Acoustic monitoring of Amazonian wildlife in human-modified landscapes

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Acoustic monitoring of Amazonian wildlife in human-modified landscapes

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requirements of Manchester Metropolitan
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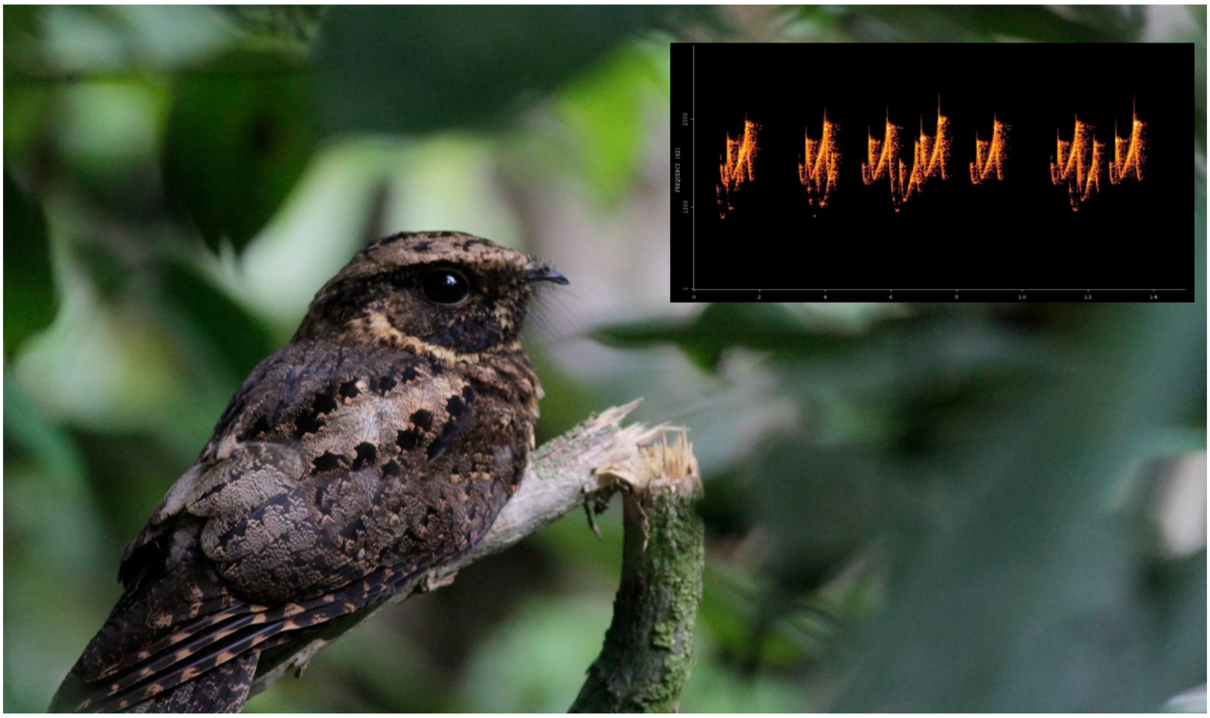

Silky-tailed nightjar Antrostomus sericocaudatus*, and a spectrogram of a duet between two individuals recorded during passive acoustic monitoring.*

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Abstract

Tropical forest covers just 12% of the planet's land surface, but disproportionately host the planet's biodiversity, including around two thirds of all terrestrial species. Amazonia retains the largest extent of remaining tropical forest globally, but just over 50% of all tropical forest loss since 2002 has been in the region. Deforestation and disturbance result in significant loss in forest biodiversity, but quantifying the exact nature of those changes can be complex. The Amazon represents a particularly challenging case in which to assess biodiversity change due to the spatiotemporal scales being assessed, because of the high proportion of rare species, and the challenging conditions for conducting biodiversity surveys in tropical forest.

Ecoacoustics has been championed as a valuable tool to overcome the difficulties of monitoring in such conditions and at large spatio-temporal scales, but applied analytical methods often remain underdeveloped. In this this thesis I develop and use a range of ecoacoustic methods to help understand the impact of anthropogenic disturbance on Amazonian wildlife, using an extensive audio dataset collected from survey points spanning a degradation gradient in the Eastern Brazilian Amazon. In Chapter 2 I introduce a quick and simple method for the detection of rainfall, tested for efficacy globally and with an accompanying R package. In Chapter 3 I present a new approach to subsampling of acoustic data for manual assessment of avian biodiversity, finding that using a high number of short repeat samples can detect approximately 50% higher alpha diversity than more commonly used approaches. In Chapter 4 I assess the sensitivity and fidelity of two commonly used acoustic indices to biodiversity responses to forest disturbances, finding that measuring indices at narrower, ecologically appropriate time-frequency bins avoids problems with signal masking. In Chapter 5 I use a two-stage, random forest based method to build a multi-taxa classifier for the nocturnal avifaunal community in the study region, and use the classifier-derived data to reveal that the nocturnal bird community is largely robust to less intense forms of forest disturbance. Overall, in this thesis I demonstrate that ecoacoustics can be a highly effective method for inventorying and monitoring biodiversity in one of the most diverse and challenging regions on the planet.

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Preface

I have written this thesis as a series of chapters, formatted in the style of stand-alone scientific papers, prefaced by an introduction and concluded with a discussion of the results and recommendations for future research. I am fortunate that two of the papers have already been published (Chapters 2 and 4, published versions included as appendices), with a third (Chapter 3) in review. This does however result in some degree of overlap between the chapters, particularly in the Methods section in relation to data collection. Each of the data chapters is formatted in the style of the journal it is published in or the target journal, so there may be some small differences in style, although all of the journal styles are similar.

The work presented in this thesis is predominantly my own. This includes all of the writing, with the exception of the ‘Package Description’ section and Table 2.4 in Chapter 2, which were written by Christian Devenish. In addition, I designed the studies, undertook the data collection for all of the acoustic data used in this study except the data from Java in Chapter 2, and undertook the data analysis. However, many other people contributed directly to this work, most notably my supervisory team, Alexander Lees, Jos Barlow and Stuart Marsden, who assisted with the study design, advised on analytical methods and provided revisions to draft versions of all of the chapters. Yves Bas, Christian Devenish, Erika Berenguer, Joice Ferreira, and Nárgila Gomes De Moura have also provided substantial input, advise and revisions at various points throughout.

I use the pronoun ‘we’ in most chapters in this thesis, with the exception of the Introduction and Discussion. There are several reasons for this, the most significant being that it maintains consistency between those chapters already published or in revision, and those yet to be, or not intended to be, published. It is also appropriate recognition for the input of others as discussed above, and the collaborative nature of modern conservation ecology, and the substantial role the Sustainable Amazon

Network (www.rasnetwork.org) has played in making this thesis possible. It should not however be interpreted as an indication that the work is not predominantly and substantially my own, in keeping with the requirements for a PhD thesis.

Publication outputs

Accepted articles

Metcalf, Oliver C., Barlow, J., Devenish, C., Marsden, S., Berenguer, E., Lees, A.C., 2020a. Acoustic indices perform better when applied at ecologically meaningful time and frequency scales. Methods Ecol. Evol. 12, 421–431. https://doi.org/10.1111/2041-210X.13521

Metcalf, Oliver C., Lees, A.C., Barlow, J., Marsden, S.J., Devenish, C., 2020b. hardRain: An R package for quick, automated rainfall detection in ecoacoustic datasets using a threshold-based approach. Ecol. Indic. 109, 105793. https://doi.org/10.1016/j.ecolind.2019.105793

In review

Metcalf, Oliver C, Barlow, J., Marsden, S., Moura, N.G. De, Berenguer, E., 2020. Optimising tropical forest bird surveys using passive acoustic monitoring and repeated short-duration point counts. bioRxiv 2020.08.24.263301. https://doi.org/10.1101/2020.08.24.263301

Chapter 1:

Introduction

The Tapajós National Forest

1.1. Tropical forests in the Anthropocene

Tropical forest covers just 12% of the planet’s land surface, but is disproportionately important in provisioning ecosystem services (Malhi et al., 2014). Tropical forests hold 34% of the terrestrial carbon store (Janetos et al., 2010), and offer some of the greatest opportunities for forest regeneration to sequester carbon and reduce warming (CBD, 2010). They also provide important services regulating waterflows and rainfall (Foley et al., 2007; Locatelli and Vignola, 2009) - vital for agriculture in tropical regions and beyond, are a vital source of medicines (Albuquerque et al., 2012), as well as providing a buffer against the spread of infectious disease (Ellwanger et al., 2020; Guégan et al., 2020; Swift et al., 2007). Tropical forests disproportionately host the planet’s biodiversity (Gentry, 1992; Mittermeier et al., 1998) including around two thirds of all terrestrial species (Gardner et al., 2009)

