., Okuda, K., Maruyama, T. and Okuda, K.N., 2019. An evaluation of the efficiency of passive acoustic monitoring in detecting deer and primates in comparison with camera traps. *Ecological Indicators*, *98*, pp.753-762.

Farina, A., 2013. *Soundscape ecology: principles, patterns, methods and applications*. Springer Science & Business Media. Berlin.

Gill, S.A. and Bierema, A.M.K., 2013. On the meaning of alarm calls: a review of functional reference in avian alarm calling. *Ethology*, *119*(6), pp.449-461.

Haimoff, E.H., 1987. A spectrographic analysis of the loud calls of helmeted hornbills Rhinoplax vigil. *Ibis*, *129*(2), pp.319-326.

Hebets EA. 2011. Current status and future directions of research in complex signaling. *Curr. Zool.* **57**, i–v.

Helenbrook, W.D., Linck, N.A., Pardo, M.A. and Suarez, J.A., 2019. Spatial variation in black-headed night monkey (Aotus nigriceps) vocalizations. *bioRxiv*, p.688333.

Higham, J.P. and Hebets, E.A., 2013. An introduction to multimodal communication. *Behavioral Ecology and Sociobiology*, *67*, pp.1381-1388.

Job, J.R., Myers, K., Naghshineh, K. and Gill, S.A., 2016. Uncovering spatial variation in acoustic environments using sound mapping. *PloS one*, *11*(7), p.e0159883.

Knight, E., Hannah, K., Foley, G., Scott, C., Brigham, R. and Bayne, E., 2017. Recommendations for acoustic recognizer performance assessment with application to five common automated signal recognition programs. *Avian Conservation and Ecology*, *12*(2).

Knight, E.C. and Bayne, E.M., 2019. Classification threshold and training data affect the quality and utility of focal species data processed with automated audio-recognition software. *Bioacoustics*, *28*(6), pp.539-554.

Krebs, J.R. and Kroodsma, D.E., 1980. Repertoires and geographical variation in bird song. In *Advances in the Study of Behavior* (Vol. 11, pp. 143-177). Academic Press. Cambridge, Massachusetts.

Metz, C.E., 1978, October. Basic principles of ROC analysis. *In Seminars in nuclear medicine* (Vol. 8, No. 4, pp. 283-298). WB Saunders. London.

Mullet, T.C., Gage, S.H., Morton, J.M. and Huettmann, F., 2016. Temporal and spatial variation of a winter soundscape in south-central Alaska. *Landscape Ecology*, *31*(5), pp.1117-1137.

Nolan, V., Scott, C., Yeiser, J.M., Wilhite, N., Howell, P.E., Ingram, D. and Martin, J.A., 2022. The development of a convolutional neural network for the automatic detection of Northern Bobwhite Colinus virginianus covey calls. *Remote Sensing in Ecology and Conservation*, 9(1), pp. 46–61

Norouzzadeh, M.S., Nguyen, A., Kosmala, M., Swanson, A., Palmer, M.S., Packer, C. and Clune, J., 2018. Automatically identifying, counting, and describing wild animals in camera-trap images with deep learning. *Proceedings of the National Academy of Sciences,* 115(25), pp.E5716-E5725.

Pérez-Granados, C. and Schuchmann, K.L., 2021. Passive acoustic monitoring of Chaco Chachalaca (Ortalis canicollis) over a year: vocal activity pattern and monitoring recommendations. *Tropical Conservation Science*, *14*, p.19400829211058295.

Pijanowski, B.C., Farina, A., Gage, S.H., Dumyahn, S.L. and Krause, B.L., 2011. What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology*, *26*(9), pp.1213-1232.

R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.C. and Müller, M., 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics*, *12*(1), pp.1-8.

Rodriguez, A., Gasc, A., Pavoine, S., Grandcolas, P., Gaucher, P. and Sueur, J., 2014. Temporal and spatial variability of animal sound within a neotropical forest. *Ecological Informatics*, *21*, pp.133-143.

Ruxton, G.D. and Schaefer, H.M., 2013. Game theory, multi-modal signalling and the evolution of communication. *Behavioral Ecology and Sociobiology*, *67*(9), pp.1417-1423.

Rycyk, A.M., Berchem, C. and Marques, T.A., 2022. Estimating Florida manatee (Trichechus manatus latirostris) abundance using passive acoustic methods. *JASA Express Letters*, *2*(5), p.051202.

Shonfield, J. and Bayne, E., 2017. Autonomous recording units in avian ecological research: current use and future applications. *Avian Conservation and Ecology*, *12*(1).

Smith, D.H., Borkin, K.M. and Shaw, W.B., 2020. A comparison of two bat detectors: which is most likely to detect New Zealand's Chalinolobus tuberculatus? *New Zealand journal of zoology*, *47*(3), pp.233-240.

Sousa-Lima, R.S., Norris, T.F., Oswald, J.N. and Fernandes, D.P., 2013. A review and inventory of fixed autonomous recorders for passive acoustic monitoring of marine mammals. *Aquatic Mammals*, *39*(1).

Sueur, J., Farina, A., Gasc, A., Pieretti, N. and Pavoine, S., 2014. Acoustic indices for biodiversity assessment and landscape investigation. *Acta Acustica United with Acustica*, *100*(4), pp.772-781.

Suzuki, T.N., Wheatcroft, D. and Griesser, M., 2016. Experimental evidence for compositional syntax in bird calls. *Nature Communications*, *7*(1), pp.1-7.

Towsey, M., Znidersic, E., Broken-Brow, J., Indraswari, K., Watson, D.M., Phillips, Y., Truskinger, A., Roe, P. and Street, G., 2018. Long-duration, false-colour spectrograms for detecting species in large audio datasets. *Journal of Ecoacoustics*, *2*(1), pp.1-1.

Wilhite, N.G., Howell, P.E. and Martin, J.A., 2020. Evaluation of acoustic recording devices to survey northern bobwhite populations. *Wildlife Society Bulletin*, *44*(1), pp.200-207.

Zhong, M., Taylor, R., Bates, N., Christey, D., Basnet, H., Flippin, J., Palkovitz, S., Dodhia, R. and Ferres, J.L., 2021. Acoustic detection of regionally rare bird species through deep convolutional neural networks. *Ecological Informatics*, *64*, p.101333.

Zwart, M.C., Baker, A., McGowan, P.J. and Whittingham, M.J., 2014. The use of automated bioacoustic recorders to replace human wildlife surveys: an example using nightjars. *PloS one*, *9*(7), p.e102770.

Chapter 5

Evaluating the impact of infrastructure expansion on the Helmeted Hornbill and the Great Argus using species-specific acoustic recognisers

5.1 Abstract

Brunei, like much of the world, is currently experiencing a major infrastructure expansion shift. A bridge linking Temburong, a rural district with limited direct connectivity, to the rest of Brunei was opened in 2020. This connection of Temburong to the rest of the country is expected to drive infrastructure development in the region, which could impact biodiversity. Here, we explore how two bird species of special conservation value – Helmeted Hornbills (*Rhinoplax vigil*) and Great Argus (*Argus argusianus*) – are affected by infrastructure expansion. We make and use two species-specific recognisers to automate the detection of the study species' calls in an audio dataset, collected using Autonomous Recording Units (ARUs) at 69 sites along an infrastructure expansion gradient. We explored how call counts for each species, derived from the recognisers, were related to the distance to the nearest main road and nearest building, as well as to above-ground biomass. We also explored the diurnal vocal activity pattern for both species. We found that distance to nearest main road and building significantly impacted the number of Helmeted Hornbill calls, with more being detected as remoteness increased. Distance to main road was also related to the number of Great Argus calls, as was biomass, with more being detected further from roads and at sites with higher biomass. Our findings fit with the ecology of these species, as both prefer undisturbed forests, which tend to contain ecologically beneficial elements such as large nesting trees for Helmeted Hornbills and a deeper leaf-litter for foraging for Great Arguses. Additionally, both species, but particularly the Helmeted Hornbill, are at risk of poaching, a threat exacerbated by roads and proximity to human settlements. Here we demonstrate the potential vulnerability of these two threatened species to further development and show how ARUs, coupled with semi-automated processing and identification, presents a possible solution to ongoing monitoring.

5.2 Introduction

With steadily increasing human populations (having exceeded 8 billion individuals in November 2022 (United Nations, 2022)), global urbanisation and infrastructure expansion has also experienced recent rapid growth (Gerten *et al*., 2019). This is an expected outcome of human population growth but is not without consequence on the natural world that surrounds it. People move to urban areas principally to seek greater chances of prosperity. The concomitant urban sprawl that comes with such levels of rural exodus is leading to what has been described as a “suburban planet” (Keil, 2017). As discussed in Chapter 1, these trends are heightened in the tropics due to greater human population densities (Harding *et al.*, 2020) and greater numbers of developing countries found in this region of the world, in which rural exodus is more prominent (Park, 2002). Increased urbanisation also leads to increased transport infrastructure to link urban zones together. All these land use changes have direct and indirect deleterious impacts on tropical rainforest ecosystems and the biodiversity they harbour. Impacts include deforestation, habitat fragmentation, roadkill, changes to predator-prey interactions, and increased hunting pressures (Laurance *et al.*, 2009).

Brunei is currently experiencing a major infrastructure expansion shift. With the opening of the SOAS bridge in 2020, the currently rural and sparsely populated Temburong District is now directly connected by road to the highly urbanised districts of Belait, Tutong, and Brunei-Muara. This new road infrastructure has linked the Eastern part of Brunei to the capital city Bandar Seri Begawan, making Temburong a more desirable place to live, work, and visit (Polgar & Jaafar, 2018). Despite this being a positive change for the socio-economic development of the country, the bridge presents a potentially concerning ecological problem. Increased traffic density and infrastructure development is expected in response to the inevitable rise of Temburong’s population (Sembiring, 2021). This area hosts pristine rainforests, containing some of the highest levels of biodiversity globally (Dykes, 1996), and maintains remote and mountainous natural areas. Urban sprawl in Brunei-Maura has already reduced pristine rainforest cover in the country to less than 50% of the land area (Aban *et al*., 2011). This not only impacts biodiversity but also causes disruption to local climates and ecosystem services the rainforest usually provides, such as heat and water absorption and soil protection. To date, there has not been an assessment of the impact of infrastructure expansion in Temburong, possibly because it has not been a cause for concern until the last few years which coincided with heavy Covid-19 restrictions in Brunei, preventing any research being undertaken (Omar & Halim, 2021).

In this chapter, we study the potential impact of infrastructure expansion on two tropical birds of special conservation interest in Borneo. We use distances to main roads and buildings, as well as biomass as proxies for infrastructure expansion and habitat quality respectively. The species studied are the Helmeted Hornbill (*Rhinoplax vigil*) and the Great Argus (*Argusianus argus*). Both species are charismatic and emblematic of Borneo's tropical rainforests, often deeply embedded in local culture, making them key flagship species for conservation efforts (Philovenny & Mohd-Azlan, 2021; Aihara *et al*., 2008). The Helmeted Hornbill is part of the Hornbill (*Bucerotidae*) family of birds and has a range extending across the Sundaic lowlands, namely Thailand, Myanmar, Malaysia, Indonesia, Brunei, but is considered extinct in Singapore (BirdLife International, 2001). This species resides in primary semi-evergreen and evergreen lowland forest in rugged terrain up to elevations of 1 500m a.s.l. (BirdLife International, 2020$_{A}$). However, the species only remains in small pockets of forest across its range due to factors such as habitat loss and poaching. The Helmeted Hornbill is the only species in the Hornbill family to have a solid 'horn', or casque, which it uses for aerial jousting when competing for mates, territories, or food. This solid casque has resulted in Helmeted Hornbills being heavily poached due to the casque's value in the illegal wildlife trade market (Beastall *et al*., 2016); it is estimated to be worth five times more than elephant ivory (Collar, 2015). This trade is considered a primary reason for the plummet of the species' population. There has been a sharp increase in illegal Helmeted Hornbill trafficking since 2011, coinciding with BirdLife International's decision to change the species' conservation status to Critically Endangered (Jain *et al*., 2018; BirdLife International, 2020$_{A}$).

The Great Argus is also suffering from the twin threats of habitat loss and poaching – although not to the same extent as the Helmeted Hornbill – and is listed as Vulnerable on the IUCN Red List (BirdLife International, 2020$_{B}$). This species is ground living and shares a very similar geographic range to the Helmeted Hornbill, residing in lowland rainforests up to elevations of around 900m a.s.l. (BirdLife International, 2020$_{B}$). The Great Argus is constituted of two subspecies: the Bornean Great Argus (*Argusianus argus grayi*), studied here, and the Malay-Sumatra Great Argus (*Argusianus argus argus*) (Winarni *et al*., 2009) and is one of the largest of the *Phasianidae* family of birds. Although this species is cage-trapped for the sale of feathers and for food, this harvesting appears to be for ceremonial reasons rather than commercial (BirdLife International, 2020$_{B}$). The bird is known for its exploded-lek mating system whereby the males perform dances at designated sites which they clear on the forest floor (Johnsgard, 2002). Despite the mating system being polygynous, the female only lays 2 eggs a year, making Great Argus a *K*-selected species and, thus, less resilient to sudden environmental change than similar, but more fecund, species.

Acoustic communication is key to fundamental biological functions across many taxa, including mate attraction, territorial defence, interactions with conspecifics, and during foraging (Wilkins *et al.*, 2013). The use of Autonomous Recording Units (ARUs) in ecological studies has revolutionised the study of vocalising but otherwise cryptic species in a cost-efficient manner (Sugai *et al.*, 2019). ARUs are similarly well suited to monitoring species concurrently across extensive remote regions. Both of these above characteristics are relevant to the two focal study species in Brunei. Both species are also well suited to censusing using ARUs as they produce distinct, long, and far-carrying loud calls. The Helmeted Hornbill call has been described as the “most distinctive call in Borneo” (Phillipps, 2014) and is the loudest sound made by any animal in the rainforest, carrying up to 2 km (Haimoff, 1987). Typically, the Helmeted Hornbill call can be divided into two distinct phases: a series of hoots and a cackle (Figure 4.1). The hoot phase comes first and consists of a long series of low-pitched hoots which start off very widespread and accelerate in frequency over time until they reach a climax, otherwise known as the cackle phase. Although it is thought that this unique call is used mainly by males to defend territories and attract a mate, breeding pairs have been seen to engage in calling duets (Haimoff, 1987). The Great Argus has several different calls and although the species is heavily sexually dimorphic with males calling before performing mating dances (Davison, 1981_{B}), females are also known to be vocal to defend foraging territories (Davison, 1981_{A}).

Recent advances in the field of bioacoustics have resulted in the development of a variety of software packages (Knight *et al.*, 2017) with which users can construct recognisers: algorithms capable of automatically detecting and extracting target calls from audio data. Kaleidoscope Pro is one of the commercially available software packages (US$300 annual license, Wildlife Acoustics, USA) which aids in acoustic data processing namely by providing a ready-to-use algorithm to detect and classify acoustic sounds through Hidden Markov Models. Using this software, we develop and use recognisers designed specifically to identify the calls of the two species respectively. Using these recognisers, the primary objective of this chapter is to evaluate the impact of infrastructure expansion on the distribution and regularity of persistence at sites of the two species. A secondary aim is to explore their diurnal calling patterns to widen ecological knowledge for these elusive species.

5.3 Methods

5.3.1 Data collection

For details on the study site, sampling protocols, and data pre-processing, see Chapter 2.

5.3.2 Recognisers

In order to detect the relevant calls for the two focal species from the audio data collected, a variety of recognisers were developed using the software Kaleidoscope Pro 5.4.8 (Wildlife Acoustics Inc., Maynard, MA, USA). For details about the workflow of constructing recognisers in Kaleidoscope Pro, see Chapter 4: *section 4.3.2*. To be able to differentiate between target and non-target calls, recognisers must be provided with training data, within which the user manually labels what is a target call to 'train' the recogniser to automatically detect these in future audio data provided.

The recognisers for both species were provided with the same set of data collected from the study site as training data. The training data were obtained from five ARUs. The localities of these five sites, all of which included some Helmeted Hornbill and Great Argus vocalisations, are not specified here to avoid informing future persecution. The training sites tended, from preliminary data exploration, to have more frequent calls than other sites. Although the selected sites were grouped, they were nonetheless selected as training data following the recommendation of Enari *et al*. (2019), as typically the more calls that are used to build a recogniser, the better it performs.

To detect the Helmeted Hornbill calls, we selected the best performing recogniser (Recogniser A) from the six that were developed in Chapter 4. This recogniser was built with prior labelling of a sample of Helmeted Hornbill calls of varying quality, all derived from recordings collected within the study region. To detect Great Argus calls, another recogniser was created, using a similar protocol, i.e. built with prior labelling of a sample of Great Argus calls of varying quality within the data collected in the study region. However, in the case of the Great Argus recogniser, the training calls were augmented with a sample of high-quality Great Argus calls from the Xeno-Canto online audio repository (www.xeno-canto.org); the latter collected from across the species range. Despite the assessment of performance metrics in Chapter 4 indicating that the best performing recogniser was built using only data collected in the local study region, Great Argus calls from further afield were included in recogniser training due to the low numbers of Great Argus calls found within the data collected from the study region. This was therefore a compromise between having sufficient calls to build a working recogniser initially and the type of calls used in the building phase. We were granted special access to Great Argus calls from Xeno-Canto as the availability of these calls are restricted to protect the species from persecution arising from playback being used to detect or attract individuals.

To make the data processing more efficient, signal parameters (frequency band of call, length of call, and time between calls) are entered into Kaleidoscope Pro before the scanning process begins, thus reducing the output detections to sounds that fit those criteria. See Chapter 4 for details about the signal parameters used for the Helmeted Hornbill recogniser. The signal parameters used to find Great Argus calls were acquired by observing example calls from Xeno-Canto through the Kaleidoscope Pro viewer window. The signal parameters of the Great Argus call were measured using the spectrograms of a sample of example Great Argus calls (See Figure 5.1 for an example Great Argus call). The measurements were narrowed down to maximum precision through repeated trials using the clustering function. The final signal parameters used to detect Great Argus calls were as follows: 600 Hz minimum frequency, 1200 Hz maximum frequency, 15 s minimum detection length, 90 s maximum detection length, and 1.2 s maximum inter-syllable gap. A 21.33 ms Fast Fourier Transform window was used during the clustering phase of recogniser construction as this was the best setting for low frequency sounds because it provides higher resolution of frequency (see Kaleidoscope Pro user manual). The maximum distance to cluster centre for building clusters was set to 0.5 (recommended setting) and the maximum number of states was set to 15. See Chapter 4: *4.3 Methods* for justification details about these parameters.

Unlike Helmeted Hornbills who have a single, distinct call, Great Arguses typically produce three call types (Clink *et al.*, 2021). To build the recogniser we focussed solely on the most common call type (‘kwow kwow’ call; Figure 5.1). This is the call type used by both sexes for territorial demarcation and during inter-pair disputes, whereas the other calls are produced by males only during mate attraction (Davison, 1981$_{A}$). Hence, this was a more frequent call and, as a result, considered likely to be better at confirming the species presence at a site.

5.3.3 Call count data

The Helmeted Hornbill and the Great Argus recognisers were individually applied to the full audio dataset collected. All the outputs classified as positive detections were manually verified by the same observer (LE) and, hence, the true positive detections were differentiated the from the false positive detections. Detections were verified both auditorily and visually, the latter using the spectrogram viewer in Kaleidoscope Pro. We collated the data to record the total number of calls for each species for each recoding day, time of day, and site. We used total call count instead of presence/absence of calls at sites to have a higher resolution in our call count data as we assumed more calls at a site was indicative of greater use of that area. However as there was no way of differentiating individuals based on the calls recorded, we could not use number of calls to estimate population densities. Due to slight variation in battery life and occasional malfunctions, not all the ARUs recorded for exactly the same number of days (See Appendix B for a list of deviations from the programmed regime). To standardise the measurements across all recording sites, we divided the total number of calls detected by the number of recording days and then multiplied that result by 30 (the average ARU deployment period) for both species at each site respectively. This calling rate was considered a proxy for the distribution and regularity of persistence at sites for each species and was then used as the dependant variable in models to relate each species vocal detection rate to habitat covariates. The data points were considered independent as they were placed sufficiently distant from each other to avoid duplicate detections of any vocalisation event and deployed following a stratified random distribution.

5.3.4 Habitat variables & correlation

Six habitat covariates were initially measured: *Distance to Nearest Main Road, Distance to Nearest Road, Distance to Nearest Building, Nearest Road Type, Infrastructure Pressure Zone,* and *Biomass* (See Chapter 3: s*ection 3.3.3* for details). Due to high correlation between many of these variables (See Chapter 3: *section 3.3.4* and Appendix C), only *Distance to Nearest Main Road, Distance to Nearest Building,* and *Biomass* were retained and used in statistical analysis as they were deemed to be the most relevant to the research question.

5.3.5 Statistical analysis

To investigate the impact of infrastructure expansion (measured by distances to main roads, buildings, and biomass) on the distribution and regularity of persistence at sites of Helmeted Hornbills and Great Arguses, we fitted the most appropriate model form for the analysis of each species. All statistical analyses and graphics were undertaken in R version 4.1.2 (R Core Team, 2022). For the Helmeted Hornbill call count data we fitted a Generalized Linear Model (GLM) with a Negative Binomial distribution using the *glm.nb* function from the *MASS* package as this was the model type that best fitted the distribution of this dataset. Despite the zero-inflated distribution of this data (Figure 5.2A), we did not fit a zero-inflated model here as the results did not converge. For the Great Argus call count data, we fitted a GLM with a Zero-inflated Negative Binomial distribution using the *zeroinfl* function from the *pscl* package, with *Distance to Nearest Main Road, Distance to Building,* and *Biomass* as predictors for the Poisson process, and *Distance to Nearest Main Road* as the predictor for the Bernoulli process. The Bernoulli process tries to model out the over-inflation from the large number of zeros in the dataset and looks at presence/absence of calls. Only one variable was used for the Bernoulli process due to a lack of degrees of freedom: with only 69 data points we could only fit models with a maximum of 6-7 degrees of freedom, following Harrell's (2001) rule of 10 observations per parameter. The Poisson process considers how many times the birds have called if there is the presence of call(s). Additionally, using the mean and standard deviation of the call count data per 1-hour slot across all sites with at least one call recorded, diurnal calling patterns were explored for both species. Sites with no calls at all were disregarded for this part of the analysis as otherwise the data would be too zero-inflated.