Figure 1.1. *Primary forest viewed from a canopy tower in the Tapajós National Forest, Pará, part of our study area.*

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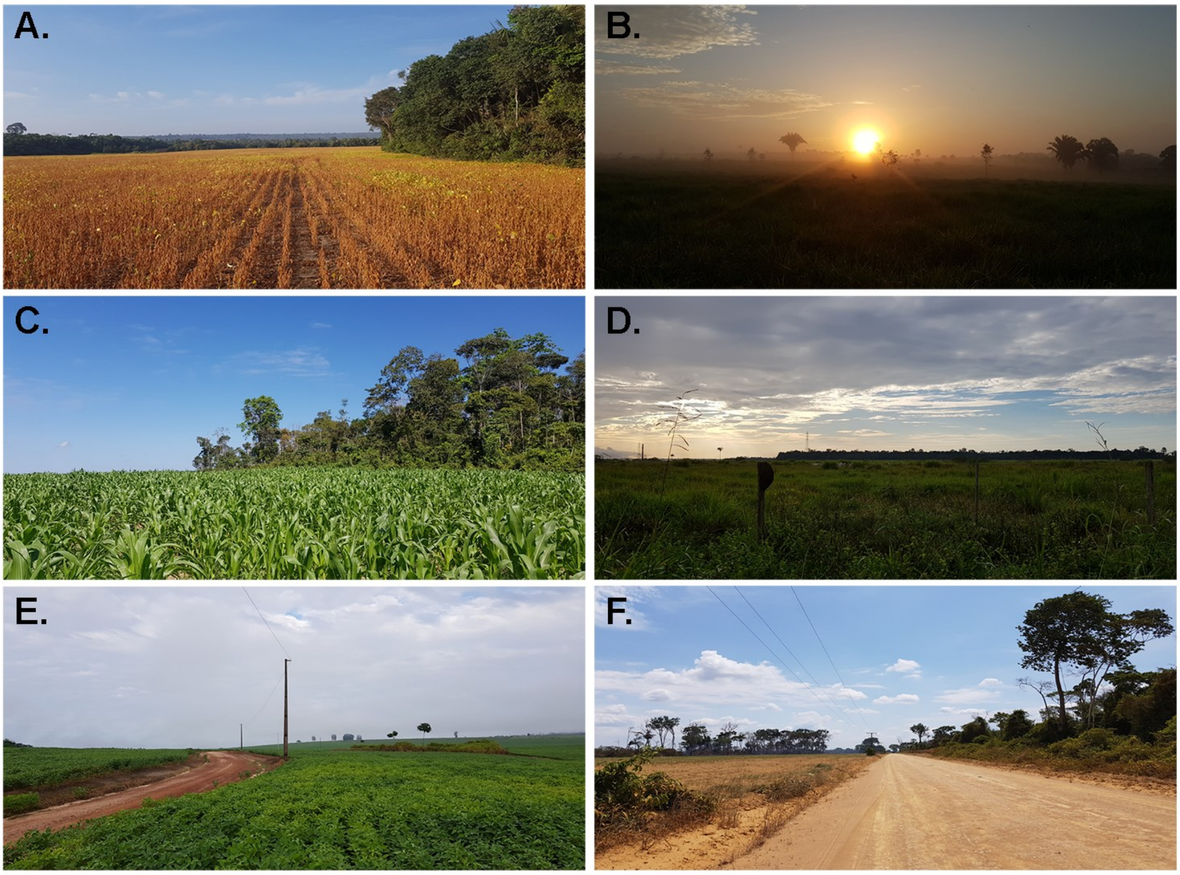
1.1.1. Brazil and deforestation

Amazonia retains the largest extent of remaining tropical forest globally and accounts for just over 50% of the loss of tropical forest cover globally since 2002 (Global Forest Review, 2020). About 60% of the Amazon is in Brazil (FAO, 2010), where most forest loss in South America between 2001-2010 occurred (Aide et al., 2013), and was until the middle of the last decade the world's most active deforestation frontier (Barlow et al., 2011; Hansen et al., 2010). Approximately 20% of primary forest in the Brazilian Amazon has already been lost (PRODES, 2020). Amazonian deforestation is driven by conversion of forest to pasture or soy, immigration leading to rapid increases in the regional population, expansion of road networks , and increases in industrial logging and mining (Andersen, 1996; Barona et al., 2010; Bowman et al., 2012; Laurance et al., 2001). Deforestation risks the region becoming a net source of carbon emissions reducing the chances of reaching the Paris Agreement target of limiting global warming to 1.5 degrees Celsius (Brienen et al., 2015; Maxwell et al., 2019; UNEP, 2019); of destabilising precipitation patterns with potentially disastrous consequences for agriculture in South America (Lapola et al., 2018; Staal et al., 2020; Vergara, 2009); and of irreversible biodiversity loss (IPBES, 2019; Moura et al., 2014; Wearn et al., 2012).

Brazil was able to successfully reduce the rate of deforestation between 2004 and 2012 by 79% (Aragão et al., 2018; Berenguer et al., 2014; Nepstad et al., 2014). The reduction is commonly ascribed to policy changes and strict enforcement, as well as a rapid reduction in the price of soy in 2004-2005 (Nepstad et al., 2014). These measures were headlined by the Action Plan for the Prevention and Control of Deforestation, extension of protected areas and an Amazonian soy moratorium, (Assuncąo et al., 2015; Boucher et al., 2013; Gollnow and Lakes, 2014; Heilmayr et al., 2020; Tacconi et al., 2019). Although the current Brazilian political situation is antipathetic towards environmental concerns (Anon., 2018) and deforestation rates have recently increased dramatically again (Silva Junior et al., 2020), the prior efficacy of the legislation means that there is a viable road map to ending deforestation in the Brazilian Amazon (Nepstad et al., 2009) given future political will.

Figure 1.2. *Forest conversion to agropastoral matrix in our study region.*



A.Soy field and forest fragment. B. Extensive cattle pasture. C. Maize and highly degraded forest fragment. D. Cattle pasture. E. Soy field F. A road running through the forest/agriculture matrix. Copyright: OCM

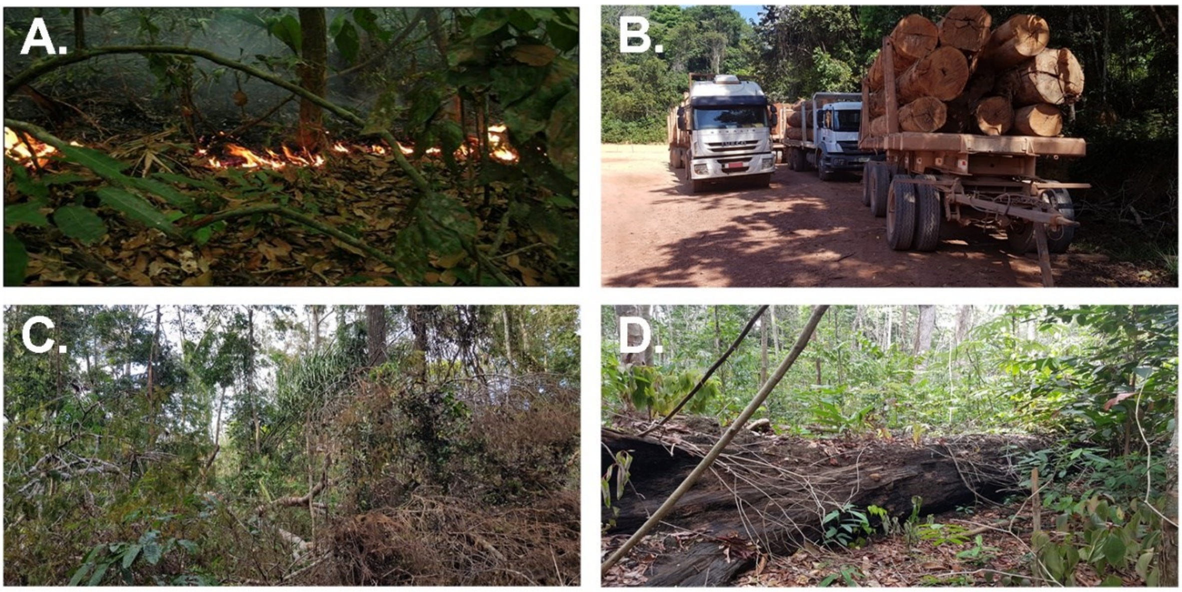
1.1.2. Forest disturbance in the Brazilian Amazon

Legislation and processes regulating deforestation were primarily concerned with land-use and forest cover, as were conservation organisations and researchers, paying only limited attention to the quality of the forest that was being protected. For example, in 2008 the area of forest impacted by disturbance in Brazil was double that of forest that was cleared for another land use (Berenguer et al., 2014). Consequently forest disturbance, primarily caused by logging and wildfires, has affected an area greater than that deforested in the Brazilian Amazon to date (Bullock et al., 2020; Matricardi et al., 2020).

Selective logging is the most widespread form of forest disturbance (Asner et al., 1999; Foley et al., 2007; Veríssimo et al., 2008), with some annual harvests prior to 1997 greater than 40 million m^3 (Merry et al., 2006). Illegal logging is ubiquitous in

Amazonia, with some estimates suggesting the majority of all logging is illegal in the region (Brancalion et al., 2018; Santos de Lima et al., 2018). Logging can lead to severely reduced carbon stocks in forest (Rappaport et al., 2018), and lead to the creation of road networks to facilitate access and logging tracks to remove timber (Arima et al., 2005) with associated edge effects (Murcia, 1995), and severely altered forest structure with increased canopy openness and higher abundance of lianas (Gerwing, 2002). Even best-practice reduced impact logging can still have significant detrimental impact on forest structure (Boltz et al., 2003; Sist and Ferreira, 2007).

Figure 1.3. *Anthropogenic forest disturbance.*



A: forest fires can often be very small, but still have a major impact on forest structure. B: Timber from low-impact logging waiting to be extracted from the Tapajós National Forest. C and D: Forest recovery. Copyright: A. Jos Barlow. B-D. OCM

Logging also contributes to forest degradation by fire, as it creates the microclimatic conditions in which uncontrolled fires can take hold within standing forests (Barlow et al., 2020; Uhl and Kauffman, 1990). Forest fires do not occur naturally in Amazonia, and generally require an anthropogenic ignition source, such as fires escaping from pasture management or secondary forest clearing, and occur usually when forest conditions have been altered through logging or drought to allow fires to take hold (Barlow et al., 2020). Even small understorey forest fires have been shown to have a dramatic impact on forest structure, causing up to 50% increased tree mortality

(Barlow et al., 2003; Silva et al., 2018). There is also an additive effect, once an area of forest has been burnt, it becomes drier and therefore more vulnerable to catching fire again, with greater intensity (Gerwing, 2002). The extent of forest wildfires can be extremely difficult to monitor as they occur below the forest canopy but can cover vast areas. For example, at the epicentre of the 2015 El Niño events, 1 million ha of forest burnt in the Santarém region of Para, Brazil (Barlow et al., 2020; Withey et al., 2018). Furthermore, as global warming exacerbates El Niño events and creates increasingly warmer and drier conditions, the regularity, intensity, and extent of wildfires are only likely to increase (Silva et al., 2018). In synergy, logging and fires can have severe consequences for tropical forests, reducing their aboveground carbon storage capacity by up to 40% (Berenguer et al., 2014), reductions in forest biomass which may last decades (Silva et al., 2018) in addition to causing potentially permanent alterations in forest structure (Barlow and Peres, 2008; Prestes et al., 2020).

1.1.3. Forest regeneration

Forest cover in the Brazilian Amazon is not uniformly declining (Aide et al., 2013; Chazdon, 2014). Regenerating secondary forests on abandoned agricultural land are a feature of many frontier areas in Amazonia (Lucas et al., 2002; Nunes et al., 2020). Although the scale of regeneration does not match that of deforestation or disturbance, secondary forest covered 129,361 km^2 in the Brazilian Amazon in 2017, or 3.8% of total forest cover (Smith et al., 2020). Secondary forest can provide many of the ecosystem services of primary forest, and are often vital resources in otherwise deforested landscapes (Börner et al., 2007; Chazdon et al., 2009; Gardner et al., 2009). However, secondary forest have distinct structure and composition to primary forest, and may never recover the same qualities as the original primary forest (Elias et al., 2020; Lennox et al., 2018).

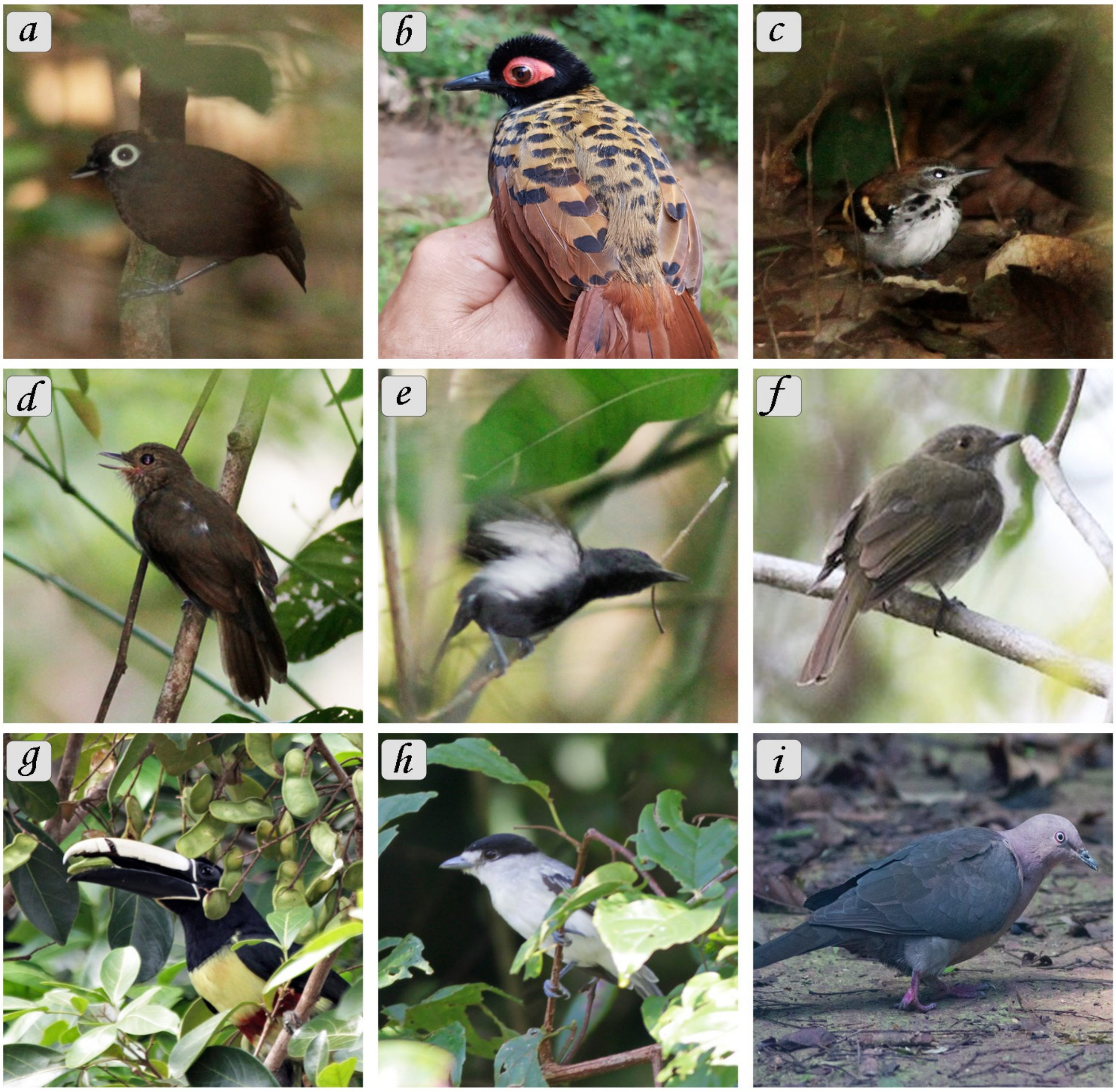
1.1.4. Biodiversity impacts of deforestation and disturbance

Deforestation and disturbance result in significant biodiversity loss (Gibson, 2011), but quantifying the exact nature of those changes can be complex - dependant on the type of impact and on the spatial and temporal scales being assessed. The starkest impacts on biodiversity occur with large-scale deforestation, universally resulting in steep declines in species richness and almost complete turnover in biotic communities, as complex ecosystems of forest specialists give way to homogenised communities of a handful of species (Gardner et al., 2013; Moura et al., 2013; Peres et al., 2010).