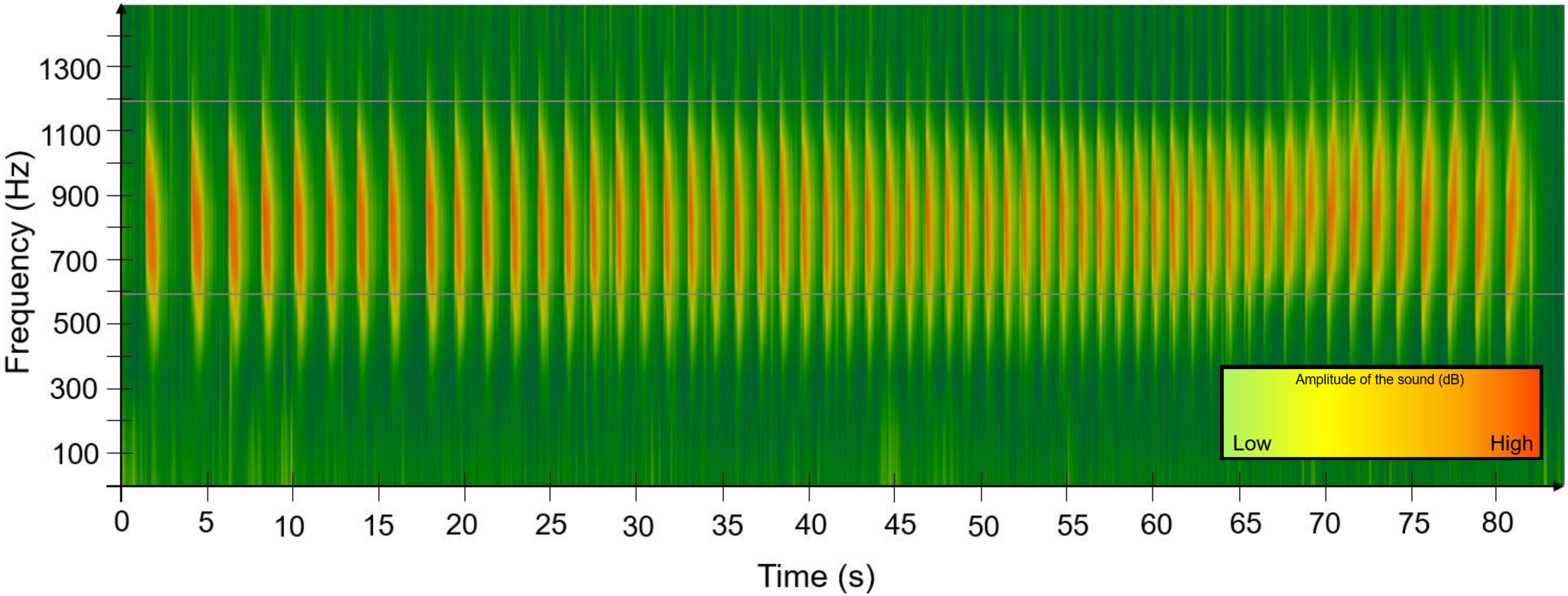


Figure 5.1 Sound spectrogram of an example ‘kwow kwow’ Great Argus call acquired using Kaleidoscope Pro 5.4.8 software (the acoustic analysis software used in this study). The two horizontal lines indicate the frequency range (600 - 1200 kHz) used in the construction of the Great Argus recogniser (algorithm to detect and extract target calls from audio data) used for the detection of the target calls during analysis. This is one of several calls made by this species.

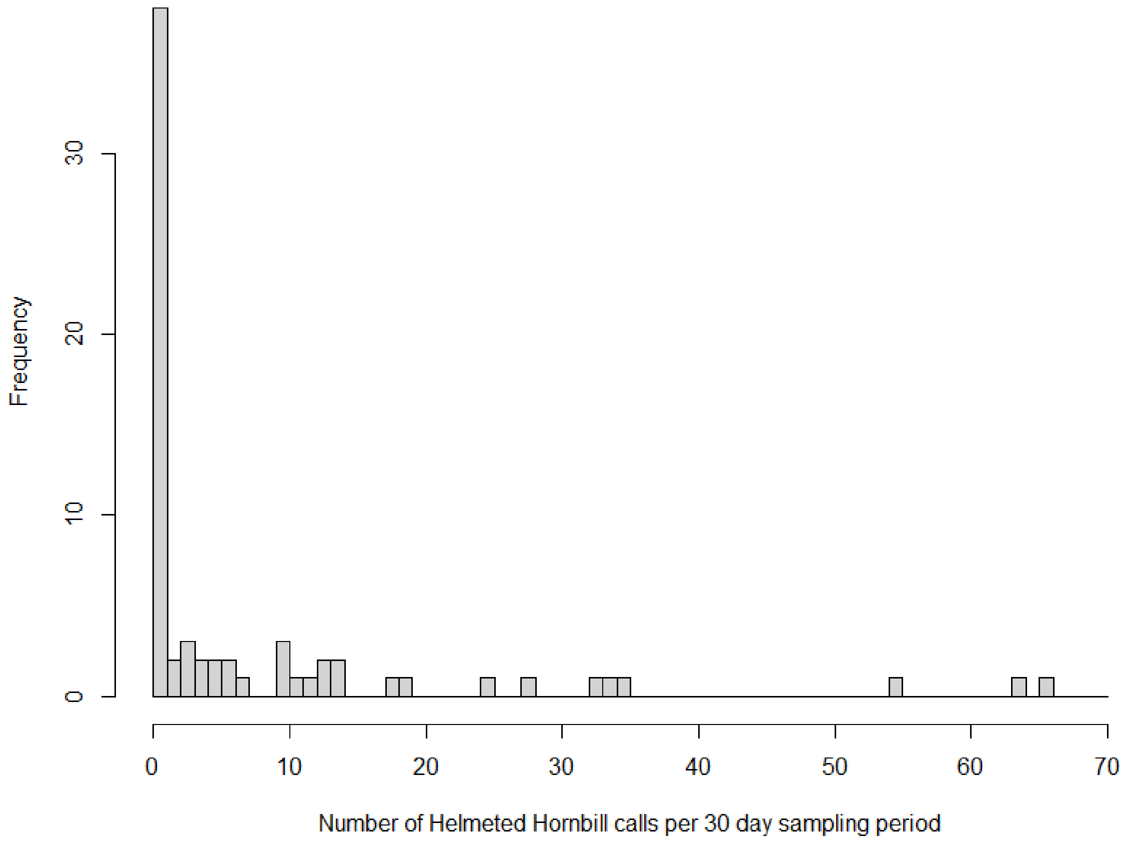
5.4 Results

5.4.1 Model results

Zero-inflation and tests of normality

The numbers of calls for both Helmeted Hornbills and Great Arguses within recording segments were highly zero inflated: over 49% and 63% of sites had no Helmeted Hornbill or Great Argus calls respectively. A Shapiro-Wilk test showed significant evidence of non-normality for both the Helmeted Hornbill call count variable (W = 0.60, $p = 2.02^{-12}$) and the Great Argus call count variable (W = 0.58, $p = 9.56^{-13}$); see also Figure 5.2.

A)



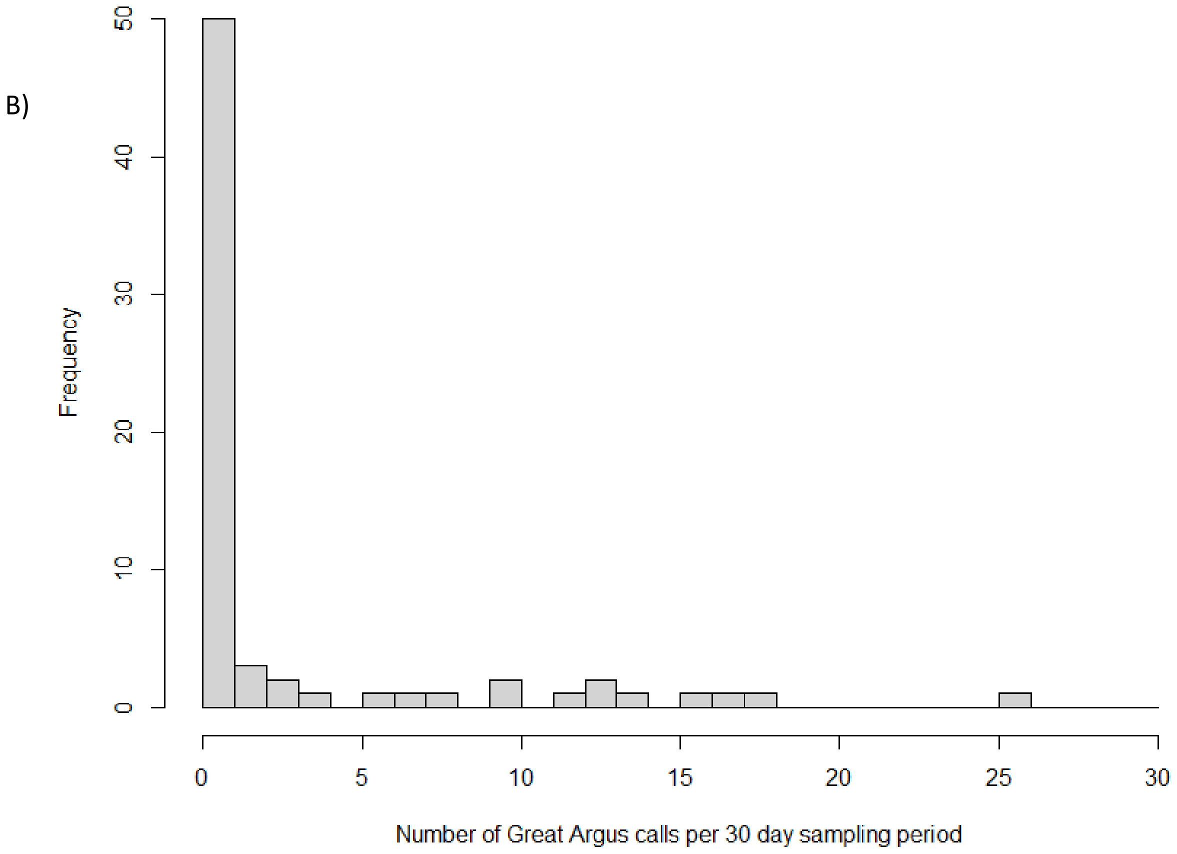


Figure 5.2 Distribution of the number calls per 30 day sampling period for A) the Helmeted Hornbill and B) the Great Argus. Frequency on the Y-axis refers to the number of sites (i.e. Autonomous Recording Units) which registered the call frequencies displayed on the X-axis, i.e. the majority of sites didn't register a call for either species. Both histograms are zero-inflated and highly suggestive of non-normality.

Helmeted Hornbill

The Negative Binomial GLM for the Helmeted Hornbill call count data indicated that *Distance to Building* was significantly positively related to call frequency, with the call count being greater further away from buildings (Z-value = 3.545; Table 5.1), for example with call count increasing by 11.12 calls for an increase of 10km from nearest building. Similarly, the Negative Binomial GLM for the Helmeted Hornbill call count data indicated that *Distance to Nearest Main Road* was significantly positively related to call frequency, with the call count being greater further away from roads (Z-value = 4.864; Table 5.1), for example with call count increasing by 5.445 calls for a 10km increase of distance from the nearest main road. *Biomass*, by contrast did not have a significant impact on the number of calls. Nevertheless, all three variables were positively correlated with the number of calls (Figure 5.3), meaning that the greater the distance from the nearest main road or building and the greater the biomass, the higher the number of Helmeted Hornbill calls. This model was slightly over dispersed (dispersion Statistic = 1.139), but this was the best fitting model for this dataset and all the variables converged.

Table 5.1 Statistical results from the Generalized Linear Model with a Negative Binomial distribution applied to the Helmeted Hornbill call count data. The target calls were extracted from the vast amounts of audio data using a species-specific recogniser (algorithm to detect and extract target calls from audio data) made in Kaleidoscope Pro (the acoustic analysis software used in this study). Distance to building is the distance between each site and the nearest building, distance to nearest main road is the distance between each site and the nearest main road to that site, and biomass is the total above ground biomass calculated using an allometric equation previously used in tropical forests in conjunction with data collected in the field. The distance variables were measured using Google Earth Pro. The null deviance was 108.20 on 68 degrees of freedom and the residual deviance was 64.13 on 65 degrees of freedom. AIC was 333.46. $R^2 = 0.407$ (McFadden's pseudo R^2). Significant effects are shown in green ($p < 0.05$).

	Estimate	**Standard Error**	**Z value**	***p*-value**
(Intercept)	-1.346	0.437	-3.077	0.002093
Biomass	2.834^{-05}	1.693^{-05}	1.674	0.094059
Distance to Building	1.112^{-03}	3.136^{-04}	3.545	0.000392
Distance to Nearest Main Road	5.445^{-04}	1.119^{-04}	4.864	1.15^{-06}

Great Argus

The Poisson count component of the Zero-Inflated Negative Binomial GLM for Great Argus call count data indicated that *Biomass* was weakly significantly positively related to call frequency, with the call count being greater with increasing levels of biomass (Z-value = 5.144; Table 5.2A), for example with call count increasing by 0.09366 call for a 10 000 Mg increase of biomass per 400m^2 plot. The model also indicated that *Distance to Nearest Main Road* was significantly positively related to call frequency (Table 5.2A), with the call count being greater with increasing distance to nearest main road (Z-value = 2.430; Table 5.2A), for example with call count increasing by 2.96 calls for a 10km increase in distance to nearest main road. *Distance to Building*, by contrast, did not have a significant impact on the number of calls (Table 5.2A). Nevertheless, all three variables were positively correlated with the number of calls (Figure 5.4), meaning that the greater the distance from the nearest main road or building and the greater the biomass, the higher the number of Great Argus calls. The model also suggested for the Bernoulli (zero-inflated, binary component) that *Distance to Nearest Main Road* had a significant but very small negative effect on the occurrence of calls (Table 5.2B), meaning that the likelihood of there being any Great Argus calls decreased as the distance from the nearest main road increased. Overall, this model was slightly under dispersed (dispersion Statistic = 0.930) but this was the best fitting model for this dataset and all the variables converged.

Table 5.2 Statistical results from the Generalized Linear Model with a Zero-Inflated Negative Binomial distribution applied to the Great Argus call count data for A) the Poisson process (count model) and for B) the Bernoulli process (zero-inflated model). The target calls were extracted from the vast amounts of audio data using a species-specific recogniser (algorithm to detect and extract target calls from audio data) made in Kaleidoscope Pro (the acoustic analysis software used in this study). Distance to building is the distance between each site and the nearest building, distance to nearest main road is the distance between each site and the nearest main road to that site, and biomass is the total above ground biomass calculated using an allometric equation previously used in tropical forests in conjunction with data collected in the field. The distance variables were measured using Google Earth Pro. Log-likelihood was -96.73 on 7 degrees of freedom. R^2 = 0.971 (adjusted R^2 obtained using the *r2_zeroinflated* function from *performance* package in R). Significant effects are shown in green ($p < 0.05$).

A	Estimate	Standard Error	Z value	***p*-value**
(Intercept)	1.274^{-02}	3.959^{-01}	0.032	0.9743
Biomass	9.366^{-06}	1.821^{-06}	5.144	2.70^{-07}
Distance to Building	3.924^{-04}	2.285^{-04}	1.717	0.0859
Distance to Nearest Main Road	2.960^{-04}	1.218^{-04}	2.430	0.0151
Log (theta)	8.841^{-01}	2.070^{-01}	4.271	1.94^{-05}

B	Estimate	Standard Error	Z value	***p*-value**
Intercept	2.0751212	0.5269815	3.938	8.22^{-05}
Distance to Nearest Main Road	-0.0008758	0.0002151	-4.072	4.67^{-05}

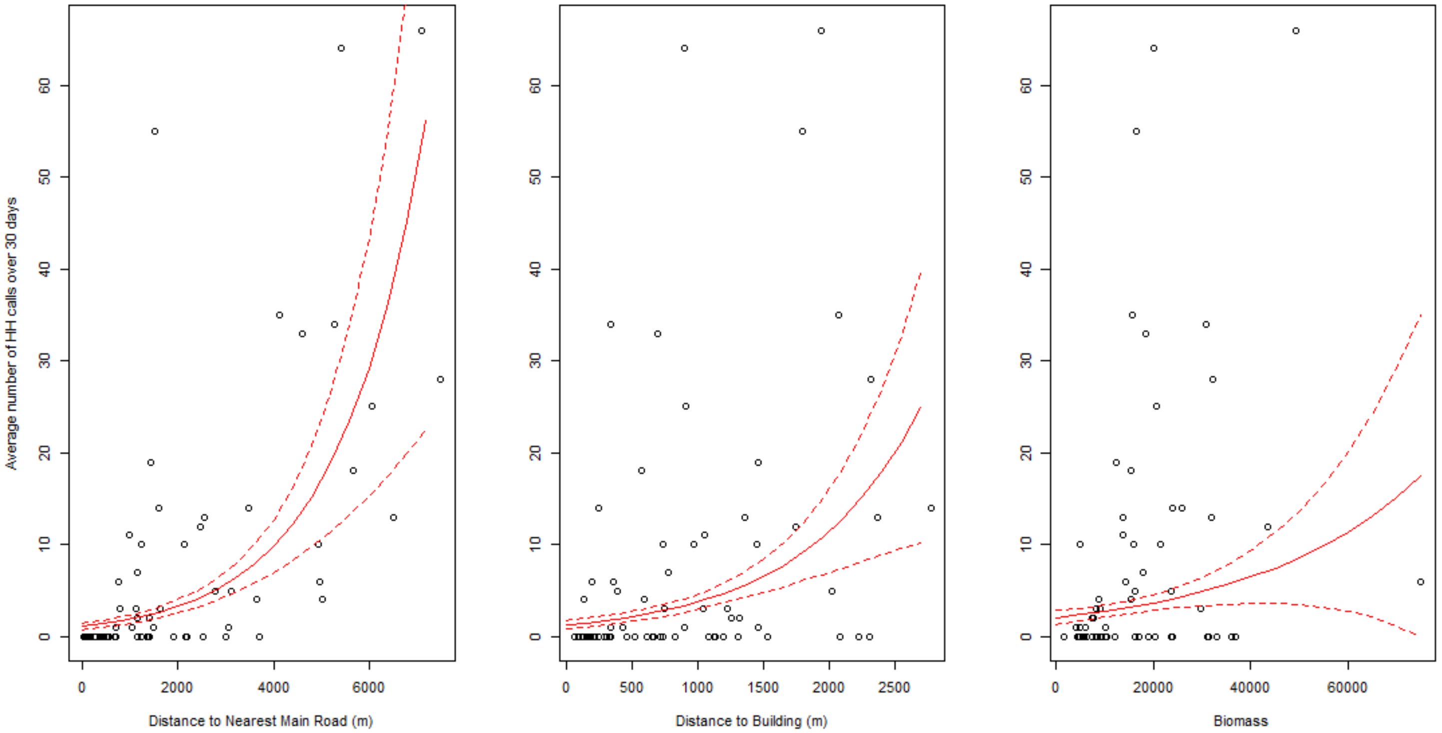


Figure 5.3 Relationship between the average number of Helmeted Hornbill calls per 30-day sampling period (at n = 69 recording sites) and the *Distance to Nearest Main Road, Distance to Nearest Building,* and *Biomass* respectively. The target calls were extracted from the vast amounts of audio data using a species-specific recogniser (algorithm to detect and extract target calls from audio data) made in Kaleidoscope Pro (the acoustic analysis software used in this study). Distance to building is the distance between each site and the nearest building, distance to nearest main road is the distance between each site and the nearest main road to that site, and biomass is the total above ground biomass calculated using an allometric equation previously used in tropical forests in conjunction with data collected in the field. The distance variables were measured using Google Earth Pro. The solid lines are the predicted model lines plotted using the predicted values from the Generalised Linear Model with a negative binomial distribution fitted to the Helmeted Hornbill call count data. Each one is plotted whilst keeping the other variables at their mean. The dotted lines represent standard error. R^2 = 0.407 (McFadden’s pseudo R^2).

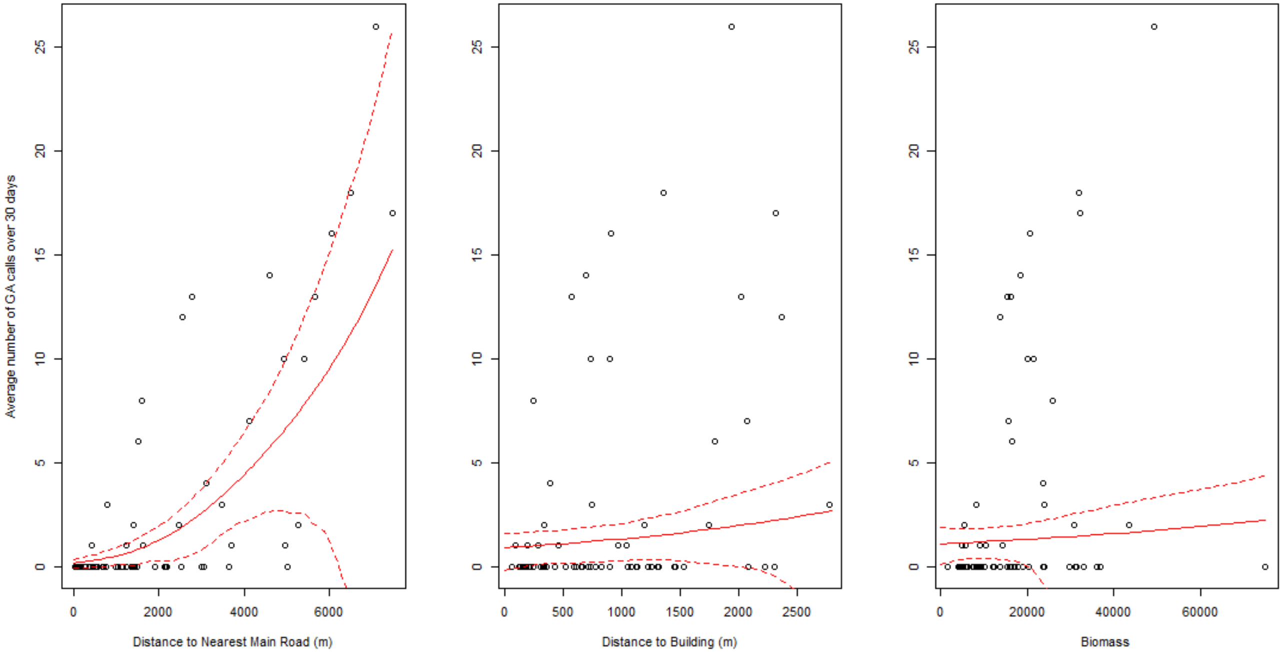
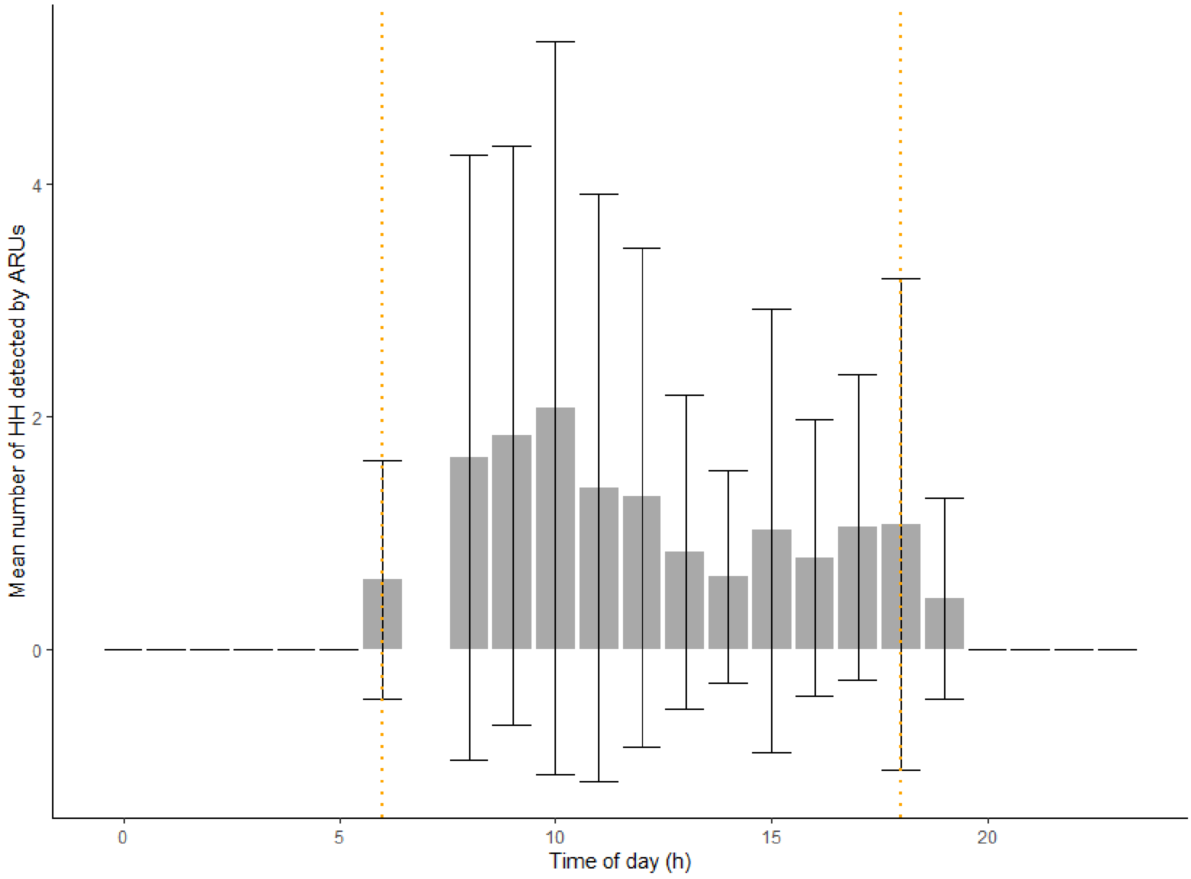