Biodiversity response to forest disturbance is substantially more complex than the response to deforestation. There is a high degree of idiosyncrasy in species response to disturbance (Gardner et al., 2009); with some species - particularly specialist species - declining quickly, whilst more generalist species are unaffected or even able to proliferate in degraded forests (Bicknell et al., 2015; Moura et al., 2016). At the community level, species richness often increases with disturbance at small spatial scales, as habitat diversity increases. Selective reduced-impact logging can have a relatively minor impact on biodiversity at local scales, often having no impact on overall assemblages in vegetation and terrestrial vertebrates (Azevedo-Ramos et al., 2006; Bicknell et al., 2015; Vasconcelos et al., 2000; Wunderle et al., 2006), although most vertebrates decline as logging intensity increases (Burivalova et al., 2014). Logging can have more substantial impacts on bat and fish communities (Dias et al., 2010; Peters et al., 2006; Presley et al., 2008), and invertebrates are rarely studied, despite making up the majority of the species pool (Andersen and Majer, 2004; Rappaport et al., 2021; Solar et al., 2016), although one study has shown a change in acoustic space use between logged and unlogged forest, likely driven by insects (Campos-Cerquiera et al., 2020). In contrast fires can cause significant decreases in fauna (Barlow and Peres, 2004a; Haugaasen et al., 2003; Peres et al., 2003), and recurrent fires can cause up to 100% turnover in understorey avian composition, and dramatic shifts in tree composition (Barlow and Peres, 2008, 2004b).

Deforestation and disturbance impacts biodiversity at a landscape scale however, with forest patch size, extent of forest fragmentation and corresponding edge effects, and quality of the surrounding agropastoral matrix strongly impacting regional biodiversity (Peres et al., 2010). The landscape scale factors drive homogenisation of biodiversity, reducing gamma diversity as primary forest specialists are lost and replaced by generalist species (Solar et al., 2015; Tabarelli et al., 2012). However, there are very few studies that have conducted research at landscape scales in the Amazon, and limited to a few locations (Peres et al., 2010), and in landscapes that do not always represent the full range of threats to biodiversity in the Amazon. For example, the longest running of such projects in the Amazon, the Biological Dynamics of Forest Fragmentation Project north of Manaus (Stouffer, 2020), extensively studies the impact of forest fragmentation and secondary forest, but does not consider disturbance. When all of the impacts are considered across a matrix of varying habitats and disturbance intensities at a landscape scale, the impact of disturbance can be severe - doubling the loss of conservation value compared to deforestation alone (Barlow et al., 2016).

Figure 1.4. *Many bird species show species specific responses to forest fragmentation and disturbance.*



Top row: understory insectivores have been shown to be highly sensitive, **a**; the interfluvial endemic Bare-eyed Antbird *Rhegmatorhina gymnops*, **b**; Black-spotted Bare-eye *Phlegopsis nigromaculata* and **c**; Banded Antbird *Dichrozona cincta*. **Middle row:** other species shown to decline with forest disturbance include **d**; Cinereous Antshrike *Thamnomanes caesius*, **e**; White-flanked Antwren *Myrmotherula axillaris* and **f**; Screaming Piha *Lipaugus vociferans*. **Bottom row:** a smaller number of species actually increase in human-modified forest including **g**; Black-necked Aracari *Pteroglossus aracari*, **h**; Black-capped Becard *Pachyramphus marginatus* and **i**; Plumbeous Pigeon *Patagoienas plumbea. Copyright: OCM*

1.1.5. Challenges of monitoring biodiversity loss through forest degradation

As species respond in such idiosyncratic ways to disturbance, monitoring a wide number of species is of vital importance. However, there are some substantial challenges to monitoring the impact of forest degradation on biodiversity in the Amazon. Foremost of these is the scales at which it is necessary to monitor. Because of the complex sink-source dynamics that can play out across landscape habitat matrices, the survey areas required can be huge. For example, the Sustainable Amazon Network (www.rasnetwork.org) plots covered ca 10,000 ha in 2010 in order to incorporate a full range of deforestation and disturbance factors at an appropriate landscape scale (Gardner et al., 2013). Similarly, as the impacts of deforestation and disturbance play out over extended timescales as forests regenerate, recover and/or are subjected to repeated disturbance events and further degrade, understanding the impacts of disturbance may require repeat surveys over decades (Campos-Cerqueira et al., 2021; de Camargo et al., 2019; Stouffer, 2020; Stouffer et al., 2009). This requires a huge amount of effort, logistical and planning challenges, and can be prohibitively expensive.

The second, more prosaic problem relates to the nature of tropical forest. Towering forest, often with dense stands of shady understory vegetation presents a severe challenge in which to survey any species, whilst in burnt or logged forest, fallen trees can be formidable barriers and dense understory regeneration can reduce visibility down to a few metres. High humidity and regular intense downpours, so characteristic of rainforest, are a stern test for any equipment. In combination, this makes observational studies difficult, and contributes to a lack of even basic natural history knowledge for many species (Lees et al., 2020), making interpretation of study results more difficult.

Figure 1.5. *Visibility can be greatly reduced in disturbed forest due to dense understory. A. Undisturbed forest. B. Logged forest. C. Logged and burned forest. D. Secondary forest. All photographs taken from 10m.*

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Finally, understanding the impact of forest degradation in the Amazon is challenging because whilst the Amazon is hyperdiverse, many species are cryptic, and/or occur at low abundances (Robinson et al., 2000; Terborgh et al., 1990). This means that accumulating sufficient inventory completeness can be challenging without extensive surveying efforts (Robinson et al., 2018). Rare and cryptic species are often under-sampled and hence discounted from studies due to insufficient detections for appropriate analysis. This is an important problem as the systematic disregard of rare species which are more likely to be dietary or habitat specialists are likely to be more vulnerable to forest disturbance.

1.2. Ecoacoustics as a tool for monitoring biodiversity in tropical forests

Ecoacoustics has been proposed as a valuable tool in overcoming the difficulties in monitoring in such conditions (Burivalova et al., 2019a; Deichmann et al., 2018;

Wagner Ribeiro Jr et al., 2017). Here I use the broadest definition of ecoacoustics following the originators of the term;

“Ecoacoustics is defined as a theoretical and applied discipline that studies sound along a broad range of spatial and temporal scales in order to tackle biodiversity and other ecological questions. The use of sound as a material from which to infer ecological information enables ecoacoustics to investigate the ecology of populations, communities and landscapes.” (Sueur and Farina, 2015).

This stands in contrast to other authors (e.g. Eldridge et al., 2018, Sugai et al., 2019) that have used ecoacoustics to refer to the study of patterns across entire soundscapes, and usually implies the use of acoustic indices. It also differentiates the field from bioacoustics, also commonly used as a catch-all term for ecological studies using acoustics (e.g. Burivalova et al., 2019), but which is more appropriately used in describing animal behaviour studies that have sound as a focus, and which can be considered a sub-discipline of ecoacoustics (Sueur and Farina, 2015). Ecoacoustic methods for marine and volant mammals are generally considerably more advanced than for birds, amphibians, reptiles and terrestrial mammals (Gibb et al., 2019), but this review will focus on the latter.

Sound has long been recognised as an excellent method by which to study biodiversity, with many species more easily detected audibly than visually, as they primarily communicate and signal their presence with sound (Heinicke et al., 2015; Rosenthal and Ryan, 2000; Sugai et al., 2019). Animal vocalisations also carry a wealth of information beyond species identity, including individual identity, abundance, location, size of the individual, behaviour, health, and clues to the ecological roles and niches they fill (Blumstein et al., 2011; Farina and Gage, 2017; Pérez-Granados and Traba, 2021; Rhinehart et al., 2020; Seddon, 2005; Stowell et al., 2019; Wilkins et al., 2013).

1.2.1. Passive Acoustic Monitoring

Ecoacoustics is underpinned by passive acoustic monitoring (PAM) (Sueur and Farina, 2015), the use of autonomous recording units (ARUs) to record soundscapes without the concurrent presence of a human observer. PAM has several advantages over more traditional survey methods when it comes to application in tropical forests which have been well documented in a series of recent reviews (e.g. Darras et al., 2019b, 2018; Gibb et al., 2019; Shonfield and Bayne, 2017; Sugai et al., 2019). The biggest benefit of PAM is the capacity to function for long periods without human intervention, allowing studies to more easily be conducted over larger spatiotemporal scales (Darras et al., 2019; Gibb et al., 2019). This allows surveys to be conducted in places for which regular access is logistically challenging, eases surveying at times that are unfavourable for traditional surveys and allows the collection of large quantities of data. Furthermore, pre-programmed recording schedules allow for a variety of sampling regimes, further extending the duration over which ARUs can record without human intervention - in a flexible, predictable, and replicable manner. This reduces the cost of data collection in comparison to traditional survey techniques (Darras et al., 2019), and allows for targeting of cryptic species that may only vocalise at specific times (Williams, 2016). Alternatively, most recording devices offer the capacity to record continuously and at broad frequency spectrums, meaning that PAM can be used to simultaneously monitor all soniferous species in the area, increasing the cost-efficiency of multi-taxa surveys and facilitating surveys of understudied taxonomic groups such as amphibians and insects (Moussy et al., 2021; Sugai et al., 2019).

Figure 1.6. *Deployment of a Frontier Labs Autonomous Recording Unit at one of our survey points*

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Early practical obstacles slowing uptake have been greatly diminished in recent years. Cost of recording units have fallen greatly, with some units now costing under $50 and a trend towards miniaturisation assisting with logistical challenges in field placement (Beason et al., 2019; Darras et al., 2018; Hill et al., 2018; Sethi et al., 2018; Whytock and Christie, 2016). Similarly, data storage costs have greatly reduced in recent years. Memory cards for ARU devices have increased in capacity whilst costs have fallen, as is the case for hard drives for long term storage (Walter, 2005). Meanwhile, it is increasingly clear that cloud computing represents a long-term, affordable solution for both storage and computational capacity requirements for analysis (Brown et al., 2020, www.arbimon.rfcx.org). Of course, these benefits are still tempered by the realities of field-surveys in tropical forests, where connectivity issues can render the idea of any sort of large-scale data transfer entirely impractical, and electronic hardware is still subject to the ravages of humidity and insect damage.

PAM offers several other advantages. For example, it makes standardisation of surveys easier, avoiding effects from observer presence (Alldredge et al., 2007) and observer bias in the field (Sauer et al., 1994). As there is a permanent record of the raw data, it is possible to verify and correct any bias introduced at the analysis stage (Darras et al., 2019). A permanent record of the raw data also limits the requirement for specialist observers in the field, so that a single expert observer can independently analyse a large number of surveys afterwards (Campbell and Francis, 2011; Digby et al., 2013; Wheeldon et al., 2019). This can be particularly important in the Amazon given the limited pool of experts able to identify entire taxonomic communities by ear (Robinson et al., 2018). Having a permanent record of the data also means that it is available for reanalysis in case of technological advancements, or application to a new question (Digby et al., 2013; Swiston and Mennill, 2009).

1.2.2. Ecoacoustic analysis pipelines

It is in the analysis of PAM data for ecological purposes, and corresponding survey design, where the most trenchant challenges remain (Darras et al., 2020; Gibb et al., 2019; Priyadarshani et al., 2018). Approaches to analysing ecoacoustic data can be subset into three main approaches; 1) manual review and identification, 2) statistical characterisation of the data to form acoustic indices, and 3) automated classification. Each method has benefits, disadvantages and significant knowledge gaps that could result in improved performance.

1.2.3. Manual analysis

The most technologically straightforward approach remains manually identification of the soniferous taxa of interest in the recordings. This approach has the lowest computational requirements, only needing the capacity to listen to the recordings and/or inspect the spectrograms. A range of open-source and commercial software is available to undertake the Fast-Fourier transformations required for spectrograms and to play sound files, including Audacity (www.audacityteam.org), Raven Lite and Pro (www.ravensoundsoftware.com), Kaleidoscope (www.wildlifeacoustics.com) and Adobe Audition (www.adobe.com/uk/products/audition.html). Media labelling software, such as BORIS (Friard and Gamba, 2016) can be useful in the annotation process.

Extensive comparisons have now been conducted between traditional point-count surveys and manually reviewing of PAM data, especially for the detection of species richness in birds, and in almost all major terrestrial biomes (Darras et al., 2019; Shonfield and Bayne, 2017). Although under certain conditions traditional surveys can outperform PAM, meta-analysis has shown that PAM studies generally outperform traditional counterparts (Darras et al., 2019). Manual identification can be extremely time-consuming, so the amount of audio data that can be analysed is greatly reduced in comparison to the use of acoustic indices or automated classification limiting the temporal and spatial scales at which it can be applied. The effort required often entails a subsampling approach to be taken which can limit the efficacy of the method especially when estimating species richness. This means that understanding the factors affecting sampling design, and ensuring optimal sampling regimes are vital when using manual analysis techniques, something that has been rarely addressed in relation to PAM. In addition, correct manual identification of sounds from recordings can be extremely challenging, meaning that this method of analysis requires a high degree of identification expertise.

Manual analysis of acoustic data has been used in Amazonia to investigate the multi-taxon biodiversity impacts of natural gas exploration (Deichmann et al., 2017), small-scale gold-mining (Alvarez-Berríos et al., 2016), FSC certified logging (Campos-Cerqueira et al., 2020), and assessing drivers of acoustic space use (Aide et al., 2017).

1.2.4. Acoustic Indices

The second approach is to analyse recordings at the soundscape level, using acoustic features to create statistical indices, which are used as alternatives to traditional biodiversity metrics (Farina, 2014; Farina and Gage, 2017; Sueur et al., 2008; Towsey et al., 2014). An important aspect of acoustic indices is that they are not dependent on taxon identities, so require very little effort in manually reviewing the audio data, allowing large quantities of data to be efficiently analysed (Eldridge et al., 2018; Pijanowski et al., 2011; Sueur et al., 2014). As taxon-specific identification is not required, analysis with acoustic indices potentially greatly reduce the requirements for experienced field surveyors - reducing a major resource bottleneck, and eliminating a main source of data error cause by species misidentification (Robinson et al., 2018). There are a large number of acoustic indices, and appropriate selection is dependent on the problem being addressed - there are several good papers addressing the functions of a range of indices (Bradfer-Lawrence et al., 2019; Eldridge et al., 2018, 2016).

The computational requirements and analytical expertise required are greater than manual analysis with the audio files requiring at least some sort of statistical analysis. There is limited GUI software to facilitate calculating even the commonest indices, although the Arbimon RFCx platform can calculate measures of acoustic space use (e.g. Deichmann et al., 2017). There are several R packages that make calculation of the commonest indices straightforward (Jerome Sueur et al., 2008; Villanueva-Rivera, Luis J. Pijanowski, 2018), meaning that technical expertise requirements are generally low although some of the newest proposed methods combine deep-learning with indices values (Sethi et al., 2020).

As acoustic indices infer community-level information from entire soundscapes, questions remain as to whether they are capable of accurately capturing the ecological complexities of soundscapes. For example, in some studies indices were unable to accurately differentiate between subtly different land uses such as different types of forest (Bormpoudakis et al., 2013; Do Nascimento et al., 2020; Eldridge et al., 2018), and they can be inconsistent predictors of traditionally used biodiversity metrics such as species richness (Eldridge et al., 2018; Fuller et al., 2015; Jorge et al., 2018; Mammides et al., 2017). However, many of the concerns related to studies that used sub-optimal survey design, and the requirements for optimal survey designs for indices-based studies are increasingly well understood (Bradfer-Lawrence et al., 2020; Mitchell et al., 2020; Pieretti et al., 2015). Acoustic indices have had limited usage in the Amazon beyond testing to show their efficacy, but have been shown to correlate with forest structure (Do Nascimento et al., 2020) and a recent study using acoustic space occupancy metrics showed that insects were the dominant acoustic markers of forest disturbance from fire and logging (Rappaport et al., 2021). In other tropical forest regions, acoustic indices have been able to successfully characterise ecological communities at a landscape scale across disturbance and degradation gradients (Bradfer-Lawrence et al., 2020; Burivalova et al., 2019b, 2018; Mitchell et al., 2020). Acoustic indices are also increasingly used as predictive features in deep-learning algorithms, to identify species (e.g. Brodie et al., 2020) or ‘outlying’ Anthropogenic sound events like chainsaws or gunshots (Sethi et al., 2020).