Figure 5.4 Relationship between the average number of Great Argus calls per 30-day sampling period (at n = 69 recording sites) and the *Distance to Nearest Main Road, Distance to Nearest Building,* and *Biomass* respectively. The target calls were extracted from the vast amounts of audio data using a species-specific recogniser (algorithm to detect and extract target calls from audio data) made in Kaleidoscope Pro (the acoustic analysis software used in this study). Distance to building is the distance between each site and the nearest building, distance to nearest main road is the distance between each site and the nearest main road to that site, and biomass is the total above ground biomass calculated using an allometric equation previously used in tropical forests in conjunction with data collected in the field. The distance variables were measured using Google Earth Pro. The solid lines are the predicted model lines plotted using the predicted values from the zero-inflated Generalised Linear Model with a negative binomial distribution fitted to the Great Argus call count data. Each one is plotted whilst keeping the other variables at their mean. The dotted lines represent 95% confidence intervals. R^2 = 0.971 (adjusted R^2 obtained using the *r2_zeroinflated* function from *performance* package in R).

5.4.2 Diurnal patterns

The diurnal calling patterns of both studied species was explored and indicated very different vocalising behaviour. Helmeted Hornbills are most vocal around 10h00 but maintain a relatively high level of vocal activity throughout daylight hours, with call frequency rapidly dropping after dusk (Figure 5.5A). By contrast, Great Arguses have a major peak in vocal activity after dusk, at around 19h00, and are less vocal through the day than the Helmeted Hornbill (Figure 5.5B). Nevertheless, both figures have very large standard errors, thus indicating very high inter-site variability and that these patterns are driven by a few specific sites. The standard error bars go below 0 due to standard errors being larger than the means, this does not indicate that there were negative levels of calls at a site (minimum number of calls at a site was 0).

A)



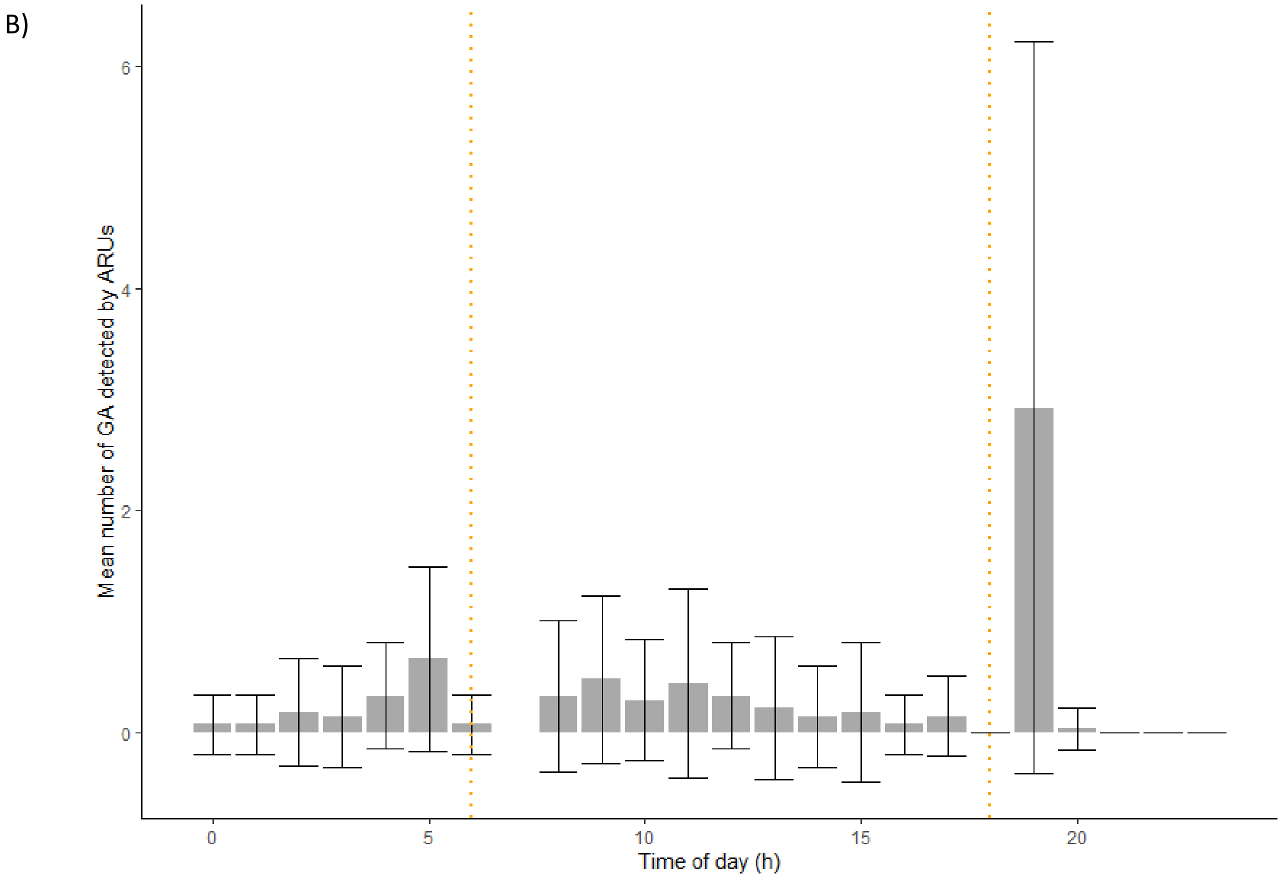


Figure 5.5 Diurnal calling patterns over the 24h period of the A) Helmeted Hornbill (Pattern calculated using n = 38 sites) and B) Great Argus (Pattern calculated using n = 27 sites). The study design included 69 randomly generated recording sites, at which one Autonomous Recording Unit (ARU) was set up to record for a 30-day period. Only the sites where at least one target species call was recorded were used in generating the diurnal calling patterns. The target calls were extracted from the vast amounts of audio data using species-specific recognisers (algorithms to detect and extract target calls from audio data) made in Kaleidoscope Pro (the acoustic analysis software used in this study). The two vertical dotted lines indicate dawn and dusk.

5.5 Discussion

Infrastructure expansion and associated forest degradation can both negatively influence the abundance and distribution of tropical bird species, ultimately homogenising the surrounding biota, resulting in a loss of biodiversity (Isaksson, 2018; Luck & Smallbone, 2010; Sewell & Catterall, 1998). In this study, we explored the effect of main roads, buildings, and biomass (taken as proxy measurements for levels of infrastructure expansion) on two such species:

the Helmeted Hornbill and the Great Argus. Both species' populations are decreasing in recent years due to widespread habitat loss and ongoing hunting pressures (BirdLife International, 2020$_{A \& B}$). It is therefore paramount that more research is conducted into these species regarding their basic ecology and what environmental factors they are sensitive to. We used call count data as a proxy for distribution (through presence/absence) and regularity of persistence (number of calls) in both species. These data cannot be used to assess the abundance as such, as there is no way of telling if the detected calls are from the same individual repeatedly or several different individuals. Furthermore, using call count presents limitations as higher call rates could also be due to fruiting events, increased behavioural activities related to breeding or offspring, or something else. Nevertheless, we assume that a higher number of calls means the bird(s) spend(s) more time in that area and thus have more regular persistence.

The three variables *Distance to Nearest Main Road, Distance to Building,* and *Biomass* each had a positive effect on the number of calls from both species (Table 5.1 & 5.2; Figure 5.3 & 5.4). Thus, the greater the distance from the nearest main road or building and the greater the biomass, the higher the number of Helmeted Hornbill and Great Argus calls (Figure 5.3 & 5.4). However, we also found that *Distance to Nearest Main Road* had a very slight negative significant effect on Great Argus call presence, meaning the greater the distance from the road, the less likely there is to be a call in the first place. Nevertheless, taken into consideration the high intercept and the positive significant effect of *Distance to Nearest Main Road* on the number of calls, this negative effect is minor.

The impacts of infrastructure expansion on the Helmeted Hornbill and the Great Argus are of concern but not surprising. Both species are threatened, with the Helmeted Hornbill listed as Critically Endangered and the Great Argus listed as Vulnerable on the IUCN Red List (BirdLife International, 2020$_{A \& B}$). This is, in part, because they both have a preference for undisturbed primary forest. Like other Hornbill species, Helmeted Hornbills need tall, large trees with large hollow cavities in which to nest (Utoyo *et* al., 2017). These are typically found in pristine, unlogged rainforests as trees need time to develop such characteristics (Chambers, 1998). Additionally, studies have shown that Helmeted Hornbills prefer large expanses of closed canopy forests (Hidayat *et al.*, 2020), thus making the species sensitive to the impacts of habitat fragmentation. Furthermore, the interaction between these two factors further worsens their individual effects, as rainforest fragmentation has been linked to die-off of larger trees (Laurance *et al*., 2000). Similarly, Great Arguses have been shown to avoid colonising disturbed habitats, as they require a deep leaf litter layer, which is characteristic of primary forests, as this provides essential foraging substrate. Moreover, primary forests tend to have a more open understory, which the birds need for their display grounds (Winarni *et al.*, 2009). An open understorey may also facilitate movement of Great Arguses, due to their large size (length of circa 70 cm for females and up to 2m for males). These characteristics are typical of pristine primary rainforests and are lost when areas are disturbed by, e.g., infrastructure expansion, selective logging, mining, agriculture and edge effects (See Chapter 1: *1.4 Threats*). Land use change – typically causing habitat loss in forest ecosystems – is one of the leading causes of biodiversity declines worldwide (Jantz *et al.*, 2015). Thus, it follows that both species would be expected to spend more time in areas further from main roads and buildings, and where the biomass is higher, as indeed we found.

A potential explanation for the slight negative significant effect of *Distance to Nearest Main Road* and Great Argus presence is the existence of primary forest-type habitats close to some parts of the highway. This therefore provides the ideal type of habitat for Great Arguses despite the proximity of a main road. Nevertheless, properly testing this hypothesis would require additional data to be collected, with perhaps a structured resurveying effort to ensure a good mix of primary and secondary forest both close to, and distant from roads. Future studies would need to ensure a balanced design of ARU deployment such that as many permutations as possible of biomass and disturbance values were sampled whilst minimising collinearity of the two variables to avoid obscuring inferences as to which factor is the primary driver of presence of the species.

Helmeted Hornbills could be disproportionally affected by another threat concomitant to the presence of roads and buildings compared to Great Arguses: easier entry ways into the forest. These often result in an associated increase in illegal hunting in these remote ecological communities (Laurance *et al.*, 2006, 2009). The hard yet easily sculpted casque of the Helmeted Hornbill is highly sort after in Chinese culture to fashion luxury, status-affirming objects and its demand has dramatically increased since 2011, with an estimated 6 000 Helmeted Hornbills killed a year in West Kalimantan, Indonesia alone (Collar, 2015). The life-history of this species worsens the impacts of such heavy poaching persecution. Even in optimal habitat conditions, the species occurs at low population densities, of between 0.05 to 2.6 individuals per km^2 (Medway & Wells 1971; Johns 2004). When exposed to slight hunting pressure, their population density has been shown to decline rapidly (Johns, 2004). Helmeted Hornbills follow a *K*-selection strategy, with individuals living up to 50 years and monogamous breeding pairs only laying one or two high-input eggs per breeding cycle, the latter lasting nearly half a year (Utoyo *et al.*, 2017; Jain *et al.*, 2018). Moreover, when nesting, the female is fully enclosed in the hollow nesting chamber, becoming completely dependant on the male for food. Thus, if one adult male is killed, this can have a cascading effect as the female and the chick cannot survive, and even if the female does, she will not breed for a long time and will be in a very poor condition due to heavy moulting (Collar, 2015). Extensive collaborative efforts have occurred between the IUCN, BirdLife International, the Helmeted Hornbill Working Group, and various other conservation organisations, to create a conservation strategy and action plan which consists of eliminating the Helmeted Hornbill trade, protecting the remaining populations and their habitats, and conducting further research into the species (Jain *et al.*, 2018), with the intention that the current work will contribute to the latter. Brunei is thought to be a stronghold for the species due to firearms being illegal and the country's financial wealth allowing it to not exploit the rainforest. There would be benefits in repeating the study in areas where the bird is less protected. The species need for high quality primary forest habitat and sensitivity to hunting pressure coupled with its highly desirable casque leaves the survival of the Helmeted Hornbill species in a very precarious state going forward. Whether the species apparent avoidance of developed areas (and/or preference for primary forests) is driven by ecological and behavioural factors, or whether it is simply an artefact of areas where persecution is likely to occur would be a relevant topic for future study.

Similarly, despite both species being negatively affected by lower *Biomass* levels, different factors could be causing these similar responses. One such of these factors could be differences in diet and foraging techniques. The Great Argus has a more varied diet than the Helmeted Hornbill, feeding on insects, shoots, flowers, fruits, and seeds, with tracked birds typically traveling less than circa 850m (± 211 m) per day (Davison, 1981$_A$; Winarni *et al.*, 2009). Whereas the Helmeted Hornbill primarily feeds on figs and is known to travel far to forage (Kitamura et al. 2011; Kaur *et al.*, 2019) – in turn making them key seed dispersers. Hence, we might expect much more variability in the consistency of Helmeted Hornbill calls at a site over longer time periods than those of the Great Argus. Although, to the best of our knowledge, Helmeted Hornbill territory size has not yet been measured, radio-tracking of the related Great Hornbill (*Buceros bicornis*) shows that its home-range can be up to 100 km^2. Given that Helmeted Hornbills likely has a narrower dietary niche (feeding mainly solely on figs (Kitamura et al. 2011; Kaur *et al.*, 2019)) it's home range could be even larger (Jain *et al.*, 2018). Thus, it might be that the Great Argus needs habitats that are locally richer and more consistent, in terms of food supply, than the Helmeted Hornbill. However the Great Argus is probably less vulnerable than the Helmeted Hornbill as the species is more generalist: as long as there is lots of something they eat, and not necessarily everything they eat, they will persist. The environmental data collected during the current study do not allow us to test this hypothesis.

The diurnal calling patterns showed that Helmeted Hornbills had a mid-morning vocalisation peak around 10h00 but that the species maintains a relatively high level of vocal activity throughout the daytime hours (Figure 5.5A). To the best of our knowledge this is the first study of diurnal vocalisation patterns in Helmeted Hornbills. Great Arguses' peak in vocal activity occurred after sunset (around 19h00) and individuals were far less vocal throughout the day than the Helmeted Hornbill (Figure 5.5B). Another study of the circadian rhythms of Great Arguses (Clink *et al.*, 2021), found contrasting results to ours, with singing events more likely in the early morning. This bout of calling mainly consisted, however, of the short call type which we did not focus on and serves a very different purpose, so is not comparable. Nevertheless, the study did find that the Great Argus was most vocal outside of daylight hours, in line with our findings.

Despite the advantages of using acoustic data, such data has limitations. Call detections, which we used to infer presence and regularity of persistence could be impacted by reduced call rates (or reduced detection) near roads. For example, detectability could be impacted by road noise pollution, though this was considered unlikely to impact the current study given the relative low traffic volumes. Birds may however have been less vocal in areas of high persecution risk, and individuals may be less vocal in areas of lower densities (e.g., less need to defend territories). Additionally, using our data we were only able to build a recogniser which detected one type of Great Argus call. Future work could focus on building recognisers for all Great Argus call types and exploring how this impacts these findings.

With global declines in diversity and abundance of species, it is becoming increasingly vital to focus conservation efforts on biodiversity hotspots like the rainforests of Borneo. Monitoring species to be able to detect changes, and to monitor the impacts of conservation interventions is vital. The current project has hopefully provided some baseline information on the occurrence of these two key species in Temburong, Brunei. This could serve as a useful baseline against which to assess changes due to infrastructure expansion, or due to conservation efforts. ARUs coupled with semi-automated processing and identification presents a possible solution to ongoing monitoring. Here, we present two recognisers built using Kaleidoscope Pro to affordably and automatically detect calls emitted by two target species: the Helmeted Hornbill and the Great Argus. The two species seem to be negatively impacted by the presence of main roads, buildings, and lower biomass levels. The former two factors potentially facilitate access to the forest namely for poachers, thus increasing the threat of hunting of both species but particularly the Helmeted Hornbill due to the high value of its solid casque. The utilisation of ARUs and recognisers for monitoring could not only be used for further research into these species' behaviours and ecologies but could inform eco-responsible policies and choices about future infrastructure development.

5.6 References

Aban, J.E., Duane, W. and Yit, G.V.Y., 2011. The potential impact of urbanisation on climate change: Brunei Darussalam case study. In *44th EAROPH & IFHP Regional Planning Conference* (pp. 1-13).

Aihara, Y., Momose, K. and Koizumi, M., 2008. Iban Knowledge of Wild Birds in a Habitat Mosaic. *Sustainability and Biodiversity Assessment on Forest Utilization Options*, p.405.

Beastall, C., Shepherd, C.R., Hadiprakarsa, Y. and Martyr, D., 2016. Trade in the Helmeted Hornbill Rhinoplax vigil: the 'ivory hornbill'. *Bird Conservation International*, *26*(2), pp.137-146.

BirdLife International. 2001. *Threatened birds of Asia: The BirdLife International Red Data Book*. BirdLife International, Cambridge, U.K.

BirdLife International, 2020A. *Argusianus argus*. *The IUCN Red List of Threatened Species* 2020: e.T22725006A183255774. https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22725006A183255774.en. Accessed on 01 December 2022.

BirdLife International. 2020B. *Rhinoplax vigil*. *The IUCN Red List of Threatened Species* 2020: e.T22682464A184587039. https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22682464A184587039.en. Accessed on 01 December 2022.

Chambers, J.Q., Higuchi, N. and Schimel, J.P., 1998. Ancient trees in Amazonia. *Nature*, *391*(6663), pp.135-136.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C. and Henry, M., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, *20*(10), pp.3177-3190.

Clink, D.J., Groves, T., Ahmad, A.H. and Klinck, H., 2021. Not by the light of the moon: Investigating circadian rhythms and environmental predictors of calling in Bornean great argus. *PloS one*, *16*(2), p.e0246564.

Collar, N.J., 2015. Helmeted Hornbills Rhinoplax vigil and the ivory trade: the crisis that came out of nowhere. *BirdingASIA*, *24*, pp.12-17.

Davison, G.W.H., 1981A. Diet and dispersion of the great argus Argusianus argus. *Ibis*, *123*(4), pp.485-494.

Davison, G.W.H., 1981B. Sexual selection and the mating system of Argusianus argus (Aves: Phasianidae). *Biological Journal of the Linnean Society*, *15*(2), pp.91-104.

Dykes, A.P., 1996. Brunei's Temburong rainforests and implications for conservation and development. *Environmental change in South-East Asia: People, Politics and Sustainable Development*, p.301.

Enari, H., Enari, H.S., Okuda, K., Maruyama, T. and Okuda, K.N., 2019. An evaluation of the efficiency of passive acoustic monitoring in detecting deer and primates in comparison with camera traps. *Ecological Indicators*, *98*, pp.753-762.

Gerten, C., Fina, S. and Rusche, K., 2019. The sprawling planet: Simplifying the measurement of global urbanization trends. *Frontiers in Environmental Science*, *7*, p.140.

Haimoff, E.H., 1987. A spectrographic analysis of the loud calls of helmeted hornbills Rhinoplax vigil. *Ibis*, *129*(2), pp.319-326.

Harding, S., Penny, A., Hunt, E., Diop, H., Kalanzi, B., Touitha, Y., Archer, C., Jackson, A., McHugh, J., Chang, O. and Mohamed, A., 2020. State of the Tropics.

Harrell, F.E., 2001. *Regression Modeling Strategies: with Applications to Linear Models, Logistic Regression, and Survival Analysis* (Vol. 608). New York: springer.

Hidayat, R.A., Febriani, N., Hanif, M. and Rahman, H., 2020. Modeling of Conservation Priority Zone for the Helmeted Hornbill (Rhinoplax Vigil) In Silokek Geopark Area, West Sumatra. *Preprints*

Isaksson, C., 2018. Impact of urbanization on birds. *Bird Species*, *235*, p.257.

IUCN, 2022. The IUCN Red List of Threatened Species. Version 2022-1. https://www.iucnredlist.org. Accessed on 06 December 2022.

Jain, A., Lee, J.G. and Chao, N., 2018. Helmeted hornbill (Rhinoplax vigil): status review, range-wide conservation strategy and action plan (2018–2027).

Jantz, S.M., Barker, B., Brooks, T.M., Chini, L.P., Huang, Q., Moore, R.M., Noel, J. and Hurtt, G.C., 2015. Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation. *Conservation Biology*, *29*(4), pp.1122-1131.