1.2.5. Automated classification

The final broad approach is automated classification of species, sonotypes or sound events. There are a range of approaches, including clustering, template matching, machine-learning techniques – in particular Random Forests, and deep-learning algorithms, primarily convolutional neural networks. All of the methods have high computational requirements and require a high level of expertise. In the case of clustering, template matching and machine-learning techniques there are several programs with GUI interfaces to facilitate their use (e.g. Tadarida, Bas et al., 2017, ASI, Ovaskainen et al., 2018, Arbimon, Mitchell-Aide 2013, Kaleidoscope Pro, https://www.wildlifeacoustics.com/products/kaleidoscope-pro,) and packages in R (e.g. Clink and Klinck, 2019; Hafner and Katz, 2018).

However, these approaches have proven to be difficult to apply successfully in complex acoustic environments such as tropical forests (Priyadarshani et al., 2018) and classification accuracy can be extremely difficult to replicate when the same algorithms are used in new areas or different habitats (Eldridge et al., 2016; Towsey et al., 2014). Instead, when adopting these user-friendly approaches to classification, many researchers have adopted semi-automated classification, in which positive identifications are manually verified post-classification to eliminate false positives. This can greatly improve the accuracy and usability of the data obtained, but can be quite time consuming. This approach has been used successfully in a range of studies in tropical forests (e.g. Campos-Cerqueira et al., 2021; Campos-Cerqueira and Aide, 2016; Pérez-Granados et al., 2021; Pérez-Granados and Schuchmann, 2020). To date very few studies have been conducted without manual post-classification validation in the tropics; a template-based study monitoring the space use of *Ramphastos tucanus* in human-modified forests (Ducrettet et al., 2020), and the Animal Sound Identifier (Ovaskainen et al., 2018), a machine-learning approach, comparing nocturnal and diurnal bird communities in fragmented forests in the central Amazon (de Camargo et al., 2019; Ovaskainen et al., 2018).

Recently, deep-learning techniques have shown that fully automated classification can attain high degrees of accuracy (Kahl et al., 2020.; LeBien et al., 2020; Ruff et al., 2020; Zhong et al., 2020), although no specialist software or packages exist to facilitate the production of deep learning algorithms for ecology, and the expertise required can be prohibitive. There are limited examples of ecological applications of this technology anywhere globally for multi-taxa studies (Florentin et al., 2020; Ruff et al., 2020), and one study in Puerto Rico achieved excellent accuracy for a range of frog and bird species in tropical forest (LeBien et al., 2020b) although it was not applied to ecological questions.

Figure 1.7. *Two of the nightjar species I created automated classifiers for; Common Pauraque Nyctidromus albicollis and Silky-tailed Nightjar Antrostomus sericocaudatus.*

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1.3. Thesis' Objectives

This thesis sets out to explore and resolve methodological obstacles to the application of acoustic technology in answering applied ecological questions in relation to the impact of forest disturbance on biodiversity in the Amazon.

To do so I have collaborated with the Sustainable Amazon Network (Rede Amazonia Sustanteval/RAS), a project initiated in 2009 to undertake a social and ecological assessment of tropical land uses at multiple scales. I have collected over eight terabytes of audio data from pre-existing transects along a disturbance gradient spanning approximately 10,000 km^2 of the eastern Brazilian Amazon in the municipalities of Santarém, Belterra, and Mojuí dos Campos (latitude ~ -3.046, longitude -54.947 WGS 84) in the Brazilian state of Pará.

I use this data to investigate and propose solutions to four significant hurdles to the widespread application of ecoacoustic techniques in answering ecological questions in Amazonia:

- First, I address a somewhat unexpected problem. Despite being an eponymous feature of rainforest impacting both bird vocalization rates and recording capability, there are limited options for the automated detection of rainfall in acoustic datasets. I present a new R package for easy, quick and accurate detection of rainfall in just a few lines of code, and test the method on datasets collected across the globe.

-Secondly, I investigate optimal sampling strategies in manual analysis of audio data. I compare two alternative strategies, one using a small number of samples with a duration analogous to traditional point counts, the second using a far higher number of very short samples, but with the same total amount of audio data sampled. I investigate how these strategies impact species richness detected at alpha and gamma scales, how often species are undetected, and the impact the new method has on detection of rarer species.

-Thirdly, I look at the use of acoustic indices in ecologically complex environments, and in particular whether the fidelity and sensitivity of acoustic indices to biodiversity responses can be improved through the use of *a priori* ecological knowledge to determine the temporal and frequency bins at which to measure the indices.

-Fourthly, I build an automated classification algorithm for the nocturnal avifaunal community using a two-step process, to overcome the twin challenges of high false positive rate, and heterogeneous false positive rates. I apply the classifier to a large acoustic dataset collected across a forest disturbance gradient in the eastern Brazilian Amazonia without post-classification manual validation to investigate the impact of forest disturbance on the Amazonian nocturnal bird community.

Finally, I discuss the challenges that remain in applying ecoacoustic techniques to applied ecological questions in the Amazon, with particular reference to the application of ecoacoustics to studies conducted over large spatio-temporal scales.

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Chapter 2:

hardRain: an R package for quick, automated rainfall detection in ecoacoustic datasets using a threshold-based approach

A heavy rain storm in the study area

2.1. Abstract

The increasing demand for cost-efficient biodiversity data at large spatiotemporal scales has led to an increase in the collection of large ecoacoustic datasets. Whilst the ease of collection and storage of audio data has rapidly increased and costs fallen, methods for robust analysis of the data have not developed so quickly. Identification and classification of audio signals to species level is extremely desirable, but reliability can be highly affected by non-target noise, especially rainfall.

Despite this demand, there are few easily applicable pre-processing methods available for rainfall detection for conservation practitioners and ecologists. Here, we use threshold values of two simple measures, Power Spectrum Density (amplitude) and Signal-to-Noise Ratio at two frequency bands, to differentiate between the presence and absence of heavy rainfall. We assess the effect of using different threshold values on Accuracy and Specificity. We apply the method to four datasets from both tropical and temperate regions, and find that it has up to 99% accuracy on tropical datasets (e.g. from the Brazilian Amazon), but performs less well in temperate environments. This is likely due to the intensity of rainfall in tropical forests and its falling on dense, broadleaf vegetation amplifying the sound.

We show that by choosing between different threshold values, informed trade-offs can be made between Accuracy and Specificity, thus allowing the exclusion of large amounts of audio data containing rainfall in all locations without the loss of data not containing rain. We assess the impact of using different sample sizes of audio data to set threshold values, and find that 200 15s audio files represents an optimal trade-off between effort, accuracy and specificity in most scenarios.

This methodology and accompanying R package ‘hardRain’ is the first automated rainfall detection tool for pre-processing large acoustic datasets without the need for any additional rain gauge data.

2.2. Introduction

Ecological questions are increasingly being answered using large datasets (Hampton et al., 2013; McCallen et al., 2019; Villanueva-Rosales et al., 2014), and faced with an ongoing biodiversity crisis, cost-effective collection of ecological data to address conservation challenges is vital (Gardner et al., 2008). The recent rapid development of cost-effective ecoacoustic sampling methods has facilitated collection of acoustic big data (Burivalova et al., 2019; Deichmann et al., 2018) and catalysed an increase in ecoacoustic monitoring. Despite the cost-effective nature of this sampling method (Deichmann et al., 2018; Hill et al., 2018), there are still significant challenges associated with the analysis of large acoustic datasets,. Automated detection and classification using machine or deep-learning techniques has been widely touted as one answer to this challenge (Priyadarshani et al., 2018). However, large datasets often require initial data cleaning to remove 'noise' (sounds which are not of interest), such as engines, wind and even electrical noises produced by the recorder (Stowell et al., 2016). The presence of hard rainfall (HR) is a significant contributor to noise as it can entirely mask all signals of interest or hinder their identification, and it can be especially problematic in both biodiverse and pluviose ecosystems such as tropical forests where our knowledge of biodiversity is most limited and acoustic data may be most useful. The use of acoustic indices, a common technique for quantifying biodiversity in large datasets without recourse to species level identification (Sueur et al., 2014; Towsey et al., 2014), have also been shown to be biased by the presence of heavy rainfall (Depraetere et al., 2012; Fairbrass et al., 2017; Towsey et al., 2014). Automated detection and excision of audio data at times of high rainfall is therefore often desirable before further analyses are undertaken, especially when using automated classifiers for detection of ecological sounds, as it reduces the potential for false identifications and increases processing time.