Johns, A.G., 1997. *Timber Production and Biodiversity Conservation in Tropical Rain Forests*. Cambridge University Press.

Johnsgard, P.A., 2002. The pheasants of the world: Biology and natural history. *History and Philosophy of the Life Sciences, 23(3/4,* pp. 547

Kaur, R., Singh, S., Ramli, R., Hassan, H., Majinun, A., Ancrenaz, M., Ratag, M., Rauf, H.A., Jamal, J., Rauf, A.S.A. and Yunus, M.D.M., 2019. Observations at a nest of Helmeted Hornbill Rhinoplax vigil in Borneo, Malaysia. *Forktail*, *34*, pp.68-73.

Keil, R., 2017. *Suburban Planet: Making the World Urban from the Outside In*. John Wiley & Sons. Hoboken, New Jersey.

Kitamura, S., Thong-Aree, S., Madsri, S. and Poonswad, P., 2011. Characteristics of hornbill-dispersed fruits in lowland dipterocarp forests of southern Thailand. *The Raffles Bulletin of Zoology*, *24*, pp.137-147.

Knight, E., Hannah, K., Foley, G., Scott, C., Brigham, R. and Bayne, E., 2017. Recommendations for acoustic recognizer performance assessment with application to five common automated signal recognition programs. *Avian Conservation and Ecology*, *12*(2).

Laurance, W.F., Delamônica, P., Laurance, S.G., Vasconcelos, H.L. and Lovejoy, T.E., 2000. Rainforest fragmentation kills big trees. *Nature*, *404*(6780), pp.836-836.

Laurance, W.F., Croes, B.M., Tchignoumba, L., Lahm, S.A., Alonso, A., Lee, M.E., Campbell, P. and Ondzeano, C., 2006. Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology*, *20*(4), pp.1251-1261.

Laurance, W.F., Goosem, M. and Laurance, S.G., 2009. Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution*, *24*(12), pp.659-669.

Luck, G.W. and Smallbone, L.T., 2010. Species diversity and urbanisation: patterns, drivers and implications. In *Urban Ecology*. Cambridge: Cambridge University Press, pp.88–119.

Medway, L. and Wells, D.R., 1971. Diversity and density of birds and mammals at Kuala Lompat, Pahang. *Malayan Nature Journal*, *24*, pp.238-247.

Omar, A.M. and Halim, A., 2021. Whole-of-nation approach in COVID-19 management: The case of Brunei Darussalam. In *Global Perspectives on Change Management and Leadership in the Post-COVID-19 Era* (pp. 35-55). IGI Global.

Park, C.C., 2002. *Tropical rainforests*. Routledge. Oxford.

Phillipps, Q., 2014. Phillipps' field guide to the birds of Borneo, 3rd edn. John Beaufoy. Oxford.

Philovenny, P. and Mohd-Azlan, J., 2021. How do people in the "Land of Hornbills" perceive Hornbills? *Bird Conservation International*, *33,* pp.1-15.

Polgar, G. and Jaafar, Z., 2018. Ecotonal Networks (ENTs). In *Endangered Forested Wetlands of Sundaland* (pp. 41-55). Springer, Cham. NY.

R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Sembiring, M., 2021. Smart City Development: Supporting Climate Resilience in Southeast Asia? In *Non-Traditional Security in the Asia-Pacific: A Decade of Perspectives.* S. Rajaratnam School of International Studies. Singapore, pp. 47-51.

Sewell, S.R. and Catterall, C.P., 1998. Bushland modification and styles of urban development: their effects on birds in south-east Queensland. *Wildlife Research*, *25*(1), pp.41-63.

Sugai, L.S.M., Silva, T.S.F., Ribeiro Jr, J.W. and Llusia, D., 2019. Terrestrial passive acoustic monitoring: review and perspectives. *BioScience*, *69*(1), pp.15-25.

United Nations (2022). *Population*. [online] United Nations. Available at: https://www.un.org/en/global-issues/population.

Utoyo, L., Marthy, W., Noske, R.A. and Surahmat, F., 2017. Nesting cycle and nest tree characteristics of the Helmeted Hornbill Rhinoplax vigil, compared to the Wreathed Hornbill Rhyticeros undulatus, in Sumatran lowland rainforest. *Kukila*, *20*, pp.12-22.

Wilkins, M.R., Seddon, N. and Safran, R.J., 2013. Evolutionary divergence in acoustic signals: causes and consequences. *Trends in Ecology & Evolution*, *28*(3), pp.156-166.

Winarni, N.L., O'brien, T.G., Carroll, J.P. and Kinnaird, M.F., 2009. Movements, distribution, and abundance of Great Argus Pheasants (Argusianus argus) in a Sumatran rainforest. *The Auk*, *126*(2), pp.341-350.

Chapter 6

Comparing detection rates of Great Argus from audio recorders and camera traps

6.1 Abstract

Monitoring vulnerable rainforests is vital in implementing effective conservation strategies, yet traditional surveying methods present many limitations. Remote sensing technologies, such as camera traps and Autonomous Recording Units (ARUs), allow standardised, semi-autonomous high-resolution monitoring of wildlife in hard-to-access habitats. These surveying methods are becoming commonplace for assessing species occurrences, whilst providing vital data about animal activity budgets, habitat use, and potentially densities. Here, we explore the suitability of two remote sensing methods to monitor Great Argus (*Argusianus argus*), a ground-dwelling pheasant of conservation concern. We quantitatively compared the number of days camera traps and ARUs detected at least one Great Argus to assess their utility and potential complementarity in monitoring. We applied a Great Argus recogniser to automate call detection within an audio dataset. We then statistically compared number of detection days from paired camera traps and ARUs deployed across 26 forest sites for which there was at least one record of the species. We also contrasted diurnal detectability patterns from the two surveying methods. We found that ARUs were significantly more likely to detect Great Arguses than camera traps but that the diurnal detection patterns differed between the methods. The greater detection rate of ARUs is likely principally to be due to their greater detection area and their reduced sensitivity to microtopographic barriers. Whilst camera traps did not provide additional sites of detection, compared to ARUs alone, they did provide records at times when the species was not vocalising (or when the ARU wasn't recording), and hence provided a better understanding of the species' ecology. However, once a recogniser has been developed for a species, data extraction from ARUs has low personnel overheads, whereas, in the absence of auto-image classification, camera traps have an ongoing processing time cost. Hence, if resources are limited for monitoring of rare vocal species, we suggest ARUs are preferable to use to detect species presence but, if resources allow, adding camera traps can provide additional information.

6.2 Introduction

Tropical rainforests are essential ecosystems for both biodiversity and humanity. As well as comprising key habitats and possessing high intrinsic value, tropical rainforests provide a multitude of vital ecosystem services, including climate regulation (Foley *et al*., 2002). In spite of this, today's tropical rainforests face a plethora of threats, including deforestation (Hansen *et al*., 2013), slash-and-burn agriculture (Brady, 1996) and overexploitation of non-woody resources (Ripple *et al*., 2015). Despite existing on four of the world's seven continents (Hazarika, 2013), tropical rainforests remain understudied (Brodie *et al*., 2012). Tropical rainforests are thought to harbour approximately half of global biodiversity (Wilson & Peter, 1988; Pillay *et al*., 2022) but many species remain undescribed (Giam *et al*., 2012). This is thought, in part, to be due to the extreme environmental conditions found in tropical rainforests ecosystems. With high annual temperatures and humidity levels, dense vegetation and often treacherous terrain, tropical rainforests are difficult to access and, thus, to monitor. Furthermore, most of them are in developing nations that lack the funding and capacity to conduct and publish scientific research, aggravating this issue. Consequently, given both their biodiversity and ecosystem service values, it is vital to develop survey techniques to help the scientific community gain a better understanding of these crucial ecosystems, to inform effective conservation strategies.

A variety of survey techniques have been used to study wildlife in tropical rainforests. Traditional line transects are often used, whereby researchers look and listen for animals of interest along walked or driven routes (Anderson, 1976). Alternatively, point count samples are frequently used to monitor birds from fixed points (Ralph *et al*., 1995). At night, eyeshine surveys can be conducted using flashlights or headtorches to detect nocturnal animals' eyes, using the reflective surface – tapetum lucidum – located behind their retina, which reflects the shined light towards the observer (Subalusky *et al*., 2009). Trap systems have also been used, such as mist nest for birds and bats (Karr, 1981; Mancini *et al*., 2022), pitfall traps for invertebrates (Woodcock, 2005), or baited traps used to attract and capture target taxa, such as butterflies (Lucci Freitas *et al*., 2014) as well as scat sampling, namely for elusive mammals (Janečka *et al.*, 2008). Surveying rainforests canopies is often challenging but critical for biodiversity assessment, as most vertebrate rainforest species spend most of their time off the ground (Lowman & Moffett, 1993). Such monitoring requires more skills, often involving elaborate equipment – such as climbing gear, cranes, and canopy walkways – resulting in higher costs and safety risks (Houle *et* al., 2004; Lowman, 2009; Parker *et al*., 1992). All of these traditional survey methods are time consuming, subject to observer bias, require expertise, and data collection protocols are often not so easily systematically reproducible.

Remote sensing surveys present a potential solution to these survey issues for some taxa by reducing time and field skill demands, and thus costs. They can also reduce observer bias and data can be collected in a repeatable and systematic way. Additionally, remote sensing technologies are less invasive than traditional surveys, which can provide less biased information. They also provide the users with a digital dataset, aiding downstream data processing and analysis.

One method of remote-sensed wildlife monitoring is camera trapping. Although often regarded as a relatively new technology, camera traps have been used for over 100 years by hunters and then biologists (Sanderson & Trolle, 2005; Noss *et al.*, 2013) to gain an insight into the lives of cryptic, rare, and shy species. Today's digital camera traps are equipped with infrared sensors which, when triggered by a passing animal, take a photograph (WWF, 2018). Camera traps can be deployed in the field for months at a time and have become a commonplace tool to assess species diversity and abundance, whilst also providing vital data about animals' activity budgets and habitat use (Noss *et al.*, 2013). This survey method helps biologists to inventory and monitor wildlife, both furthering ecological knowledge of study species, which, in turn, can inform conservation strategies. Nevertheless, camera trapping remains an underutilised technology due to the misalignment between the technological progress made in cameras, batteries, and data storage versus downstream data management tools (Harris *et al.*, 2010). The speed of image processing is not keeping pace with the technological developments of camera hardware.

Until recently, camera traps were the only automated wildlife monitoring tool in widespread use to conduct large scale spatiotemporal sampling. More recently, another remote sensing technology which now also allows users to conduct large spatiotemporal wildlife monitoring, is Autonomous Recording Units (ARUs). Used for bioacoustical monitoring, ARUs have revolutionised the field of wildlife remote sensing in the past decade and given rise to the new discipline of soundscape ecology (Pijanowski *et al.*, 2011$_{A}$). Like camera traps, ARUs can be left unattended in the field for long periods of time (Sidie-Slettedahl *et al.*, 2015), recording the soundscape around them. A soundscape has been defined as "collection of sounds that emanate from landscapes" – namely biophony, geophony, and anthrophony: sounds produced by biological, geophysical and anthropological sources respectively (Pijanowski *et al.*, 2011$_{B}$). Thus, ARUs present themselves as a comparable technology to camera traps but allow researchers to detect species acoustically instead of visually. Like camera traps, the use of ARUs is currently limited by acoustic processing software lagging behind the rapid technological advances of ARU hardware. Nevertheless, ARUs and camera traps are proving to be an essential tool to further wildlife monitoring in hard-to-access ecosystems such as tropical forests.

Camera traps and ARUs present similar surveying capabilities but have rarely been used in conjunction (See Buxton *et al*., 2018 for literature review of studies that have compared these methods; Enari *et al*., 2019; Crunchant *et al*., 2020; Garland *et al*., 2020), with most finding ARUs to be more sensitive in species detection when studying vocalising animals. Here, we present the first study, to the best of our knowledge, where both methods were deployed simultaneously in Bruneian forests of Temburong, Borneo. We chose to focus this comparison on one species, the Great Argus (*Argusianus argus*). This was due to the species local cultural and conservation value, as well as its forest floor habitat use and its regular vocalization behaviour. The Great Argus is one of the largest species in the *Phasiabidae* family of birds and is given special ceremonial importance in local cultures. The species is listed as Vulnerable on the IUCN Red List (BirdLife International, 2020) due to habitat loss and poaching. Great Arguses are ground dwelling birds with distinct and loud calls (Clink *et al*., 2021), making them well suited to both camera trapping and ARU monitoring. Comparative studies of Great Argus vocalisations, conducted using traditional survey methods, suggested that line transects gave higher density estimates than point counts (Nijman, 2007). This study is a first step in conducting a similar study using remote sensing technologies. Our primary goal here is to evaluate which remote surveying method is best suited to the study of Great Arguses by comparing respective detection rates in order to guide future ecological studies on Great Arguses and similar species. A secondary aim is to give an overview of the advantages and disadvantages of both remote surveying methods.

6.3 Methods

6.3.1 Data collection

For details on the study site, sampling protocols and data pre-processing, see Chapter 2.

6.3.2 Great Argus detections

Camera trap data

To compare the audio survey results and camera images, we deployed camera traps at the same sites as the ARUs (See Chapter 2). The resultant images were sorted and identified manually. Photographs including all ground-foraging avian species were identified to species level where possible. Photographs including Great Arguses were separated, and the data aggregated to record the total number of days at each site that had at least one Great Argus detected. We chose to do this to control for duplicate events (resampling the same individual multiple times). If only part of the bird was visible on the camera trap photograph, it was counted as a detection. Due to slight variation in battery life and occasional malfunctions, not all the camera traps recorded for exactly the same number of days (See Appendix B for a list of deviations from the programmed regime). To standardise the measurements across all sites, we divided the total number of detection days by the total number of surveying days and then multiplied that result by 30 (the average camera trap deployment period) at each site.

Audio data

To automate – and thus significantly accelerate – the detection of Great Argus calls in the audio data collected, we constructed a recogniser (as described in Chapter 5) in Kaleidoscope Pro 5.4.8 (Wildlife Acoustics Inc., Maynard, MA, USA), which is an automated signal recognition software to aid in audio data analysis. A recogniser was trained by the user to extract target sounds from the audio dataset. The recogniser was trained with prior labelling of a sample of Great Argus calls of varying quality from within the study region, augmented with a sample of high-quality calls from an audio repository (Xeno Canto (www.xeno-canto.org)), the latter collected from across the species range (For details see Chapter 4 & 5: *Methods*). Great Argus typically produces three different call types (Clink *et al*., 2021). To build the recogniser, we focussed solely on the most common call type ('kwow kwow' call; Figure 5.1). This is the call type used by both sexes for territorial demarcation and during inter-pair disputes. Other calls are produced by males but only during mate attraction (Davison, 1981). Hence, the 'kwow kwow' call was a much more frequent call and, as a result, considered likely to be better at confirming the species presence at a site.

The resultant recogniser was applied to the full audio dataset collected. All the outputs classified as positive detections were manually verified and, hence, true positive detections were differentiated from false positive detections. Detections were verified both auditorily and visually, the latter using the spectrogram viewer in Kaleidoscope Pro. As with the camera traps, we collated the call detection data to record the total number of days at each site that had at least one call detected. We chose to do this to control for duplicate events, particularly as we then compared these results to camera trap photographs. Similarly to camera traps, due to slight variation in battery life and occasional malfunctions, not all the ARUs recorded for exactly the same number of days (See Appendix B for a list of deviations from the programmed regime). To standardise the measurements across all recording sites, we divided the total number of detection days by the total number of recording days and then multiplied that result by 30 (the average ARU deployment period) at each site.

As discussed in Chapter 2, the ARUs were pre-programmed with a subsampling recording regime. This was to maximise survey efforts across the whole camera trap deployment period whilst reducing maintenance requirements, as well as to maintain sufficient digital data storage space and battery life. Nevertheless, this presents a limitation to the study. Camera traps operated 24/7 and were constantly able to detect Great Arguses if present, whilst ARUs detection rates will tend to represent an underestimate of Great Argus calls present – an issue encountered in other comparison studies using similar survey methods (Enari *et al.*, 2019). Nevertheless, ARUs have a greater sampling range (discussed later) than camera traps so they still provide a good index.

6.3.3 Statistical analysis

Given the data recording approach adopted, we were able to pair daily detections of Great Arguses from cameras and ARUs at each site. Sites with no Great Argus detections arising from either survey methods (n = 43) were discarded from analysis as they were of no relevance to the study question, leaving 26 sites with Great Argus detections from a least one of the methods on at least one day (ARU n = 24 and camera trap n = 11). Thus, to test whether ARU and camera trap Great Argus detection rates differ, on average, in number of days with at least one detection, a Wilcoxon signed ranked test was fitted. To produce the diurnal activity pattern graphs, more sites were used for the ARU-produced pattern (n = 27) than were used in the statistical analysis (n = 24). This is due to times when recording pairs were redeployed due to camera trap malfunctions, despite the paired ARU functioning correctly in both deployments. There were 3 sites where this was the case and where the ARU in question captured some Great Argus calls. Thus, as data duplication wasn’t an issue here (as we were not comparing sites but rather observing overall calling patterns), these extra 3 audio surveys were retained to increase the dataset. All statistical analyses and graphics were undertaken in R version 4.1.2 (R Core Team, 2022).

We also graphically explored how detection rates changed between survey methods according to distance to road and qualitatively compared diurnal patterns obtained using both surveying methods respectively. No statistical tests were conducted for these analyses.

6.4 Results

Camera traps were able to detect a large variety of bird species, of different sizes and behaviours, despite only being able to survey the forest floor and the lower parts of the understory (Table 6.1). There were 24 different species detected by our camera traps in total as well as 388 individual birds detected in total.

Table 6.1 Species detected by camera traps across all sites. The study design included 69 randomly generated recording sites, at which one camera trap was set up to record for a 30-day period. Photographs obtained from all camera traps were processed manually and species identified on a case-by-case basis. The species below are ordered from greatest to lowest number of detections.

Species	**Common name**	**Number of detections**
Pitta sordida	Hooded Pitta	73
Pellorneum malaccense	Short-tailed babbler	66
Pellorneum capistratum	Black-capped babbler	60
Rollulus rouloul	Crested Partridge	52
Lophura ignita	Bornean Crested Fireback	32
Argusianus argus	Great Argus	26
Chalcophaps indica	Emerald Dove	21
Larvivora cyane	Siberian Blue Robin	12
Copsychus,malabaricus	White-rumped Shama	8
Rallina fasciata	Red Legged Crake	8
Erythropitta granatina	Garnet Pitta	5
Kenopia striata	Striped Wren-Babbler	5
NA	Non-identifiable	3
Pycnonotus plumosus	Olive-Winged Bulbul	3
Carpococcyx radiceus	Bornean Ground Cuckoo	1
Cyanoptila cyanomelana	Blue and White Flycatcher	1
Stachyris maculata	Chestnut-rumped Babbler	1
Ketupa sumatranus	Barred Eagle Owl	1
Alophoixus phaeocephalus	Yellow-Bellied Bulbul	1
Stachyris nigricollis	Black-Throated Babbler	1
Malacopteron magnum	Rufous-crowned Babbler	1
Pellorneum bicolor	Ferruginous Babbler	1
Centropus sinensis	Greater Coucal	1
Gorsachius melanolophus	Malaysian Night Heron	1

Tests of normality

A Shapiro-Wilk test showed evidence of non-normality for both the audio (W = 0.90, $p < 0.01652$) and camera trap (W = 0.55, $p < 8.218^{-08}$) Great Argus detection rate (Figure 6.1), thus justifying the use of a non-parametric statistical test.

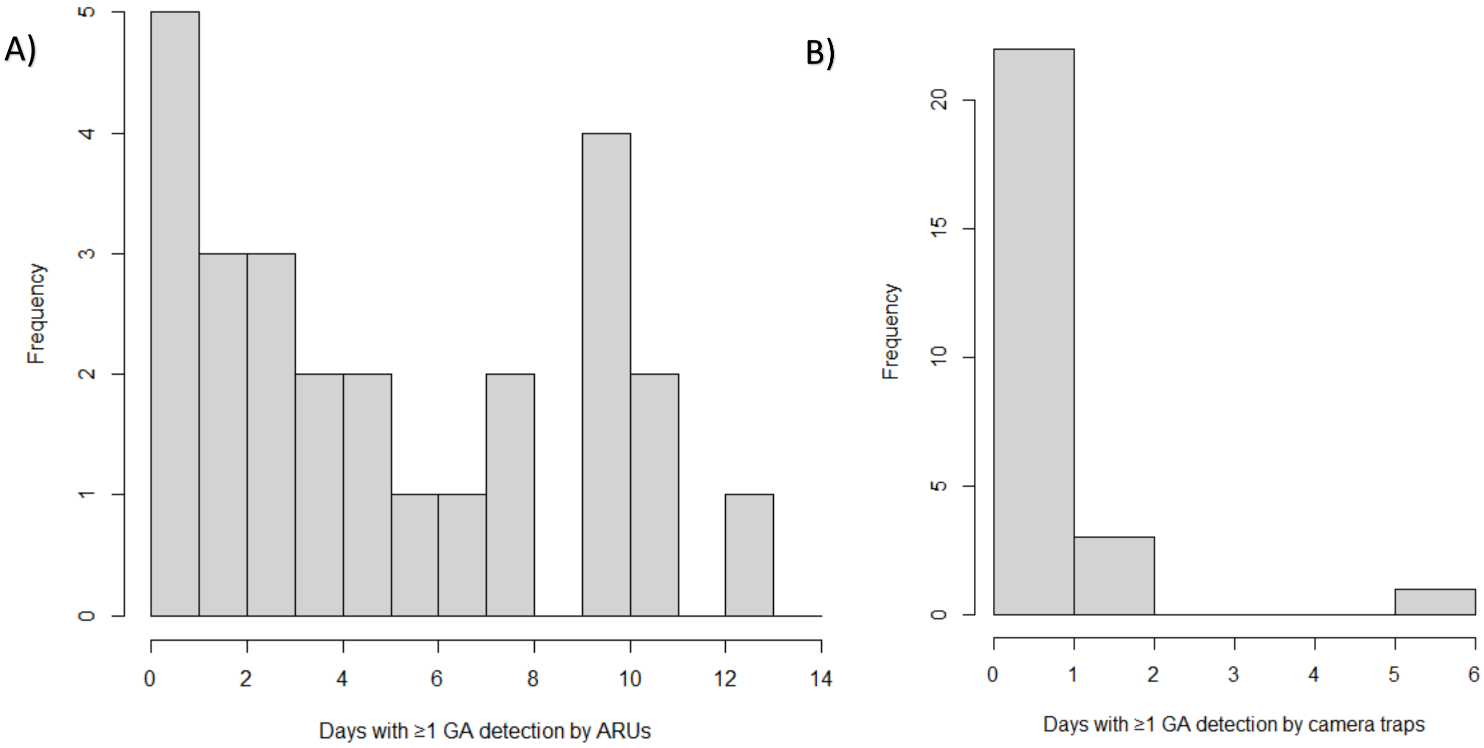


Figure 6.1 Detection frequency of Great Argus across the 26 study sites by A) Autonomous Recording Units (ARUs) and B) camera traps. The study design included 69 randomly generated recording sites, at which one Autonomous Recording Unit (ARU) and one camera trap were set up to record for a 30-day period. A detection day was counted as such when one or more Great Argus was/were detected by the survey method in question. Sites with no Great Argus detections arising from either survey methods (n = 43) were discarded from analysis as they were of no relevance to the study question, leaving 26 sites with Great Argus detections from a least one of the methods on at least one day out of the 30-day study period (ARU n = 24 and camera trap n = 11).

Detection rates

Example samples of a Great Argus camera trap images obtained (Figure 6.2) and a Great Argus call (Figure 5.1) are presented for reference. The Wilcoxon signed rank test revealed a significant difference in the Great Argus detection rates between the two survey methods

(ARUs and camera traps): V = 340, $p < 1.639^{-06}$, with ARUs being significantly more likely to detect Great Arguses if present (Figure 6.3).

Additionally, the ARU detection rate seems to vary with distance between the recording site and the nearest main road, with more Great Argus calls being detected at sites further away from the nearest main roads (Figure 6.4). The camera trap detection rate however does not seem to be affected in the same way, remaining relatively constant – but lower than that of ARUs – in relation to distance between the recording site and the nearest main roads (Figure 6.4). However, as stated in the methods, these trends were obtained through graphical observations and were not statistically tested in this study.

Figure 6.2 Sample camera trap photographs of A) male Great Argus B) female Great Argus C) a female Great Argus with her two chicks at night using infrared photography. The study design included 69 randomly generated recording sites, at which one camera trap was set up to record for a 30-day period. Great Argus were detected at 11 sites. Photographs obtained from all camera traps were processed manually and species identified on a case-by-case basis.

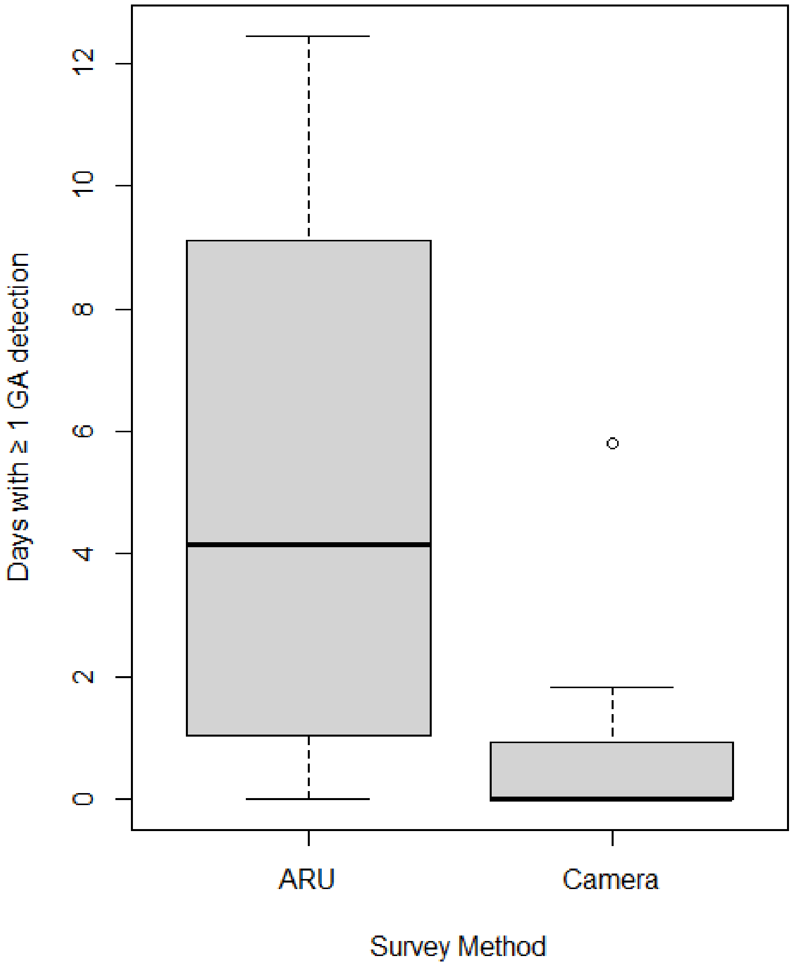


Figure 6.3 Detection rates of Great Argus by Autonomous Recording Units (ARU) and camera traps (camera) at the 26 recording sites with at least one Great Argus detection by either surveying method. The study design included 69 randomly generated recording sites, at which one ARU and one camera trap were set up to record for a 30-day period. A detection day was counted as such when one or more Great Argus was detected by the survey method in question. Sites with no Great Argus detections arising from either survey methods (n = 43) were discarded from analysis as they were of no relevance to the study question, leaving 26 sites with Great Argus detections from a least one of the methods on at least one day out of the 30-day study period (ARU n = 24 and camera trap n = 11).

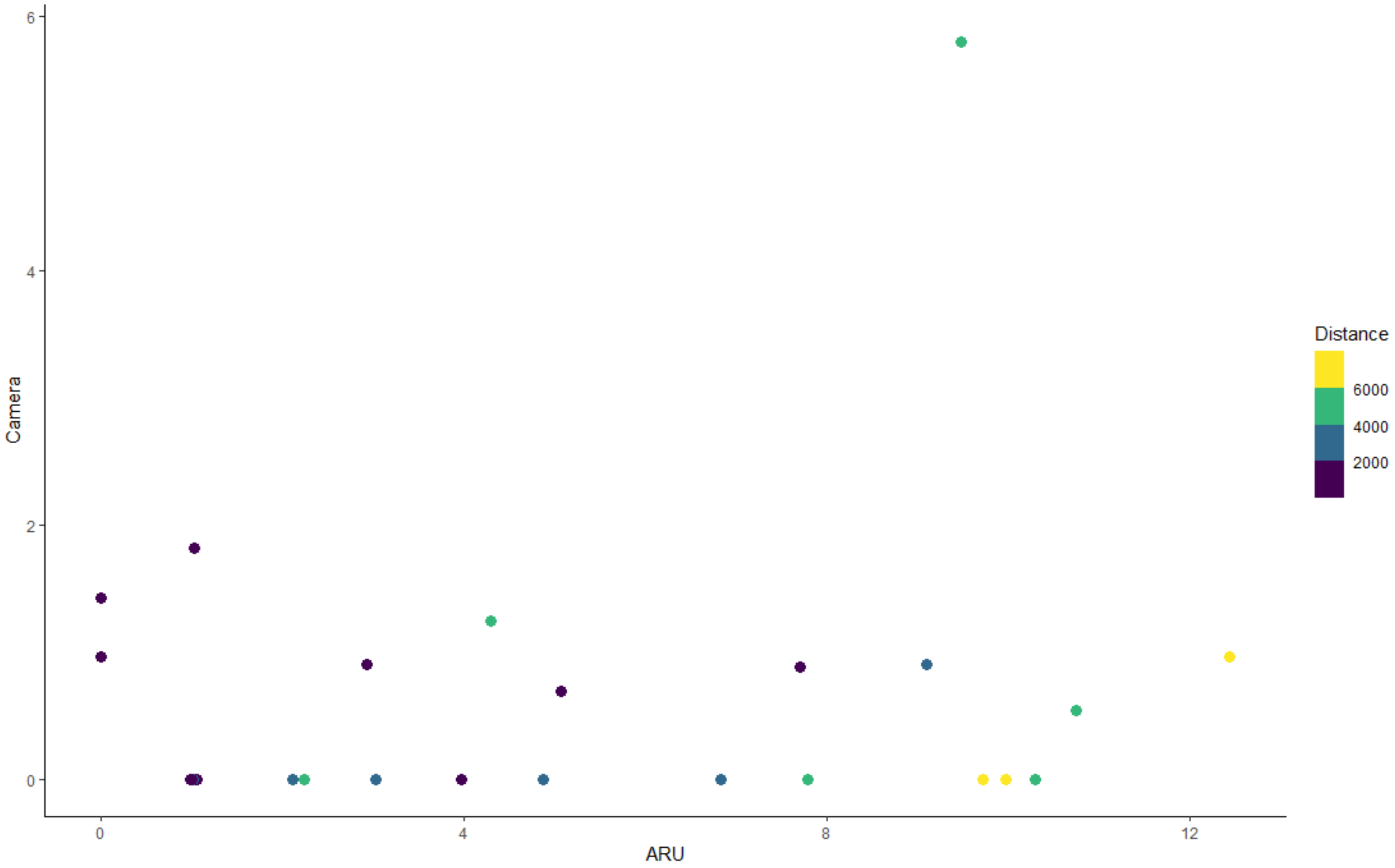
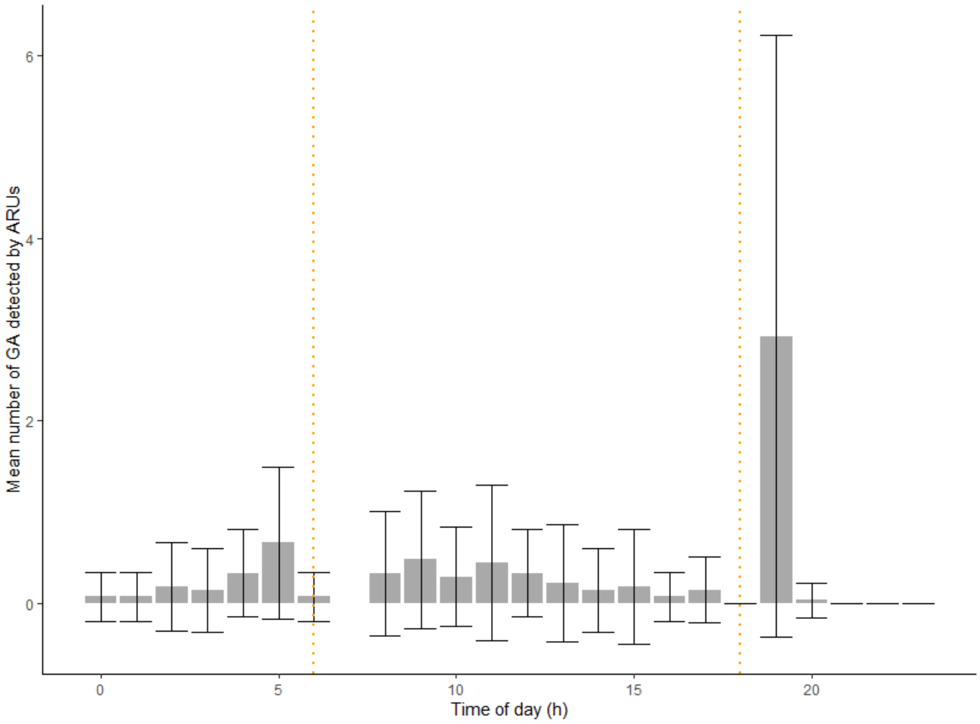


Figure 6.4 Average number of days on which Great Arguses were detected by camera traps (camera) and/or by Autonomous Recoding Units (ARU) at each site, coloured according to *Distance to Nearest Main Road* (N = 26, some points are overlain by other). Each data point refers to a site. The general trend observed here is that as the distance to the nearest main road increases, ARUs detect more Great Arguses whereas the detection rate of camera traps remains stable and low. The study design included 69 randomly generated recording sites, at which one ARU and one camera trap were set up to record for a 30-day period. A detection day was counted as such when one or more Great Argus was detected by the survey method in question. Sites with no Great Argus detections arising from either survey methods (n = 43) were discarded from analysis as they were of no relevance to the study question, leaving 26 sites with Great Argus detections from a least one of the methods on at least one day out of the 30-day study period (ARU n = 24 and camera trap n = 11). *Distance to Nearest Main Road* (here, Distance) is the distance between each site and the nearest main road to that site and was measured using Google Earth Pro.

Diurnal activity patterns

ARUs showed relatively low but constant vocalisation activity through the day and night, with a large peak just after dusk at 19:00 (Figure 6.5A), In contrast, the camera traps revealed a peak of Great Argus activity at dawn and then a secondary peak mid-afternoon (Figure 6.5B), in line with findings by O'Brien & Kinnaird (2008) and depicting Great Arguses as mostly diurnal. The standard error bars go below 0 due to standard errors being larger than the means, this does not indicate that there were negative levels of calls at a site (minimum number of calls at a site was 0). These trends were made through graphical observations and were not statistically tested in this study.

A)



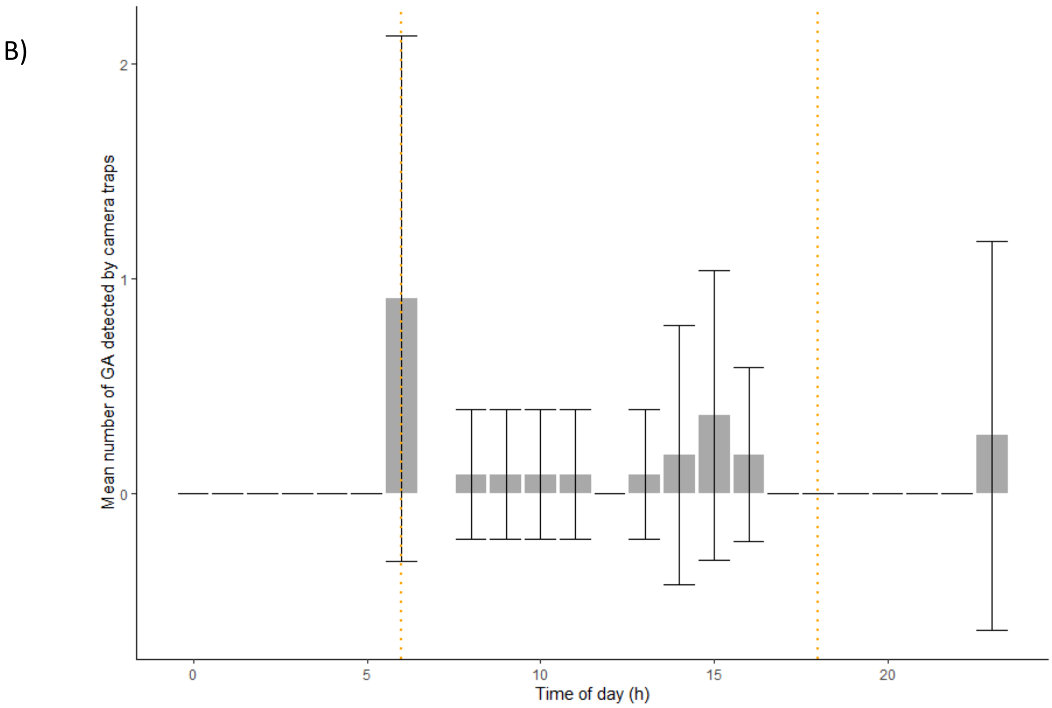


Figure 6.5 Diurnal patterns of Great Argus detected by A) Autonomous Recording Units (ARUs) (194 calls across 27 sites) and B) camera trap (26 photographic bursts across 11 sites, excluding consecutive bursts of the same individual(s)). The study design included 69 randomly generated recording sites, at which one Autonomous Recording Unit (ARU) and one camera trap were set up to record for a 30-day period. Only the sites where at least one Great Argus was detected were used in generating the diurnal patterns. For the call diurnal pattern, Great Argus calls were extracted from the vast amounts of audio data using a species-specific recogniser (algorithms to detect and extract target calls from audio data) made in Kaleidoscope Pro (the acoustic analysis software used in this study). For the camera trap diurnal pattern, photographs obtained from all camera traps were processed manually and species identified on a case-by-case basis. The two vertical dotted lines indicate dawn and dusk.

6.5 Discussion

Monitoring tropical forests presents many challenges due to extreme terrain and climatic conditions, usually resulting in data on this biome – and the often cryptic and elusive animals it contains – being scarce (Stork *et al*., 2007; Shoo *et al*., 2005; Zinger *et al*., 2020). Our study demonstrated that, although ARUs had a higher Great Argus detection rate, on average, than camera traps (Figure 6.3), using the two remote sensing survey methods concurrently enabled a broader approach of monitoring rare tropical rainforest ground birds, such as the Great Argus. The two surveying methods revealed different diurnal activity patterns (Figure 6.5), meaning they were detecting Great Arguses at different times of day, thus revealing the benefit of deploying both methods of remote-sensed wildlife monitoring tools. These differences could be due to several different factors discussed below. This study focuses on vertebrate taxa only and we acknowledge this as a limitation.

Firstly, ARUs possess, on average, much greater detection areas than camera traps, of up to 100 – 7 000 times greater (Enari *et al*., 2019). This allows them to detect Great Arguses, and other wildlife, further afield than camera traps can. Maximum camera trap sensor detection ranges vary between 9.1 – 30.5 m (Meek *et al*., 2012), with ours being 24 m in this study, but are frequently reduced to even smaller ranges when deployed in forest habitats because their field of view is often obstructed by vegetation or microtopography. By contrast ARUs possess much greater detection areas as they are less impaired by terrain and vegetation. Nevertheless, sound waves can also be attenuated by topography and vegetation and a greater detection range is not always advantageous. Camera traps' restricted detection range can help pinpoint the location of animals to a much smaller area and thus allow more precise model results. Secondly, ARUs are not constrained by directionality. Unlike camera traps, which can only detect a target within a fixed field of view, ARUs have a 360-degree detection scope, thus providing a much larger detection circumference. Thus, the two survey methods are clearly not sampling the same areas, with ARUs – unlike camera traps – having the capabilities of detecting targets further afield and in all directions.

The advantages of ARUs over cameras extends beyond their greater detection ranges. ARUs are able to provide additional information that other remote sensing technologies cannot. Although camera traps can help estimate factors such as breeding success – such as the photograph of the Great Argus with chicks in Figure 6.2C – and sex ratios through images, acoustic data enables researchers to investigate information that can only be extracted from auditive cues. For instance, socio-behavioural information can provide high resolution data about wild populations and individuals, such as state-specific signals. Although occupancy data is key to assess species distribution and abundance (Devarajan *et al*., 2020), it cannot explain the reasons behind population trends. Different types of calls from certain species are indicative of certain population dynamics, behavioural states and contexts, or life history events (Teixeira *et al*., 2019), such as male sika deer (*Cervus nippon*) calls signifying the density of potential breeding males and presence of females (Enari *et al.*, 2019) or curlew (*Numenius arquata*) calls indicating fledging success or predator activity (Grant *et al.*, 2000). Moreover, due to their greater detection ranges discussed above, ARUs are a great advantage in conducting population density estimates of thinly distributed and/or cryptic vocalising species with small but non-contiguous territories, such as Dupont's

Lark (*Chersophilus duponti*) (Pérez-Granados *et al.*, 2018). Nevertheless, phenology must be considered when using vocalisations for population estimates as these may vary according to other factors, such as breeding seasons. Thus, acoustic socio-behavioural data could provide further information and begin to close the gap of knowledge about the factors that drive population trends, hence helping authoritative bodies to better manage wildlife populations and their habitats going forward.

Additionally, ARUs can be used to survey animals that do not live at ground level. Although arboreal camera traps – camera traps placed above ground level – have recently been emerging as an effective monitoring methodology for non-ground species (Bowler *et al.*, 2017; Moore *et al.*, 2020; Monteza-Moreno *et al.*, 2022; Zhu *et al.*, 2022), most research projects set up camera traps up at ground level. Ground-level camera trapping is less resource intensive, accident prone, and logistically complex than arboreal camera trapping; especially in tropical rainforest where some trees are extremely tall and require specialist tree climbers or stands for access, making projects more costly (Houle *et al.*, 2004; Moore *et al.*, 2021). Although not as relevant for all habitat types, being able to easily survey non-ground dwelling species is particularly advantageous in forest ecosystems. Forests are structurally complex habitats (McCleary & Mowat, 2002) – driving microhabitat and microclimatic heterogeneity (Ishii *et al.*, 2004) – in turn creating greater number of refuges and niches (Pace *et al.*, 1999), consequentially driving biodiversity (Tscharntke *et al.*, 2012). This is particularly the case in tropical rainforests where many taxa exhibit strong preferences for height (Lowman & Moffett, 1993) and thus often occupy the canopy and understory vegetative strata instead of the forest floor. ARUs enable users to monitor non-ground dwelling vocalising species with greater ease than arboreal camera traps due to their ability to detect targets which are out of sight. Furthermore, studies have found that animals show response to camera traps (Meek *et al.*, 2014), suggesting they can detect them, potentially biasing data collected and disturbing wildlife. ARUs are more discrete than camera traps due to their small size, inconspicuous appearance, and silent operating. Thus, ARUs present themselves as a remote sensing technology with a broader and less biased potential surveying capability than camera traps, although restricted to use on vocalising species.

Despite the greater surveying range and capability of ARUs, and the additional resolution of data they provide, study designs incorporating both remote sensing surveying methods remain advantageous as ARUs present some limitations. Some of the facets that make ARUs such good surveying tools also limit their use. As discussed above, ARUs provide vital socio-behavioural data via the analysis of acoustic cues, which can be vital in management and conservation decision-making (Teixeira *et al.*, 2019) due to the relative ease of obtaining high resolution data on cryptic and elusive vocal species using such tools. Inversely, this means that unless the target animal is communicating, or otherwise engaging in auditive social behaviours, they cannot be surveyed using ARUs as they are acoustically inconspicuous and thus will be non-detectable by ARUs. This could mean that, even if the study species is very vocal, only certain individuals could be detectable at certain times. For instance, in primates, dominance is a key predictor of vocal use (Kavanagh *et al*., 2021), meaning that subordinate individuals will be less likely to be detected by ARUs. Similarly, vocalisation levels of given species - such as the tropical oriol *Icterus icterus* – can vary with seasons, often being more frequent in breading season when mate attraction and territorial defence are at stake (Odom *et al*., 2017). Sex and age can also influence vocalisation rates (Enari *et al*., 2019; Bezerra *et al*., 2009). Camera traps, although having a reduced detection range compared to ARUs, will detect animals passing in front of them irrespective of what behaviour it is engaging in – given they are big enough to be captured by such a camera. Camera traps will reliably detect animals even if they are simply walking past or foraging, whereas ARUs mainly detect animals when they are engaging in a specific behaviour requiring the production of vocalisations, such as territorial or personal defence, mating and alarm calls, or other communications with conspecifics.

As animals spend the majority of their time resting, traveling, feeding/foraging, and being vigilant (Wahungu *et al*., 2001; Kulp & Heymann, 2015; Rupert *et al*., 2018), it is reasonable to suggest that camera traps do present some unique benefits to remote sensing wildlife, as ARUs would not be able to detect vocal animals when engaging in these daily non-acoustic activities. This is evidenced by the misalignment of Great Argus diurnal activity patterns found using ARUs versus camera traps (Figure 6.5): the two survey methods are detecting the birds at different times of the day. Thus, together the two surveying methods provide a broader understanding of Great Argus ecology and activity patterns. ARUs and camera traps used in isolation would suggest very different activity patterns of the species. Using both in combination aids inference and understanding. Hence, camera traps provide a good complementary survey method for vocal species during their non-vocal activities (Colyn *et al*., 2020).