Despite the need for effective tools to identify and remove audio segments containing heavy rain, little research currently exists on the topic. Other published methods have different objectives; focussing on detection of rainfall as an objective in its own right (Brown et al., 2019), finding a proxy variable for quantification of total rainfall, or being designed to function in specific geographic areas to study the effect of rainfall within a wider soundscape (Bedoya et al., 2017). This has resulted in prioritising optimisation of accuracy of detection over ease of use and specificity. Other methods, such as the ecoacoustic event detection approach (Farina et al., 2018) allow a holistic approach to identification of all acoustic events, in which rainfall identification becomes a secondary benefit. We argue that many ecologists and conservation practitioners will primarily be interested in quickly identifying the majority of rain files rather than ascertaining the presence or absence of rain, to allow for better classification of ecological sounds and unbiased indices. For these users, the priority will be minimizing effort and maximising specificity –e.g. ensuring that false positive rates are very low so that ecological data are not removed from a dataset to achieve a higher overall accuracy of rainfall detection. Therefore, the most successful reported method of automated rainfall classification Brown et al. (2019), which involves a complex machine-learning approach and an extensive feature set, could be prohibitive for non-specialists. Many users may be willing to trade-off a small amount of accuracy in return for much lower analytical effort and greater ease of comprehension.

A simpler, quicker approach to classification has been proposed by Bedoya et al. (2017). This utilizes two acoustic measures indicative of rainfall taken at a single frequency band to set a decision threshold above which rainfall is determined to be present. However, this method uses minimum values over a period of acoustic data with rain of known intensity (using a rain gauge) to set the decision threshold. Obtaining verified rainfall data may not be possible in many cases, and requires additional cost and effort – especially in closed canopy ecosystems. Additionally the use of minimum values to set thresholds prioritizes accuracy over specificity, potentially leading to avoidably high false positive rates for relatively small gains in accuracy and the exclusion of potentially informative audio files. Setting threshold values from the second quartile of the interquartile range (Q2) may give more conservative predictions for the presence of HR, enabling a trade-off between higher specificity scores at the expense of accuracy. Furthermore, the amplitude of rainfall increases most noticeably at two frequency bands, 0.6-1.2 kHz and 4.4-5.6 kHz where the impact of raindrops hitting vegetation is most noticeable. Bedoya measures the indices at 0.6-1.2 kHz as light intensity rainfall is more noticeable, and it contains less biophony than the higher frequencies. However, it is unclear if the use of both of the frequency bands would produce better results when classifying only heavy rain, or in locations with higher levels of anthropophony (man-made noise).

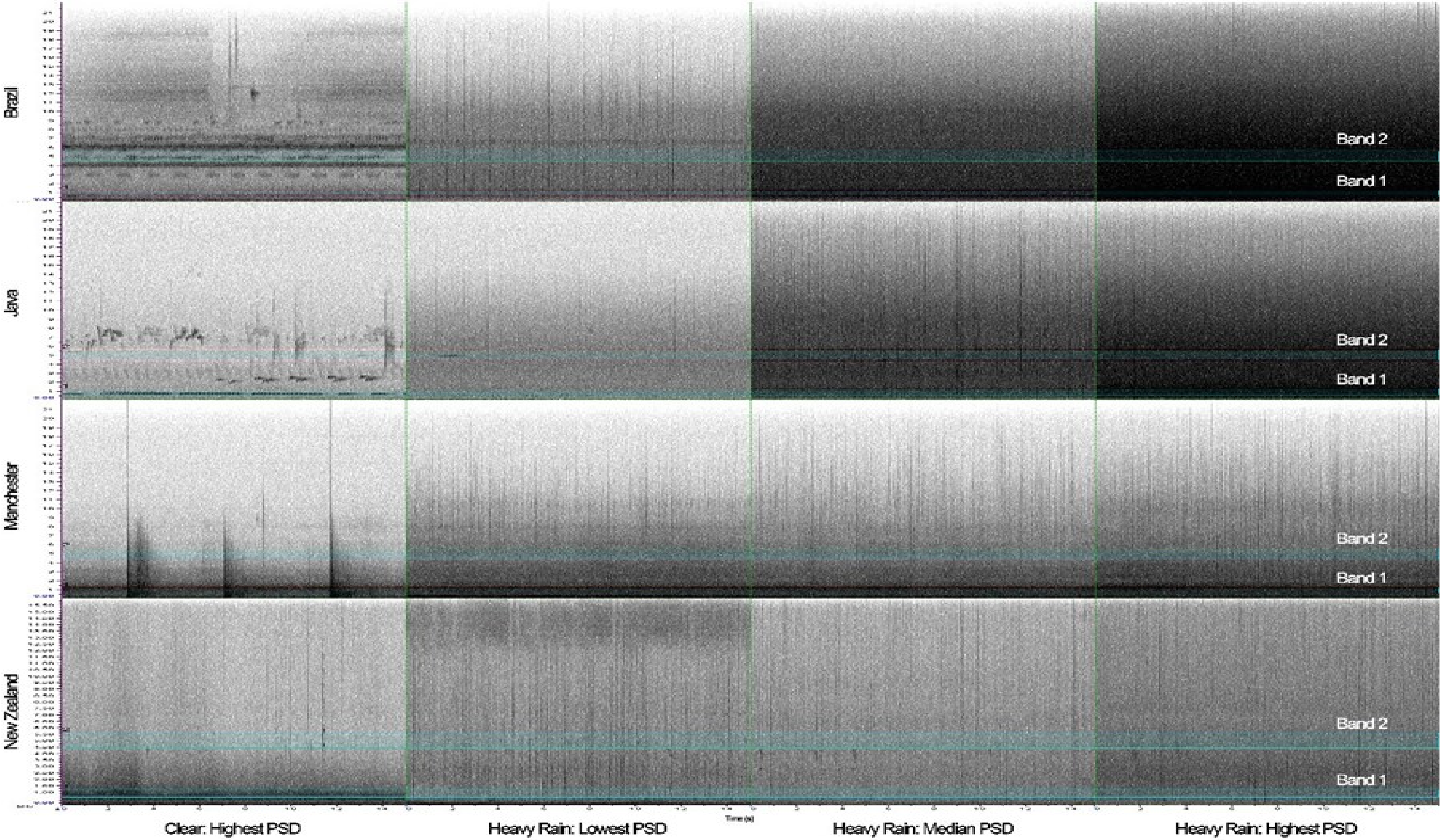
Here we present a user-friendly methodology and associated R package (R Studio Team, 2015) ‘hardRain’, for automated rainfall detection that maintains high specificity and accuracy for use with new datasets. We build on the thresholding approach of Bedoya, developing a method to remove the need for any additional data from rain gauges to set threshold values. We investigate, at multiple tropical and temperate sites, whether using both 0.6-1.2 kHz and 4.4-5.6 kHz frequency bands provide greater accuracy and specificity than using only the lower frequency band, and assess the optimal number of files containing rainfall to use as training data from which to obtain threshold values. We also explore how differences in location affect classification results, and the trade-offs in accuracy and specificity when using minimum or Q2 values for setting decision thresholds.

2.3. Methods

2.3.1. Definition of rainfall

Identifying audio files containing rain without rain gauge data is not straightforward, as light rainfall can be indistinguishable from background noise (Bedoya et al., 2017). However, in these cases, rainfall is less likely to be less disruptive for the automated classification of ecological sounds. Here, we focus on the detection of heavy rainfall, here defined as rainfall that visually masks or significantly degrades other sound events (see Figure 2.1 for examples). Audio files were manually assigned as either ‘Hard Rain (HR)’ or ‘Clear’ through visual inspection of spectrograms in Raven Pro (Cornell Bioacoustics Research Program, 2010). For consistency, a single observer (OM) undertook all manual classifications in this paper

Figure 2.1. *Examples of spectrograms assigned to rainfall present and absent taken from the combined training and test dataset of each country, ranked by power spectral density (PSD).*