Furthermore, the use of ARUs is limited to certain species and relies on greater quantities of additional biological information compared to that of camera traps. Fundamentally, ARUs can only be used to survey relatively vocal animals, which heavily restricts the potential study species. Furthermore, not all animals have distinct calls – like that of the Great Argus – and thus are either indecipherable from background noise or easily confused with that of another species. Due to the large size of most audio datasets, study species' calls cannot be too sporadic, as this would render them almost impossible to find among the vastness of other acoustic information stored in such datasets. To mitigate this issue however, audio data banks – such as Xeno Canto used here – can be utilised to enhance the number of calls and make it easier for statistically-driven recognisers to detect target calls in a dataset. Moreover, the use of ARUs to survey target species, relies on the previous knowledge of that animal's call, information which is not always known and can vary greatly between and within individuals and geographic regions (Krebs & Kroodsma, 1980; Towsey *et al.*, 2018; Helenbrook *et al.*, 2019). Without this, no information of interest can be extracted from the audio dataset, thus rendering it redundant. Conversely, camera traps do not present the same issue as, on average, photographic, pictographic, and physical descriptions of animals are more widely available.

The use of ARUs comes with technological challenges and relies on more analysis tools and skills than camera trapping. ARUs are relatively new to the field of remote sensing across large spatiotemporal scales and thus this innovative hardware is not yet answering to all the demands of the research community. For instance, battery life is severely reduced compared to that of camera traps when compared for the same surveying duration. For instance, our ARUs and camera traps were both deployed for approximately 30 days before running out of battery, with camera traps recording continuously throughout that period whilst ARUs were only recording for of total of less than 3.5 hours daily. Additionally, there is excessive attenuations of sound amplitude in ARU recordings, with sounds emitted at ground level being disproportionally attenuated compared to sounds emitted higher off the ground (Enari *et al.*, 2019), reducing the potential uses of ARUs. If this technical issue was solved, ARUs could be used more reliably for analysing species' habitat use and interactions (Rhinehardt *et al.*, 2020) as well as for distance-sampling based population density estimates (Yip *et al.*, 2020; Sebastián-González *et al.*, 2018) using microphone triangulation to calculate target location (Gayk & Mennill, 2020).

Furthermore, ARUs require heavy data processing to extract desired information. Manual processing can be very lengthy and tedious but automated processing is unreliable and often computationally complex, requiring expert knowledge (Priyadarshani *et al.*, 2018; Gibb *et al.*, 2019). Camera trap data on the other hand is quicker and easier to process but presents inter-observer biases (Zett *et al.*, 2022), especially as inexperienced volunteers are often involved (Enari *et al.*, 2019). Although many semi-automated species classification software packages are currently emerging – examples include Conservation AI (Chalmers *et al.*, 2019), Zamba (Driven Data, 2017), and more (Yu *et al.*, 2013) –, most are focused on African or temperate wildlife, cannot be trained to specific datasets, and require image data sharing (Shepley *et al.*, 2021). Thus, manually analysing camera trap images is preferred. Although not as time consuming as manually analysing audio data, it would be advantageous to concentrate efforts into a few, trusted, and high performing camera trap image classification software packages. Software packages are also available to help manage camera trap data, like the R package *camtrapR* (Niedballa et al. 2016), which also helps speed up image processing. Hence, there is progress to make for both surveying methods in terms of technological challenges and data processing, but particularly for ARUs.

Although ARUs have many advantages over the more traditional remote sensing survey method of camera trapping, using a hybrid survey design is optimal as this draws on the strengths of both surveying methods, reducing the situations where the target is imperceptible. It is worth noting however that once a recogniser has been developed for a species, data extraction from ARUs (at least in terms of checking apparent occurrences) has low personnel overheads, whereas, in the absence of auto-image classification, camera traps have an ongoing processing time cost. Hence, if resources are limited for monitoring of rare vocal species, we suggest ARUs are preferable to use to detect species presence but, if resources allow, adding camera traps can provide additional information, with little additional deployment effort. Here we present a comparative study focusing on Great Argus detection rates of ARUs and camera traps. We conclude that, although ARUs are significantly more likely to detect Great Arguses if present at a site, the addition of camera traps provided a more holistic dataset, detecting Great Arguses at different times of day than ARUs. Future studies using the collected data could compare distance-sampling based population density estimates of Great Arguses acquired through ARUs and camera traps respectively and explore whether a similar density of ARU and camera trap deployment – and hence with similar set-up and monitoring costs – could serve equally well to estimate populations or distributions.

6.6 References

Anderson, D.R., 1976. *Guidelines for Line Transect Sampling of Biological Populations* (No. 9-76). Utah Cooperative Wildlife Research Unit. Utah State University. Logan, Utah.

Bezerra, B.M., da Silva Souto, A., de Oliveira, M.A.B. and Halsey, L.G., 2009. Vocalisations of wild common marmosets are influenced by diurnal and ontogenetic factors. *Primates*, *50*(3), pp.231-237.

BirdLife International. 2020. *Rhinoplax vigil*. *The IUCN Red List of Threatened Species* 2020: e.T22682464A184587039. https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22682464A184587039.en. Accessed on 16 January 2023.

Bowler, M.T., Tobler, M.W., Endress, B.A., Gilmore, M.P. and Anderson, M.J., 2017. Estimating mammalian species richness and occupancy in tropical forest canopies with arboreal camera traps. *Remote Sensing in Ecology and Conservation*, *3*(3), pp.146-157.

Brady, N.C., 1996. Alternatives to slash-and-burn: a global imperative. *Agriculture, Ecosystems & Environment, 58*(1), pp.3-11.

Brodie, J., Post, E. and Laurance, W.F., 2012. Climate change and tropical biodiversity: a new focus. *Trends in Ecology & Evolution*, *27*(3), pp.145-150.

Buxton, R.T., Lendrum, P.E., Crooks, K.R. and Wittemyer, G., 2018. Pairing camera traps and acoustic recorders to monitor the ecological impact of human disturbance. *Global Ecology and Conservation*, *16*, p.e00493.

Chalmers, C., Fergus, P., Wich, S. and Montanez, A.C., 2019. Conservation AI: Live stream analysis for the detection of endangered species using convolutional neural networks and drone technology. *arXiv Preprint arXiv:1910.07360*.

Clink, D.J., Groves, T., Ahmad, A.H. and Klinck, H., 2021. Not by the light of the moon: Investigating circadian rhythms and environmental predictors of calling in Bornean great argus. *PloS One*, *16*(2), p.e0246564.

Colyn, R., Campbell, A. and Smit-Robinson, H., 2020. The use of a camera trap and acoustic survey design to ascertain the vocalization and breeding status of the highly elusive White-winged Flufftail, Sarothrura ayresi. *Avian Conservation and Ecology*, *15*(2).

Crunchant, A.S., Borchers, D., Kühl, H. and Piel, A., 2020. Listening and watching: Do camera traps or acoustic sensors more efficiently detect wild chimpanzees in an open habitat? *Methods in Ecology and Evolution*, *11*(4), pp.542-552.

Davison, G.W.H., 1981. Diet and dispersion of the great argus Argusianus argus. *Ibis*, *123*(4), pp.485-494.

Devarajan, K., Morelli, T.L. and Tenan, S., 2020. Multi-species occupancy models: Review, roadmap, and recommendations. *Ecography*, *43*(11), pp.1612-1624.

Driven Data. Project Zamba Computer Vision for Wildlife Research & Conservation. 2017. Available online: https://zamba.drivendata.org/ (Accessed on 12 January 2023).

Enari, H., Enari, H.S., Okuda, K., Maruyama, T. and Okuda, K.N., 2019. An evaluation of the efficiency of passive acoustic monitoring in detecting deer and primates in comparison with camera traps. *Ecological Indicators*, *98*, pp.753-762.

Foley, J.A., Botta, A., Coe, M.T. and Costa, M.H., 2002. El Niño–Southern oscillation and the climate, ecosystems and rivers of Amazonia. *Global Biogeochemical Cycles*, 16(4), pp.79-1.

Garland, L., Crosby, A., Hedley, R., Boutin, S. and Bayne, E., 2020. Acoustic vs. photographic monitoring of gray wolves (Canis lupus): a methodological comparison of two passive monitoring techniques. *Canadian Journal of Zoology*, *98*(3), pp.219-228.

Gayk, Z.G. and Mennill, D.J., 2020. Pinpointing the position of flying songbirds with a wireless microphone array: three-dimensional triangulation of warblers on the wing. *Bioacoustics*, *29*(4), pp.375-386.

Giam, X., Scheffers, B.R., Sodhi, N.S., Wilcove, D.S., Ceballos, G. and Ehrlich, P.R., 2012. Reservoirs of richness: least disturbed tropical forests are centres of undescribed species diversity. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1726), pp.67-76.

Gibb, R., Browning, E., Glover-Kapfer, P. and Jones, K.E., 2019. Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods in Ecology and Evolution*, *10*(2), pp.169-185.

Grant, M.C., Lodge, C., Moore, N., Easton, J., Orsman, C. and Smith, M., 2000. Estimating the abundance and hatching success of breeding Curlew Numenius arquata using survey data. *Bird Study*, *47*(1), pp.41-51.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R. and Kommareddy, A., 2013. High-resolution global maps of 21st-century forest cover change. S*cience*, *342*(6160), pp.850-853.

Harris, G., Thompson, R., Childs, J.L. and Sanderson, J.G., 2010. Automatic storage and analysis of camera trap data. *Bulletin of the Ecological Society of America*, *91*(3), pp.352-360.

Hazarika, S., 2013. Rainforests and migration. In *The Encyclopaedia of Global Human Migration.* Blackwell Publishing Ltd. Oxford.

Helenbrook, W.D., Linck, N.A., Pardo, M.A. and Suarez, J.A., 2019. Spatial variation in black-headed night monkey (Aotus nigriceps) vocalizations. *BioRxiv*, p.1-19.

Houle, A., Chapman, C.A. and Vickery, W.L., 2004. Tree climbing strategies for primate ecological studies. *International Journal of Primatology*, *25*(1), pp.237-260.

Ishii, H.T., Tanabe, S.I. and Hiura, T., 2004. Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. *Forest Science*, *50*(3), pp.342-355.

Janečka, J.E., Jackson, R., Yuquang, Z., Diqiang, L., Munkhtsog, B., Buckley-Beason, V. and Murphy, W.J., 2008. Population monitoring of snow leopards using noninvasive collection of scat samples: a pilot study. *Animal Conservation*, *11*(5), pp.401-411.

Karr, J.R., 1981. Surveying birds with mist nets. *Studies in Avian Biology*, *6*, pp.62-67.

Krebs, J.R. and Kroodsma, D.E., 1980. Repertoires and geographical variation in bird song. In *Advances in the Study of Behavior* (Vol. 11, pp. 143-177). Academic Press. Cambridge, Massachusetts.

Kulp, J. and Heymann, E.W., 2015. Ranging, activity budget, and diet composition of red titi monkeys (Callicebus cupreus) in primary forest and forest edge. *Primates*, *56*(3), pp.273-278.

Lowman, M.D. and Moffett, M., 1993. The ecology of tropical rain forest canopies. *Trends in Ecology & Evolution*, *8*(3), pp.104-107.

Lowman, M.D., 2009. Canopy research in the twenty-first century: a review of arboreal ecology. *Tropical Ecology*, *50*(1), p.125.

Lucci Freitas, A.V., Agra Iserhard, C., Pereira Santos, J., Oliveira Carreiral, J.Y., Bandini Ribeiro, D., Alves Melo, D.H., Batista Rosa, A.H., Marini-Filho, O.J., Mattos Accacio, G. and Uehara-Prado, M., 2014. Studies with butterfly bait traps: an overview. *Revista Colombiana de Entomología*, *40*(2), pp.203-212.

Mancini, M.C.S., Hintze, F., de Souza Laurindo, R., de Macêdo Mello, R. and Gregorin, R., 2022. Tradition vs. innovation: comparing bioacoustics and mist-net results to bat sampling. *Bioacoustics*, *31*(5), pp. 575-593.

McCleary, K. and Mowat, G., 2002. Using forest structural diversity to inventory habitat diversity of forest-dwelling wildlife in the West Kootenay region of British Columbia. *B.C. Journal of Ecosystems and Management, (2)2,* pp.1-13

Meek, P.D., Fleming, P. and Ballard, G., 2012. *An introduction to camera trapping for wildlife surveys in Australia*. Canberra, Australia: Invasive Animals Cooperative Research Centre.

Meek, P.D., Ballard, G.A., Fleming, P.J., Schaefer, M., Williams, W. and Falzon, G., 2014. Camera traps can be heard and seen by animals. *PloS One*, *9*(10), p.e110832.

Monteza-Moreno, C.M., Rodriguez-Castro, L., Castillo-Caballero, P.L., Toribio, E. and Saltonstall, K., 2022. Arboreal camera trapping sheds light on seed dispersal of the world's only epiphytic gymnosperm: Zamia pseudoparasitica. *Ecology and Evolution*, *12*(3), p.e8769.

Moore, J.F., Pine, W.E., Mulindahabi, F., Niyigaba, P., Gatorano, G., Masozera, M.K. and Beaudrot, L., 2020. Comparison of species richness and detection between line transects, ground camera traps, and arboreal camera traps. *Animal Conservation*, *23*(5), pp.561-572.

Moore, J.F., Soanes, K., Balbuena, D., Beirne, C., Bowler, M., Carrasco-Rueda, F., Cheyne, S.M., Coutant, O., Forget, P.M., Haysom, J.K. and Houlihan, P.R., 2021. The potential and practice of arboreal camera trapping. *Methods in Ecology and Evolution*, *12*(10), pp.1768-1779.

Niedballa, J., Sollmann, R., Courtiol, A. and Wilting, A., 2016. camtrapR: an R package for efficient camera trap data management. *Methods in Ecology and Evolution*, *7*(12), pp.1457-1462.

Nijman, V., 2007. Effects of vocal behaviour on abundance estimates of rainforest galliforms. *Acta Ornithologica*, *42*(2), pp.186-190.

Noss, A., Polisar, J., Maffei, L., Garcia, R. and Silver, S., 2013. *Evaluating jaguar densities with camera traps.* Bronx, New York: Jaguar Conservation Program & Latin America and Caribbean Program.

O'Brien, T.G. and Kinnaird, M.F., 2008. A picture is worth a thousand words: the application of camera trapping to the study of birds. *Bird Conservation International*, *18*(S1), pp.S144-S162.

Odom, K.J., Logue, D.M., Studds, C.E., Monroe, M.K., Campbell, S.K. and Omland, K.E., 2017. Duetting behavior varies with sex, season, and singing role in a tropical oriole (Icterus icterus). *Behavioral Ecology*, *28*(5), pp.1256-1265.

Pace, M.L., Cole, J.J., Carpenter, S.R. and Kitchell, J.F., 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution*, *14*(12), pp.483-488.

Parker, G.G., Smith, A.P. and Hogan, K.P., 1992. Access to the upper forest canopy with a large tower crane. *BioScience*, *42*(9), pp.664-670.

Pérez-Granados, C., Bustillo-De La Rosa, D., Gómez-Catasús, J., Barrero, A., Abril-Colón, I. and Traba, J., 2018. Autonomous recording units as effective tool for monitoring of the rare and patchily distributed Dupont's Lark Chersophilus duponti. *Ardea*, *106*(2), pp.139-146.

Pijanowski, B.C., Farina, A., Gage, S.H., Dumyahn, S.L. and Krause, B.L., 2011$_{A}$. What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology*, *26*(9), pp.1213-1232.

Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H. and Pieretti, N., 2011$_{B}$. Soundscape ecology: the science of sound in the landscape. *BioScience*, *61*(3), pp.203-216.

Pillay, R., Venter, M., Aragon-Osejo, J., González-del-Pliego, P., Hansen, A.J., Watson, J.E. and Venter, O., 2022. Tropical forests are home to over half of the world's vertebrate species. *Frontiers in Ecology and the Environment*, *20*(1), pp.10-15.

Priyadarshani, N., Marsland, S. and Castro, I., 2018. Automated birdsong recognition in complex acoustic environments: a review. *Journal of Avian Biology*, *49*(5), pp.jav-01447.

R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ralph, C.J., Sauer, J.R. and Droege, S., 1995. *Monitoring bird populations by point counts*. Pacific Southwest Research Station. Albany, California.

Rhinehart, T.A., Chronister, L.M., Devlin, T. and Kitzes, J., 2020. Acoustic localization of terrestrial wildlife: Current practices and future opportunities. *Ecology and Evolution*, *10*(13), pp.6794-6818.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I., Levi, T., Lindsey, P.A. and Macdonald, D.W., 2015. Collapse of the world's largest herbivores. *Science Advances*, *1*(4), p.e1400103.

Ruppert, N., Holzner, A., See, K.W., Gisbrecht, A. and Beck, A., 2018. Activity budgets and habitat use of wild southern pig-tailed macaques (Macaca nemestrina) in oil palm plantation and forest. *International Journal of Primatology*, *39*(2), pp.237-251.

Sanderson, J.G. and Trolle, M., 2005. Monitoring elusive mammals: unattended cameras reveal secrets of some of the world's wildest places. *American Scientist*, *93*(2), pp.148-155.

Sebastián-González, E., Camp, R.J., Tanimoto, A.M., de Oliveira, P.M., Lima, B.B., Marques, T.A. and Hart, P.J., 2018. Density estimation of sound-producing terrestrial animals using single automatic acoustic recorders and distance sampling. *Avian Conservation and Ecology. 13(2):7*

Shepley, A., Falzon, G., Lawson, C., Meek, P. and Kwan, P., 2021. U-Infuse: Democratization of Customizable Deep Learning for Object Detection. *Sensors*, *21*(8), p.2611.

Shoo, L.P., Williams, S.E. and Hero, J.M., 2005. Climate warming and the rainforest birds of the Australian Wet Tropics: Using abundance data as a sensitive predictor of change in total population size. *Biological Conservation*, *125*(3), pp.335-343.

Sidie-Slettedahl, A.M., Jensen, K.C., Johnson, R.R., Arnold, T.W., Austin, J.E. and Stafford, J.D., 2015. Evaluation of autonomous recording units for detecting 3 species of secretive marsh birds. *Wildlife Society Bulletin*, *39*(3), pp.626-634.

Stork, N.E., Balston, J., Farquhar, G.D., Franks, P.J., Holtum, J.A.M. and Liddell, M.J., 2007. Tropical rainforest canopies and climate change. *Austral Ecology*, *32*(1), pp.105-112.

Subalusky, A., Fitzgerald, L. and Smith, L., 2009. Detection of American alligators in isolated, seasonal wetlands. *Applied Herpetology*, *6*(3), pp.199-210.

Teixeira, D., Maron, M. and van Rensburg, B.J., 2019. Bioacoustic monitoring of animal vocal behavior for conservation. *Conservation Science and Practice*, *1*(8), p.e72.

Towsey, M., Znidersic, E., Broken-Brow, J., Indraswari, K., Watson, D.M., Phillips, Y., Truskinger, A., Roe, P. and Street, G., 2018. Long-duration, false-colour spectrograms for detecting species in large audio datasets. *Journal of Ecoacoustics*, *2*(1), pp.1-1.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F. and Ewers, R.M., 2012. Landscape moderation of biodiversity patterns and processes-eight hypotheses. *Biological Reviews*, *87*(3), pp.661-685.

Wahungu, G.M., Catterall, C.P. and Olsen, M.F., 2001. Predator avoidance, feeding and habitat use in the red-necked pademelon, Thylogale thetis, at rainforest edges. *Australian Journal of Zoology*, *49*(1), pp.45-58.

Wilson, E.O. and Frances, P.M., 1988. Biodiversity Washington DC: National Academy. *Sciences.*

Woodcock, B.A., 2005. Pitfall trapping in ecological studies. *Insect Sampling in Forest Ecosystems*, *5*, pp.37-57.

WWF, 2018. *Camera trapping*. Available online at: https://www.wwf.org.uk/project/conservationtechnology/camera-trap. (Accessed on 13 January 2023).

Yip, D.A., Knight, E.C., Haave-Audet, E., Wilson, S.J., Charchuk, C., Scott, C.D., Sólymos, P. and Bayne, E.M., 2020. Sound level measurements from audio recordings provide objective distance estimates for distance sampling wildlife populations. *Remote Sensing in Ecology and Conservation*, *6*(3), pp.301-315.

Yu, X., Wang, J., Kays, R., Jansen, P.A., Wang, T. and Huang, T., 2013. Automated identification of animal species in camera trap images. *EURASIP Journal on Image and Video Processing*, *2013*(1), pp.1-10.

Zett, T., Stratford, K.J. and Weise, F.J., 2022. Inter-observer variance and agreement of wildlife information extracted from camera trap images. *Biodiversity and Conservation*, *31*(12), pp.3019-3037.

Zinger, L., Donald, J., Brosse, S., Gonzalez, M.A., Iribar, A., Leroy, C., Murienne, J., Orivel, J., Schimann, H., Taberlet, P. and Lopes, C.M., 2020. Advances and prospects of environmental DNA in neotropical rainforests. *Advances in Ecological Research*, *62*, pp.331-373.

Zhu, C., Li, W., Gregory, T., Wang, D., Ren, P., Zeng, D., Kang, Y., Ding, P. and Si, X., 2022. Arboreal camera trapping: a reliable tool to monitor plant-frugivore interactions in the trees on large scales. *Remote Sensing in Ecology and Conservation*, *8*(1), pp.92-104.

Chapter 7

General Discussion

7.1 Overview

In this thesis, we have used and applied cutting-edge remote surveying technology and analysis tools to push the boundaries of knowledge and understanding regarding the use of eco-acoustics to infer the impact of infrastructure expansion on birds in tropical rainforests ecosystems. Tropical rainforests provide an optimal challenge for eco-acoustic research as this biome presents many hotspots of biodiversity, resulting in complex soundscapes. Primarily using Autonomous Recording Units (ARUs), this project showcased two of the main audio analysis tools (acoustic indices and recognisers) and identified both the strengths and weaknesses of their implementation. Furthermore, by applying these tools to a large set of audio data, collected across an infrastructure expansion gradient in Brunei's tropical rainforests, our work has explored the impact of several spatial-temporal factors on the soundscapes and species present in the study area. Here, we discuss and summarise the findings of this thesis and place in them a wider ecological context.

7.2 Remote surveying technologies

The use of ARUs during this project enabled us to collect a vast quantity of audio data across a large spatial-temporal scale, with little previous expertise. The ease of use provided by audio recorders, allows scientists with relatively little experience in this technology and little taxonomic expertise to conduct state-of-the-art research projects, thus opening the field of conservation ecology to a wider community and – consequently – accelerating understanding. ARUs are being increasingly used by researchers due to their advantages over traditional surveying methods. These advantages include reduced observer bias, permanent record of data and larger spatial-temporal surveying capabilities coupled with less time spent in the field (Shonfield & Bayne, 2017). The use of ARUs allow scientists to monitor animal communities or individuals at both small and large scales, in turn enabling them to assess the need for – or success of – conservation programs or study animal behaviour like never before. Indeed, several large-scale audio monitoring programs have been set up, including one of the largest ecological experiments globally: The SAFE Acoustics project in the Danum Valley Conservation Area in Sabah, Malaysia (Sethi *et al.*, 2020). This project allows real-time, remote surveying of the soundscape across a network of deployed ARUs and has been used in over 200 research projects, including assessing how to balance productive palm oil plantations in parallel with healthy ecological communities (Bicknell *et al.*, 2023). ARUs have also been used to track animal communication, allowing users to track migratory birds (Buxton *et al.*, 2016; Farnsworth & Russell 2007; Sanders & Mennill 2014; Shonfield & Bayne, 2017) and even identify individuals in a non-invasive way to further infer return rates (Ehnes & Foote 2015; Petrusková *et al.*, 2016) or other behaviours of interests at a local scale, such as habitat use (Mennill *et al.*, 2006, 2012; Wang *et al.*, 2005). However, due to the relative novelty of acoustic technology, there has been discrepancies between the methods used in eco-acoustic studies, consequentially resulting in inconsistent or incomparable findings (Bradfer-Lawrence *et al.*, 2019). Thus, in Chapter 2, we outline research protocols to gather the maximum amount of data possible given the hardware and time restrictions that were present during our fieldwork, whilst trying to keep in line with best-practice guidance in the literature – bearing in mind our audio recording protocol was restricted by the camera traps we simultaneously deployed.

Using both remote surveying technologies in conjunction permitted us to conduct a comparative study between the two remote surveying methods (Chapter 6), something that has – to the best of our knowledge – never been done before on birds in tropical rainforests ecosystems. Over the last decade, a handful of studies have integrated both remote surveying techniques in the aims of answering various ecological questions, such as abundance and distribution of species, as well as behavioural studies, at multiple trophic levels (Buxton *et al.*, 2018$_{A}$), with some focusing on anthropogenic impacts (Buxton *et al.*, 2017$_{A}$; Derose-Wilson *et al.*, 2015; Francis *et al.*, 2015; Robinson *et al.*, 2015). Most studies using both camera traps and ARUs simultaneously have mammals as their focal taxon (Crunchant *et al.*, 2020; Diggins *et al.*, 2016; Enari *et al.*, 2017, 2019; Francis *et al.*, 2015; Garland *et al.*, 2020; Horton *et al.*, 2015; Isbell and Bidner 2016; Wrege *et al.*, 2017), making this study one of the few integrating these remote surveying technologies to study birds (Buxton *et al.*, 2017$_{A \& B}$; Derose-Wilson *et al.*, 2015; Robinson *et al.*, 2015). Here, using a custom-built audio recogniser (an algorithm capable of automatically detecting and extracting target calls from audio data), we tallied calls of a vulnerable ground-bird – the Great Argus – and compared the number of detection days at each site to that of camera traps. Although our findings clearly demonstrated the ARUs had a significantly higher detection rate overall, there was a divergence in the diurnal activity patterns constructed using both survey methods independently. Amalgamating data collected using both remote surveying technologies led to a more holistic understanding of the species' ecology and increased chances of detection, thus providing with the potential also to improve abundance and distribution studies. Despite the many opportunities such surveys permit, the main impediment that remains is data processing.

7.3 Acoustic analysis tools

Although recent development in acoustic technology has provided opportunities for unprecedented ‘big data’ collection, the difficulty lies in extracting information of interest from audio datasets. Two main acoustic analysis tools available to scientists today are acoustic indices and recognisers.

Acoustic indices allow researchers to quantitatively summarise aspects of audio files in a standardised way (Towsey *et al.*, 2014$_{A}$), thus making recordings easily comparable. The main advantages of acoustic indices are their simplicity and ease of computing. Despite their relatively recent development, many eco-acoustic studies now utilise these indices for rapid biodiversity assessments and exploring patterns in spatial-temporal variation (Buxton *et al.*, 2018$_{B}$). Acoustic indices have been used in many biomes across the globe, from tropical rainforests (Jorge *et al.*, 2018; Moreno-Gómez *et al.*, 2019; Retamosa Izaguirre *et al.*, 2021) and temperate grasslands (Müller *et al.*, 2022; Shamon *et al.*, 2021), to polar regions (Bolgan *et al.*, 2018; Yip *et al.*, 2021) and even urban areas (Fairbrass *et al.*, 2017; Rajan *et al.*, 2019), both in terrestrial and marine ecosystems, with some studies even starting to look at underground soil-soundscapes (Keen *et al.*, 2022). They have helped describe, summarise, and compare soundscapes around the world like never before. Additionally, long-duration false colour spectrograms present a new method for interpreting index scores, by combining them to visually display temporally large soundscapes, which indirectly provides a novel, rapid way of monitoring species without the time-consuming need to build complex recognisers (Towsey *et al.*, 2014$_{B}$, 2018). Nevertheless, there remains heavy scepticism surrounding the ecological relevance of acoustic indices, as studies have found inconsistent findings when correlating them to various bioindicators (Bradfer-Lawrence *et al.*, 2019; Buxton *et al.*, 2018$_{B}$). In Chapter 3, we applied one of the most commonly used acoustic indices, the Acoustic Complexity Index (ACI), which was developed to “produce a direct and quick quantification of the bird vocalisations by processing the intensities registered in audio files” (Pieretti *et al.* 2011). In light of the ACI’s intended focus on bird vocalisations, our findings were the opposite of what we were expecting. Particularly in terms of the diurnal patterns observed, which showed a significant decrease of ACI during daytime compared to that at night, with a notable drop at dawn. Additionally, ACI was found to decline as remoteness increased, which we also found surprising. Although other studies have found similar trends and this could be explained by several factors (including the dominance of highly vocal edge-loving species, ecotones supporting a wider community of species, or compensation against noise pollution), our findings described in Chapter 5 create a perplexing duality in our results. Using our custom-made acoustic recognisers developed in Chapter 4 and 5 for the Helmeted Hornbill (*Rhinoplax vigil*) and Great Argus (A*rgusianus argus*), we found that, in the case of these two species at least, the birds had a greater regularity of persistence at sites further from roads. However due to logistical restrictions, we did not take in situ bird species diversity and abundance measurements (namely point count surveys), as done in other studies which also used acoustic indices (Bradfer-Lawrence *et al*., 2020; Dröge *et al.*, 2021; Eldridge *et al*., 2018; Jorge *et al*., 2018; Mammides *et al*., 2017; McGrann *et al*., 2022). Hence, we cannot directly correlate our ACI findings with bird species abundance and diversity and thus cannot fully conclude as to the exact ecological meaning of ACI in this study until additional work is conducted.

The other major tool used in eco-acoustic research are recognisers. Once trained, these algorithms allow users to detect and extract target calls from large sets of audio data – a task that can otherwise take a very long time. For example, to manually listen to our dataset (7 141 hours of audio recording), excluding any identification or classification, would have taken 3.5 years (assuming a person works 5 days per week for 8 hours per day) – further highlighting the need for automated processing and identification in eco-acoustics. Nevertheless, much like acoustic indices, the reliability of recognisers has been questioned in the literature (Brooker *et al*., 2020). There is a plethora of programs that have been developed to date, based on a diversity of underlying algorithms (Brandes, 2008), which allow users to build custom-made species-specific recognisers. The main recogniser building software programs available to date are Song Scope, MonitoR, Raven Pro, Kaleidoscope Pro, and Convolutional neural networks. These programs have helped the scientific community study individuals and species within their ecosystems at a much faster pace than ever before. Kaleidoscope Pro, used in this thesis, is a commercially available software which presents a user-friendly interface – thus furthering the accessibility of eco-acoustics to a wider audience. Recognisers built using Kaleidoscope Pro's have been previously suggested to perform poorly in comparative studies (Brooker *et al*., 2020; Knight *et al*., 2017), however – to the best of our knowledge – Chapter 4 constitutes the first attempt at teasing apart which construction techniques in Kaleidoscope Pro result in better performing recognisers. Although this was not an original goal of the project, initial classifications of bird vocalisation data proved rather weak (possibly due to the complexity of rainforest soundscapes), suggesting a need for further exploration and refinement of recogniser construction. By trying different combinations of training data and labelling ('teaching' the algorithm what is and is not a target call) we concluded that using training data from the study site and labelling all types of target call, irrespective of (perceived) quality, resulted in the best performing recogniser. However, even our best performing recogniser still produced many false positives, rendering the use of our recogniser semi-automated, as we had to manually check the 'positive' output for target calls. Nevertheless, as our goal was to detect the most target calls possible, even if that meant increasing the number of false positives, this was more acceptable in this study than a more balanced (in terms of sensitivity and specificity) recogniser that missed numerous calls. Thus, research goals must be considered when constructing a recogniser, as this is not necessarily the best outcome for all projects.

7.4 Impact of infrastructure expansion on biodiversity

Aside from evaluating acoustic tools, another major focus of this thesis was applying these tools to infer the ecological impact of infrastructure expansion in the study area. To do this we used a combination of approaches, namely the Acoustic Complexity Index (ACI) to analyse the soundscape and overall bird biodiversity, as well as the use of custom-made species-specific recognisers to detect calls of the Helmeted Hornbill and the Great Argus. The ACI scores in Chapter 3 suggested a higher bird biodiversity nearer roads and in higher infrastructure pressure zones with no sensitivity to buildings or biomass. As mentioned previously, this might be due to ecotones supporting a greater diversity of species, whose vocalisations are adapted to different sound environments, and hence together they better 'fill' the soundscape. However, ACI's correlation with bird vocalisations remains theoretical, with many studies finding no such correlations, and thus high scores here could represent invertebrates or geophony. Meanwhile, our recognisers in Chapter 5 suggested both study birds had a greater regularity of persistence at sites further from roads and buildings as well as with greater biomass, thus not conforming to the overall bird biodiversity trends revealed by the ACI results. Nevertheless, this result was to be expected as the Helmeted Hornbill and Great Argus are forest interior specialists and thus are less likely to be found around the forest edge. Additionally, both methods revealed intriguing acoustic diurnal patterns. ACI showed a clear pattern of higher scores at night – theoretically indicating high bird vocalisation activity – whilst the patterns produced by our recogniser results were mixed. Helmeted Hornbills seemed to only vocalise during the daytime, whilst Great Argus vocalised through the 24h period, with their highest peak of vocal activity being after dusk.

Both the ACI analyses and the individual species studies suggested that roads had a significant impact on biodiversity, evidencing that infrastructure expansion does not go without consequence. Roads, and other anthropogenic linear clearings, cause considerable ecological disturbance – such as chemical and nutrient pollution, increasing edge habitat, increasing risks of roadkill, creating barriers or impassable clearings, changes in predator-prey interactions, increased risk of biological and human invasions, frequently leading to increased poaching – and have been suggested to disproportionally affect tropical forests biodiversity (Laurance *et al*., 2009). Nevertheless, this type of infrastructure has been repeatedly reported to cause negative consequences across many different taxa and biomes (Dean *et al*., 2019; Dickie *et al*., 2017; Dorsey *et al*., 2015; Elzanowski *et al*., 2009; He *et al*., 2019; Myers-Smith *et al*., 2006), with roads being amongst the most well understood linear disturbances. Mitigations to reduce the impact of such infrastructure include wildlife bridges and tunnels to allow for safe crossing (Teixeira *et al*., 2013; Van der Ree *et al*., 2009), limiting expansion in certain areas of special conservation value, investing in high-quality infrastructure to avoid downstream work and pollution (Laurance *et al*., 2009), and raising awareness about the issue.

7.5 Future work

The findings of this thesis provide an overview of the soundscapes across infrastructure expansion gradients (albeit a gradient towards the more undistributed end of the infrastructure expansion gradient) in Temburong, Brunei. One of the advantages of audio data, such as that collected here, is that one dataset can be used to answer numerous questions. Thus, future work could focus on further analysis of the soundscape, for example recalculating ACI over narrower ecologically relevant frequency bands (Metcalf *et al*., 2021) or by implementing frequency filters (Hyland *et al*., 2023). This could be used to block out stridulating insects, for example, and explore how this impacts current results. Additionally, the work carried out in Chapter 3 could be repeated with other acoustic indices to broaden our general understanding of Temburong's soundscapes. In terms of recognisers, future work could look at constructing Helmeted Hornbill and Great Argus recognisers using other software programs, applying them to our audio dataset, and comparing results to those produced by Kaleidoscope Pro. The ecological work carried out in Chapter 5 could be repeated with any species of interest in the study area and results compared to our focal species, as well as the ACI scores, to further explore the relationship between bird vocalisations and ACI. Similarly, a comparison study between camera trap and acoustic data could be conducted on another vocalising ground-dwelling organism of interest. Moreover, in the future, citizen science could be explored as a way of identifying vocalisation in audio datasets, similarly to how it is already being done with camera trap data. Long term, further collaboration must be undertaken between ecologists and computer scientists, sound specialists, and mathematicians to further the potential of both acoustic indices and recognisers.

7.6 Conclusion

Tropical rainforests are vital to many living organisms on Earth, including humans, providing stable, resource-rich habitats locally, as well as climate regulation globally. This biome is so vast and imposing – and is of immeasurable biological, cultural, and aesthetic value – yet is so vulnerable in the face of today’s anthropogenic threats, such as infrastructure expansion. Conserving tropical rainforest ecosystems is paramount, both for the wildlife they harbour and to maintain global ecosystem functioning. Recent progress in remote surveying technology and analysis tools have allowed researchers to monitor natural ecosystems, including hard-to-access rainforests, like never before. By using camera traps and ARUs, coupled with acoustic indices and recognisers, this thesis has depicted the advantages and disadvantages of these technologies and analysis tools, as well as showcased their practical application for exploring the sensitivity of bird communities to infrastructure expansion. The research presented here is valuable and constitutes one of the first studies of its kind in Brunei’s tropical rainforest ecosystems. Hopefully, it will act as a springboard for further research, both to continue developing the field of eco-acoustics and to gain further ecological knowledge to help mitigate the current biodiversity loss crisis.

7.7 References

Bicknell, J.E., O'Hanley, J.R., Armsworth, P.R., Slade, E.M., Deere, N.J., Mitchell, S.L., Hemprich-Bennett, D., Kemp, V., Rossiter, S.J., Lewis, O.T. and Coomes, D.A., 2023. Enhancing the ecological value of oil palm agriculture through set-asides. *Nature Sustainability*, pp.1-13.

Bolgan, M., O'Brien, J., Chorazyczewska, E., Winfield, I.J., McCullough, P. and Gammell, M., 2018. The soundscape of Arctic Charr spawning grounds in lotic and lentic environments: can passive acoustic monitoring be used to detect spawning activities? *Bioacoustics*, *27*(1), pp.57-85.

Bradfer-Lawrence, T., Gardner, N., Bunnefeld, L., Bunnefeld, N., Willis, S.G. and Dent, D.H., 2019. Guidelines for the use of acoustic indices in environmental research. *Methods in Ecology and Evolution*, *10*(10), pp.1796-1807.

Bradfer-Lawrence, T., Bunnefeld, N., Gardner, N., Willis, S.G. and Dent, D.H., 2020. Rapid assessment of avian species richness and abundance using acoustic indices. *Ecological Indicators*, 115, p.106400.

Brandes, T.S., 2008. Automated sound recording and analysis techniques for bird surveys and conservation. *Bird Conservation International*, *18*(S1), pp.S163-S173.

Brooker, S.A., Stephens, P.A., Whittingham, M.J. and Willis, S.G., 2020. Automated detection and classification of birdsong: An ensemble approach. *Ecological Indicators*, *117*, p.106609.

Buxton, R.T., Brown, E., Sharman, L., Gabriele, C.M. and McKenna, M.F., 2016. Using bioacoustics to examine shifts in songbird phenology. *Ecology and Evolution*, *6*(14), pp.4697-4710.

Buxton, R.T., Galvan, R., McKenna, M.F., White, C.L. and Seher, V., 2017$_A$. Visitor noise at a nesting colony alters the behavior of a coastal seabird. *Marine Ecology Progress Series*, *570*, pp.233-246.

Buxton, R.T., McKenna, M.F., Mennitt, D., Fristrup, K., Crooks, K., Angeloni, L. and Wittemyer, G., 2017$_B$. Noise pollution is pervasive in US protected areas. *Science*, *356*(6337), pp.531-533.

Buxton, R.T., Lendrum, P.E., Crooks, K.R. and Wittemyer, G., 2018$_A$. Pairing camera traps and acoustic recorders to monitor the ecological impact of human disturbance. *Global Ecology and Conservation*, *16*, p.e00493.

Buxton, R.T., McKenna, M.F., Clapp, M., Meyer, E., Stabenau, E., Angeloni, L.M., Crooks, K. and Wittemyer, G., 2018$_B$. Efficacy of extracting indices from large-scale acoustic recordings to monitor biodiversity. *Conservation Biology*, *32*(5), pp.1174-1184.

Crunchant, A.S., Borchers, D., Kühl, H. and Piel, A., 2020. Listening and watching: Do camera traps or acoustic sensors more efficiently detect wild chimpanzees in an open habitat? *Methods in Ecology and Evolution*, *11*(4), pp.542-552.

Dean, W.R.J., Seymour, C.L., Joseph, G.S. and Foord, S.H., 2019. A review of the impacts of roads on wildlife in semi-arid regions. *Diversity*, *11*(5), p.81.

Derose-Wilson, A., Fraser, J.D., Karpanty, S.M. and Hillman, M.D., 2015. Effects of overflights on incubating Wilson's plover behavior and heart rate. *The Journal of Wildlife Management*, *79*(8), pp.1246-1254.

Dickie, M., Serrouya, R., McNay, R.S. and Boutin, S., 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology*, *54*(1), pp.253-263.

Diggins, C.A., Gilley, L.M., Kelly, C.A. and Ford, W.M., 2016. Comparison of survey techniques on detection of northern flying squirrels. *Wildlife Society Bulletin*, *40*(4), pp.654-662.

Dorsey, B., Olsson, M. and Rew, L.J., 2015. Ecological effects of railways on wildlife. In *Handbook of Road Ecology*. John Wiley & Sons, Ltd. Hoboken, New Jersey, U.S. pp.219-227.

Dröge, S., Martin, D.A., Andriafanomezantsoa, R., Burivalova, Z., Fulgence, T.R., Osen, K., Rakotomalala, E., Schwab, D., Wurz, A., Richter, T. and Kreft, H., 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*, 120, p.106929.

Ehnes, M. and Foote, J.R., 2015. Comparison of autonomous and manual recording methods for discrimination of individually distinctive Ovenbird songs. *Bioacoustics*, *24*(2), pp.111-121.

Eldridge, A., Guyot, P., Moscoso, P., Johnston, A., Eyre-Walker, Y. and Peck, M., 2018. Sounding out ecoacoustic metrics: Avian species richness is predicted by acoustic indices in temperate but not tropical habitats. *Ecological Indicators*, 95, pp.939-952.

Elzanowski, A., Ciesiołkiewicz, J., Kaczor, M., Radwańska, J. and Urban, R., 2009. Amphibian road mortality in Europe: a meta-analysis with new data from Poland. *European Journal of Wildlife Research*, *55*, pp.33-43.

Enari, H., Enari, H., Okuda, K., Yoshita, M., Kuno, T. and Okuda, K., 2017. Feasibility assessment of active and passive acoustic monitoring of sika deer populations. *Ecological Indicators*, *79*, pp.155-162.

Enari, H., Enari, H.S., Okuda, K., Maruyama, T. and Okuda, K.N., 2019. An evaluation of the efficiency of passive acoustic monitoring in detecting deer and primates in comparison with camera traps. *Ecological Indicators*, *98*, pp.753-762.

Fairbrass, A.J., Rennert, P., Williams, C., Titheridge, H. and Jones, K.E., 2017. Biases of acoustic indices measuring biodiversity in urban areas. *Ecological Indicators*, *83*, pp.169-177.

Farnsworth, A. and Russell, R.W., 2007. Monitoring flight calls of migrating birds from an oil platform in the northern Gulf of Mexico. *Journal of Field Ornithology*, *78*(3), pp.279-289.

Francis, M.J., Spooner, P.G. and Matthews, A., 2015. The influence of urban encroachment on squirrel gliders (Petaurus norfolcensis): effects of road density, light and noise pollution. *Wildlife Research*, *42*(4), pp.324-333.

Garland, L., Crosby, A., Hedley, R., Boutin, S. and Bayne, E., 2020. Acoustic vs. photographic monitoring of gray wolves (Canis lupus): a methodological comparison of two passive monitoring techniques. *Canadian Journal of Zoology*, *98*(3), pp.219-228.

He, K., Dai, Q., Gu, X., Zhang, Z., Zhou, J., Qi, D., Gu, X., Yang, X., Zhang, W., Yang, B. and Yang, Z., 2019. Effects of roads on giant panda distribution: a mountain range scale evaluation. *Scientific Reports*, *9*(1), p.1110.

Horton, K.G., Shriver, W.G. and Buler, J.J., 2015. A comparison of traffic estimates of nocturnal flying animals using radar, thermal imaging, and acoustic recording. *Ecological Applications*, *25*(2), pp.390-401.

Hyland, E.B., Schulz, A. and Quinn, J.E., 2023. Quantifying the Soundscape: How filters change acoustic indices. *Ecological Indicators*, *148*, p.110061.

Isbell, L.A. and Bidner, L.R., 2016. Vervet monkey (Chlorocebus pygerythrus) alarm calls to leopards (Panthera pardus) function as a predator deterrent. *Behaviour*, *153*(5), pp.591-606.

Jorge, F.C., Machado, C.G., da Cunha Nogueira, S.S. and Nogueira-Filho, S.L.G., 2018. The effectiveness of acoustic indices for forest monitoring in Atlantic rainforest fragments. *Ecological Indicators*, 91, pp.71-76.

Keen, S.C., Wackett, A.A., Willenbring, J.K., Yoo, K., Jonsson, H., Clow, T. and Klaminder, J., 2022. Non-native species change the tune of tundra soils: Novel access to soundscapes of the Arctic earthworm invasion. *Science of the Total Environment*, *838*, p.155976.

Knight, E., Hannah, K., Foley, G., Scott, C., Brigham, R. and Bayne, E., 2017. Recommendations for acoustic recognizer performance assessment with application to five common automated signal recognition programs. *Avian Conservation and Ecology*, *12*(2).

Laurance, W.F., Goosem, M. and Laurance, S.G., 2009. Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution*, *24*(12), pp.659-669.

Mammides, C., Goodale, E., Dayananda, S.K., Kang, L. and Chen, J., 2017. Do acoustic indices correlate with bird diversity? Insights from two biodiverse regions in Yunnan Province, south China. *Ecological Indicators*, 82, pp.470-477.

McGrann, M.C., Wagner, B., Klauer, M., Kaphan, K., Meyer, E. and Furnas, B.J., 2022. Using an acoustic complexity index to help monitor climate change effects on avian diversity. *Ecological Indicators*, 142, p.109271.

Mennill, D.J., Burt, J.M., Fristrup, K.M. and Vehrencamp, S.L., 2006. Accuracy of an acoustic location system for monitoring the position of duetting songbirds in tropical forest. *The Journal of the Acoustical Society of America*, *119*(5), pp.2832-2839.

Mennill, D.J., Battiston, M., Wilson, D.R., Foote, J.R. and Doucet, S.M., 2012. Field test of an affordable, portable, wireless microphone array for spatial monitoring of animal ecology and behaviour. *Methods in Ecology and Evolution*, *3*(4), pp.704-712.

Metcalf, O.C., Barlow, J., Devenish, C., Marsden, S., Berenguer, E. and Lees, A.C., 2021. Acoustic indices perform better when applied at ecologically meaningful time and frequency scales. *Methods in Ecology and Evolution*, *12*(3), pp.421-431.

Moreno-Gómez, F.N., Bartheld, J., Silva-Escobar, A.A., Briones, R., Márquez, R. and Penna, M., 2019. Evaluating acoustic indices in the Valdivian rainforest, a biodiversity hotspot in South America. *Ecological Indicators*, *103*, pp.1-8.

Müller, S., Gossner, M.M., Penone, C., Jung, K., Renner, S.C., Farina, A., Anhäuser, L., Ayasse, M., Boch, S., Haensel, F. and Heitzmann, J., 2022. Land-use intensity and landscape structure drive the acoustic composition of grasslands. *Agriculture, Ecosystems & Environment*, *328*, p.107845.

Myers-Smith, I.H., Arnesen, B.K., Thompson, R.M. and Chapin III, F.S., 2006. Cumulative impacts on Alaskan arctic tundra of a quarter century of road dust. *Ecoscience*, *13*(4), pp.503-510.

Petrusková, T., Pišvejcová, I., Kinštová, A., Brinke, T. and Petrusek, A., 2016. Repertoire-based individual acoustic monitoring of a migratory passerine bird with complex song as an efficient tool for tracking territorial dynamics and annual return rates. *Methods in Ecology and Evolution*, *7*(3), pp.274-284.

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*, *11*(3), pp.868-873.

Rajan, S.C., Athira, K., Jaishanker, R., Sooraj, N.P. and Sarojkumar, V., 2019. Rapid assessment of biodiversity using acoustic indices. *Biodiversity and Conservation*, *28*, pp.2371-2383.

Retamosa Izaguirre, M., Barrantes-Madrigal, J., Segura Sequeira, D., Spínola-Parallada, M. and Ramírez-Alán, O., 2021. It is not just about birds: what do acoustic indices reveal about a Costa Rican tropical rainforest? *Neotropical Biodiversity*, *7*(1), pp.431-442.

Robinson Willmott, J., Forcey, G.M. and Hooton, L.A., 2015. Developing an automated risk management tool to minimize bird and bat mortality at wind facilities. *Ambio*, *44*(Suppl 4), pp.557-571.

Sanders, C.E. and Mennill, D.J., 2014. Acoustic monitoring of migratory birds over western Lake Erie: avian responses to barriers and the importance of islands. *The Canadian Field-Naturalist*, *128*(2), p.135.

Sethi, S.S., Ewers, R.M., Jones, N.S., Signorelli, A., Picinali, L. and Orme, C.D.L., 2020. SAFE Acoustics: An open-source, real-time eco-acoustic monitoring network in the tropical rainforests of Borneo. *Methods in Ecology and Evolution*, *11*(10), pp.1182-1185.

Shamon, H., Paraskevopoulou, Z., Kitzes, J., Card, E., Deichmann, J.L., Boyce, A.J. and McShea, W.J., 2021. Using ecoacoustics metrices to track grassland bird richness across landscape gradients. *Ecological Indicators*, *120*, p.106928.

Shonfield, J. and Bayne, E., 2017. Autonomous recording units in avian ecological research: current use and future applications. *Avian Conservation and Ecology*, *12*(1).

Teixeira, F.Z., Printes, R.C., Fagundes, J.C.G., Alonso, A.C. and Kindel, A., 2013. Canopy bridges as road overpasses for wildlife in urban fragmented landscapes. *Biota Neotropica*, *13*, pp.117-123.

Towsey, M., Wimmer, J., Williamson, I. and Roe, P., 2014$_A$. The use of acoustic indices to determine avian species richness in audio-recordings of the environment. *Ecological Informatics*, *21*, pp.110-119.

Towsey, M., Zhang, L., Cottman-Fields, M., Wimmer, J., Zhang, J. and Roe, P., 2014$_B$. Visualization of long-duration acoustic recordings of the environment. *Procedia Computer Science*, *29*, pp.703-712.

Towsey, M., Znidersic, E., Broken-Brow, J., Indraswari, K., Watson, D.M., Phillips, Y., Truskinger, A. and Roe, P., 2018. Long-duration, false-colour spectrograms for detecting species in large audio datasets. *Journal of Ecoacoustics*, *2*, pp.1-13.

Van der Ree, R., Heinze, D., McCarthy, M. and Mansergh, I., 2009. Wildlife tunnel enhances population viability. *Ecology and Society*, *14*(2), pp 7-15.

Wang, H., Chen, C.E., Ali, A., Asgari, S., Hudson, R.E., Yao, K., Estrin, D. and Taylor, C., 2005, September. Acoustic sensor networks for woodpecker localization. In *Advanced Signal Processing Algorithms, Architectures, and Implementations XV* (Vol. 5910, pp. 80-91). SPIE.

Wrege, P.H., Rowland, E.D., Keen, S. and Shiu, Y., 2017. Acoustic monitoring for conservation in tropical forests: examples from forest elephants. *Methods in Ecology and Evolution*, *8*(10), pp.1292-1301.

Yip, D.A., Mahon, C.L., MacPhail, A.G. and Bayne, E.M., 2021. Automated classification of avian vocal activity using acoustic indices in regional and heterogeneous datasets. *Methods in Ecology and Evolution*, *12*(4), pp.707-719.

Chapter 8

Appendices

8.1 Appendix A – Equipment details

SongMeter and camera trap equipment details are listed in Table 1A.1 and 1A.2 respectively.

Table 1A.1 Equipment details for the 27 SongMeters Micro and 3 Song Meter Mini used during fieldwork.

Item	SongMeter model	Serial number
1	SongMeter Micro (Wildlife Acoustics)	SMM00843
2	SongMeter Micro (Wildlife Acoustics)	SMM00787
3	SongMeter Micro (Wildlife Acoustics)	SMM01298
4	SongMeter Micro (Wildlife Acoustics)	SMM01405
5	SongMeter Micro (Wildlife Acoustics)	SMM01489
6	SongMeter Micro (Wildlife Acoustics)	SMM00775
7	SongMeter Micro (Wildlife Acoustics)	SMM00972
8	SongMeter Micro (Wildlife Acoustics)	SMM00661
9	SongMeter Micro (Wildlife Acoustics)	SMM00672
10	SongMeter Micro (Wildlife Acoustics)	SMM01402
11	SongMeter Micro (Wildlife Acoustics)	SMM00662
12	SongMeter Micro (Wildlife Acoustics)	SMM01367
13	SongMeter Micro (Wildlife Acoustics)	SMM01404
14	SongMeter Micro (Wildlife Acoustics)	SMM01381
15	SongMeter Micro (Wildlife Acoustics)	SMM00653
16	SongMeter Micro (Wildlife Acoustics)	SMM00988
17	SongMeter Micro (Wildlife Acoustics)	SMM01000
18	SongMeter Micro (Wildlife Acoustics)	SMM01296
19	SongMeter Micro (Wildlife Acoustics)	SMM02432
20	SongMeter Micro (Wildlife Acoustics)	SMM01936
21	SongMeter Micro (Wildlife Acoustics)	SMM01400
22	SongMeter Micro (Wildlife Acoustics)	SMM01906

23	SongMeter Micro (Wildlife Acoustics)	SMM01310
24	SongMeter Micro (Wildlife Acoustics)	SMM01403
25	SongMeter Micro (Wildlife Acoustics)	SMM00858
26	SongMeter Micro (Wildlife Acoustics)	SMM01483
27	SongMeter Micro (Wildlife Acoustics)	SMM00867
28	SongMeter Mini (Wildlife Acoustics)	SMA00646
29	SongMeter Mini (Wildlife Acoustics)	SMA00941
30	SongMeter Mini (Wildlife Acoustics)	SMA00521

Table 1A.2 Equipment details for the 45 camera traps used during fieldwork.

Item	**Camera trap model**	**Serial number**
1	Browning Strike Force HD Pro X BTC-5HDPX	2110053111205HDPX
2	Browning Strike Force HD Pro X BTC-5HDPX	2110066911205HDPX
3	Browning Strike Force HD Pro X BTC-5HDPX	2110201911205HDPX
4	Browning Strike Force HD Pro X BTC-5HDPX	2110065111205HDPX
5	Browning Strike Force HD Pro X BTC-5HDPX	2110036411205HDPX
6	Browning Strike Force HD Pro X BTC-5HDPX	2110041411205HDPX
7	Browning Strike Force HD Pro X BTC-5HDPX	2110054311205HDPX
8	Browning Strike Force HD Pro X BTC-5HDPX	2110040211205HDPX
9	Browning Strike Force HD Pro X BTC-5HDPX	2110042211205HDPX
10	Browning Strike Force HD Pro X BTC-5HDPX	2110049911205HDPX
11	Browning Strike Force HD Pro X BTC-5HDPX	2110293811205HDPX
12	Browning Strike Force HD Pro X BTC-5HDPX	2110050311205HDPX
13	Browning Strike Force HD Pro X BTC-5HDPX	2110032611205HDPX
14	Browning Strike Force HD Pro X BTC-5HDPX	2110302011205HDPX
15	Browning Strike Force HD Pro X BTC-5HDPX	2110066011205HDPX
16	Browning Strike Force HD Pro X BTC-5HDPX	2110301811205HDPX
17	Browning Strike Force HD Pro X BTC-5HDPX	2110295111205HDPX
18	Browning Strike Force HD Pro X BTC-5HDPX	2110066811205HDPX
19	Browning Strike Force HD Pro X BTC-5HDPX	2110050411205HDPX
20	Browning Strike Force HD Pro X BTC-5HDPX	2110094411205HDPX
21	Browning Strike Force HD Pro X BTC-5HDPX	2110032911205HDPX
22	Browning Strike Force HD Pro X BTC-5HDPX	2110288111205HDPX

23	Browning Strike Force HD Pro X BTC-5HDPX	2110217511205HDPX
24	Browning Strike Force HD Pro X BTC-5HDPX	2110421711205HDPX
25	Browning Strike Force HD Pro X BTC-5HDPX	2110298811205HDPX
26	Browning Strike Force HD Pro X BTC-5HDPX	2110068011205HDPX
27	Browning Strike Force HD Pro X BTC-5HDPX	2110043011205HDPX
28	Browning Strike Force HD Pro X BTC-5HDPX	2110036111205HDPX
29	Browning Strike Force HD Pro X BTC-5HDPX	2110043211205HDPX
30	Browning Strike Force HD Pro X BTC-5HDPX	2110034111205HDPX
31	Browning Strike Force HD Pro X BTC-5HDPX	2110052711205HDPX
32	Browning Strike Force HD Pro X BTC-5HDPX	2110093511205HDPX
33	Browning Strike Force HD Pro X BTC-5HDPX	2110300511205HDPX
34	Browning Strike Force HD Pro X BTC-5HDPX	2110333611205HDPX
35	Browning Strike Force HD Pro X BTC-5HDPX	2110292011205HDPX
36	Browning Strike Force HD Pro X BTC-5HDPX	2110334811205HDPX
37	Browning Strike Force HD Pro X BTC-5HDPX	2110024711205HDPX
38	Browning Strike Force HD Pro X BTC-5HDPX	2110041511205HDPX
39	Browning Strike Force HD Pro X BTC-5HDPX	2110067811205HDPX
40	Browning Strike Force HD Pro X BTC-5HDPX	2110046111205HDPX
41	Browning Strike Force HD Pro X BTC-5HDPX	2110051011205HDPX
42	Browning Strike Force HD Pro X BTC-5HDPX	2110009811205HDPX
43	Browning Strike Force HD Pro X BTC-5HDPX	2110033511205HDPX
44	Browning Strike Force HD Pro X BTC-5HDPX	2110052511205HDPX
45	Browning Strike Force HD Pro X BTC-5HDPX	2110334511205HDPX

8.2 Appendix B – Equipment malfunctions

A list of all the deviations from the programmed regime for SongMeters and malfunctions for camera traps can be found in Table 2B.1 and 2B.2 respectively according to recording sites. Sites LIP7.2, LIP10.2, MIP4.2, and MIP34.2 are repeats due to camera trap malfunctions, not ARUs malfunction (but the latter was redeployed to have paired datasets recorded at the same time).

Table 2B.1 All the deviations from the programmed regime for SongMeters. Rows with a ‘x’ indicates there were no deviations from the programmed regime by the SongMeter at that site. ‘Malfunctioned’ indicates when an audio file was not recorded for the correct amount of time (usually slightly shorter), often accompanied by a small, unopenable, error file. This usually happened near the end of the deployment period, when the SD card was nearly full.

Recording site	Comments
AZ1	x
AZ2	x
AZ3	Recorded an extra 1 min of audio data after each scheduled recording slot.
AZ4	x
FREME2	x
HIP1	Varying dawn recording length.
HIP38	05/12 at 10h and 15h malfunctioned.
HIP48	04/5 at 9h malfunctioned. Varying dawn recording length.
HIP49	Varying dawn recording length
HIP50	Varying dawn recording length
HIP51	x
HIP52	1 dusk file is half the length it should be. 6/13 (last day) at 16h, 18h, 19h malfunctioned
HIP53	Varying dawn recording length.
HIP54	X
HIP55	Varying dawn recording length.
HIP57	Varying dawn recording length. Recorded an extra 1 min of audio data after each scheduled recording slot.
HIP58	1 dawn file malfunctioned.
HIP59	x

HIP60	Varying dawn recording length.
HIP63	Varying dawn recording length.
HIP64	Varying dawn recording length.
HIP65	x
HIP66	Varying dawn recording length.
HIP67	Recorded an extra 1 min of audio data after each scheduled recording slot.
HIP68	x
HIP69	Varying dawn recording length.
HIP70	Varying dawn recording length.
J1	1 dawn file malfunctioned.
J10	x
J2	x
J3	x
J4	x
J5	No audio files found, possibly due to SD car corruption.
J6	x
J7	Recorded an extra 1 min of audio data after each scheduled recording slot.
J8	x
J9	Last dusk file slightly shorter than normal (98kb).
JBPLOT	x
LIP10	04/28 (last day) at 11h malfunctioned.
LIP10.2	x
LIP11	x
LIP25	x
LIP27	Varying dawn recording length.
LIP35	Varying dawn recording length.
LIP37	Varying dawn recording length.
LIP44	Varying dawn recording length.
LIP45	Varying dawn recording length.
LIP7	1 dawn file slightly longer than normal. Recorded an extra 1 min of audio data after each scheduled recording slot.
LIP7.2	x
LIP8	x
LIP9	x

MIP1	x
MIP15	x
MIP15 new	06/4 (last day) 4h malfunctioned
MIP16	Varying dawn recording length. Recorded an extra 1 min of audio data after each scheduled recording slot.
MIP22	Varying dawn recording length.
MIP27 new	x
MIP28	Varying dawn recording length.
MIP3	Varying dawn recording length.
MIP34	x
MIP34.2	x
MIP35	Varying dawn recording length.
MIP36	Only recorded for 6 days.
MIP4	Varying dawn recording length.
MIP4.2	x
MIP40	Varying dawn recording length.
MIP41	Varying dawn recording length.
MIP42	Varying dawn recording length.
MIP47	Varying dawn recording length.
MIP48	x
MIP8	Varying dawn recording length.
MIP9 (Freme1)	x
MIP9.2	x
SOAS	x

Table 2B.2 All the deviations from the programmed regime for camera traps. Rows with a ‘x’ indicates there were no deviations from the programmed regime by the camera trap at that site. ‘Glitched’ indicates that the camera trap took a very large series of images in a row without necessarily being triggered.

Recording site	**Comments**
AZ1	x
AZ2	Adjusted by a monkey (03/05/22).

AZ3	x
AZ4	x
FREME2	Adjusted by a monkey (05/05/22).
HIP1	x
HIP38	x
HIP48	x
HIP49	x
HIP50	Adjusted by monitor lizard (13/3/22).
HIP51	x
HIP52	x
HIP53	Condensation on some images.
HIP54	Night overexposure.
HIP55	x
HIP57	Glitched and date reset to 1/1/2020 during deployment. Continued recording as normal after glitch.
HIP58	x
HIP59	x
HIP60	Adjusted by monkey (26/2/22). Some grainy images.
HIP63	Night overexposure.
HIP64	x
HIP65	Night overexposure.
HIP66	Abnormal image light/quality.
HIP67	Glitched twice. Continued recording as normal after the glitch.
HIP68	Glitched and date reset to 1/1/2020 during deployment. Continued recording as normal after glitch.
HIP69	Night overexposure.
HIP70	x
J1	x
J10	Glitched and date reset to 1/1/2020 during deployment. Stops recording after glitch.
J2	Night overexposure and lots of empty images.
J3	Night overexposure.
J4	Night overexposure.
J5	Did not record any data.
J6	Night overexposure.
J7	x

J8	x
J9	Night overexposure and condensation obscuring some images.
JBPLOT	Glitched and date reset to 1/1/2020 during deployment. Continued recording as normal after glitch. Condensation on some images.
LIP10	Glitched (24/5/22). Stops recording after glitch.
LIP10.2	Glitched (30/6/22 - 01/07/22). Does not resume normal functioning.
LIP11	Night overexposure. Glitch (24/04/22) but continued recording as normal after glitch.
LIP25	Glitch (16/4/22) but continued recording as normal after glitch.
LIP27	SD card filled up on the first deployment day due to bees swarming around camera trap.
LIP35	Night overexposure and condensation obscuring some images. Glitched (19/3/22) but continued recording as normal after the glitch.
LIP37	Condensation distorting some images.
LIP44	x
LIP45	x
LIP7	Adjusted by a monkey (30/03/22).
LIP7.2	x
LIP8	Some condensation (not too bad).
LIP9	Some condensation (not too bad).
MIP1	Condensation distorting some images.
MIP15	Did not record for full deployment, may have run out of batteries.
MIP15 new	Strange image quality, some condensation.
MIP16	x
MIP22	x
MIP27 new	x
MIP28	x
MIP3	x
MIP34	Did not record any data.
MIP34.2	Glitch (27/6/22): does not reset until the end. Night overexposure.
MIP35	x
MIP36	Night overexposure.
MIP4	Glitch (6/3/22) but continued recording as normal after the glitch. Adjusted by monkey.
MIP4.2	x
MIP40	x

MIP41	x
MIP42	Night overexposure, condensation in some images. Glitch (22/2/22) but continued recording as normal after the glitch.
MIP47	x
MIP48	x
MIP8	Stopped recording early, may have run out of battery.
MIP9 (Freme 1)	x
MIP9.2	x
SOAS	Glitch (04/06/22) but continued recording as normal after the glitch.

8.3 Appendix C – Habitat covariates correlation

Statistical measures relating to the habitat covariates correlation. See Table 3C.1 for results of the Pearson's correlation conducted between the continuous variables. See Table 3C.2 for the association between the categorical variables. See Figure 3C.1 for the association between the continuation variable *Distance to Nearest Main Road* and the categorical variable *Nearest Main Road Type.*

Table 3C.1 Pearson's correlation scores between continuous variables. Red cells indicate correlation scores greater than recommended the cut-off threshold of r = 0.7, in this case resulting in the variable *Distance to nearest road* being discarded during analysis. Distance to building is the distance between each site and the nearest building, distance to nearest main road is the distance between each site and the nearest main road to that site, distance to nearest road is the distance between each site and the nearest road to that site, and biomass is the total above ground biomass calculated using an allometric equation previously used in tropical forests in conjunction with data collected in the field. The distance variables were measured using Google Earth Pro.

	Distance to nearest main road	*Biomass*	*Distance to nearest road*	*Distance to nearest building*
Distance to nearest main road	1			
Biomass	0.2831440	1		
Distance to nearest road	0.9015533	0.3418768	1	
Distance to nearest building	0.3523868	0.2685286	0.3705074	1

Table 3C.2 Association between the categorical variables *Nearest main road type* and *Infrastructure Pressure Zone*. HIP = High Infrastructure Pressure; MIP = Medium Infrastructure Pressure; LIP = Low Infrastructure Pressure.

		Infrastructure Pressure Zone		
		HIP	MIP	LIP
Nearest main road type	Highway	30	0	0
	Secondary main road	0	19	0
	Track	0	1	19

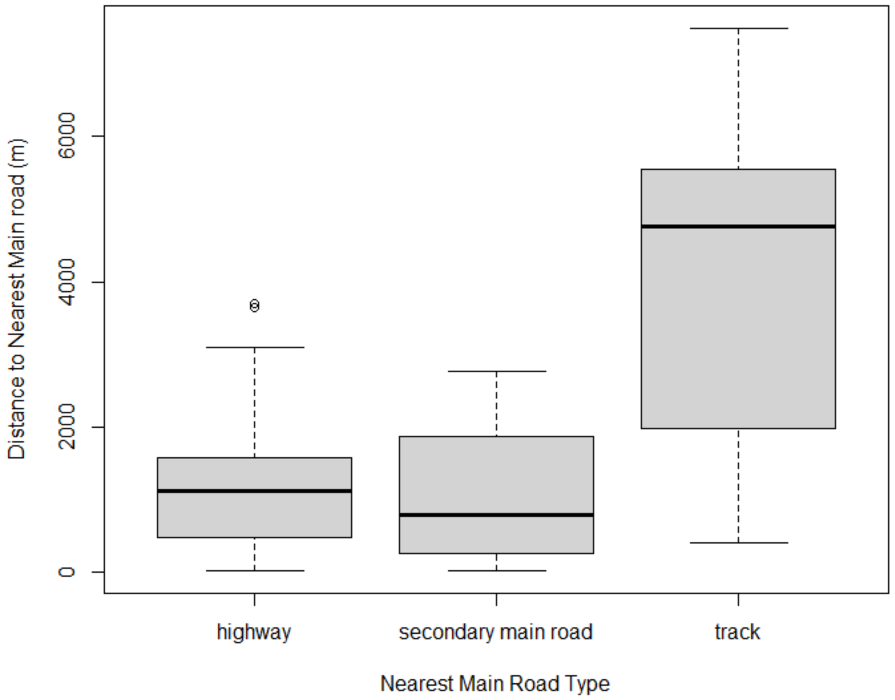


Figure 3C.1 Association between the continuation variable *Distance to Nearest Main Road* and the categorical variable *Nearest Main Road Type*. *Distance to Nearest Main Road* is the distance between each site and the nearest main road to that site. *Nearest Main Road Type* was either highway, secondary main road, or track. Distances were measured using Google Earth Pro.