2.3.2. Data

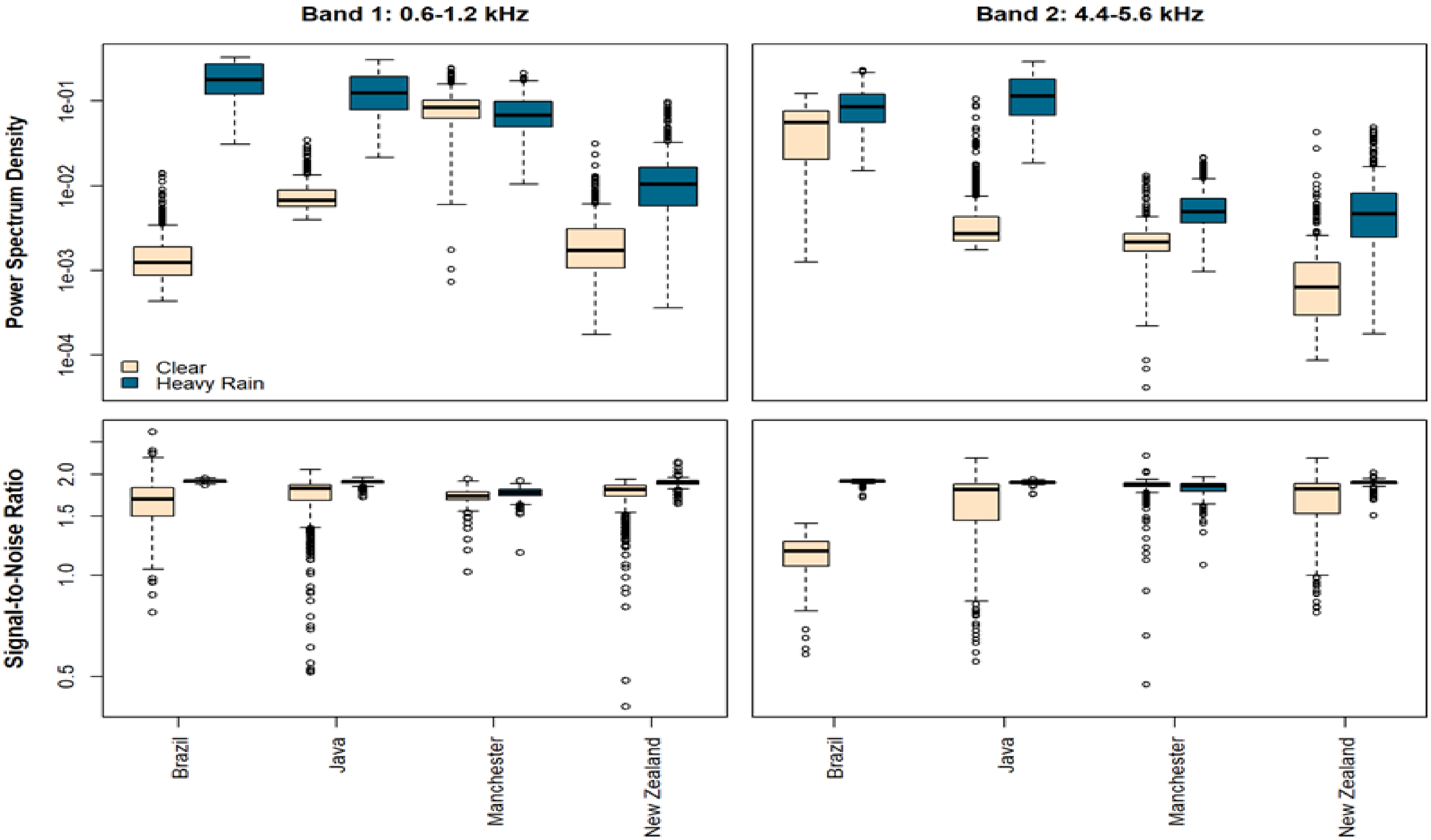
This paper uses four primary datasets; two were collected in tropical rain forest; Santarém, Pará state, Brazil (-3.046, -54.947) and West Java, Indonesia (-6.181, 106.827), and two from temperate climates; one from temperate forests in Taranaki, New Zealand (-39.448, 174.414) and one from an urban balcony in Manchester, United Kingdom (53.485, -2.228). All include periods of time when both rainfall and clear weather were prevalent. The Brazil dataset comprises more than 10,000 hrs of data from 29 sites, the Java data set consists of more than 10,000 hours of data from 11 sites in montane forests in West Java with 12 recorders per site, Manchester over 600 hrs from one site and New Zealand over 3,900 hrs from 31 recorders at one site. For further information on data collection locations and durations at each of the sites see Appendix S2.1. Data were collected using Frontier Labs Bioacoustic Audio recorders (Frontier Labs, 2015), with the exception of the New Zealand dataset which used NZ Department of Conservation recorders (see Metcalf et al., 2019 for more information). All audio data were recorded at a sampling rate of 44.1 kHz except the New Zealand data set recorded at 32 kHz. All audio data were subdivided into 15 s sound files.

2.3.3. Threshold Setting and Optimisation

From each primary dataset, a training and test dataset were selected. The test and training datasets comprised 1000 files each. We manually selected 1,500 files that were then randomly split into 1,000 training files and 500 test files. A further 500 files that had been manually selected as being Clear (of Heavy Rainfall) were included in the test dataset, so that both the training and test dataset are composed of 1000 files. The Brazilian training dataset comprised 13 sites including both undisturbed primary and heavily degraded primary forests. The test dataset comprised eight sites and three sites for HR and Clear files respectively. Java training data came from 11 sites, whilst the test dataset used data from eights sites for HR and one site for Clear data. Manchester HR data were collected between 25th-28th April 2019, whilst Clear data was from 4th November 2018. The New Zealand training data were from 18 sites, whilst HR test data came from 16 sites and Clear from 18 sites.

We followed Bedoya et al., (2017) in using power spectral density (PSD) and signal-to-noise ratio (StN) as acoustic indices. The PSD of an acoustic file increases with rainfall intensity, while StN is useful to differentiate files that have high PSD because of continuous rainfall versus those that have high PSD because of non-continuous loud sound sources, such as biophony (e.g. animal vocalisations) or anthropophony. The PSD values in both 0.6-1.2 kHz and 4.4-5.6 kHz frequency bands were calculated for every file with the ‘spectro’ function from the seewave package in R (Sueur et al., 2008). The window length used to calculate PSD values was set to equal the duration of the audio file (typically 15 s segments – see package documentation; Figure 2.2 shows these values from the test datasets). We used mean divided by standard deviation of the PSD for the Signal-to- Noise ratio, following Bedoya et al., (2017), although we note a typographical error in point 3 of Algorithm 2.1 as the deviation of the mean is not squared in the standard deviation formula.

Figure 2.2. *Power Spectral Density and Signal-to-Noise Ratio values for audio files containing heavy rain and clear files from the test datasets. The y-axes are presented on a log scale.*



In predicting the presence of heavy rain, we followed Bedoya et al., (2017) in using thresholds for PSD and StN, so that if any of the measured values from an audio file exceed the threshold, they were predicted to contain heavy rain. We used mean balanced accuracy (Accuracy) and specificity (Specificity) (Velez et al., 2007) to assess the performance of classifier models. Although accuracy is the primary objective of classification, in some uses the penalty for the rejection of useable data (false-positives) may be far higher than the consequences of keeping files containing rain in the dataset (false-negatives), and specificity is the best measure for that circumstance (Fielding and Bell, 1997).

We tested classification performance using thresholds of PSD and StN from frequency band 1 (e.g. values had to exceed two thresholds to be classified as HR) against classification using PSD and StN from frequency bands 1 and 2 (e.g. values have to exceed four thresholds to be classified as HR) using a paired Wilcoxon rank test. To assess the effect, we took 100 subsamples of n=500 from each of the four countries' training datasets. Minimum and Q2 threshold values were then obtained and used to classify the applicable test dataset. Accuracy and specificity values were calculated by country, threshold choice and the mean of all countries combined.

To optimise the number of training samples required, we assessed the relationship between the number of training samples and accuracy/specificity with the aim of balancing the effort of manually selecting training data and the susceptibility of threshold values to outliers and variation in data sets. For each training dataset, 100 subsamples of size n= 10, 20, 30, 40, 50, 75, 100, then increasing increments of 50 to 1000, were taken and threshold values obtained using both frequency band 1 and 2 and these used to classify the applicable test dataset. Mean accuracy, specificity and their standard deviations were then calculated for each sample size by country and threshold choice. The sample size of n=500 was tested for significant differences in classification Accuracy and Specificity between the countries using Kruskal-Wallis and pairwise Wilcoxon tests, significant at <0.05.

In order to assess if there was overtraining between the test and training datasets, we conducted a case study using the Brazilian primary data. A random sample set of 6,960 files (1 hour from each transect), independent from the test and training data, was taken from the Brazilian primary dataset and manually labelled. A further subsample of 500 files was taken from the Brazilian training dataset to obtain threshold values, and these were used to predict the presence and absence of rainfall in the Brazilian random sample.

2.4. Results

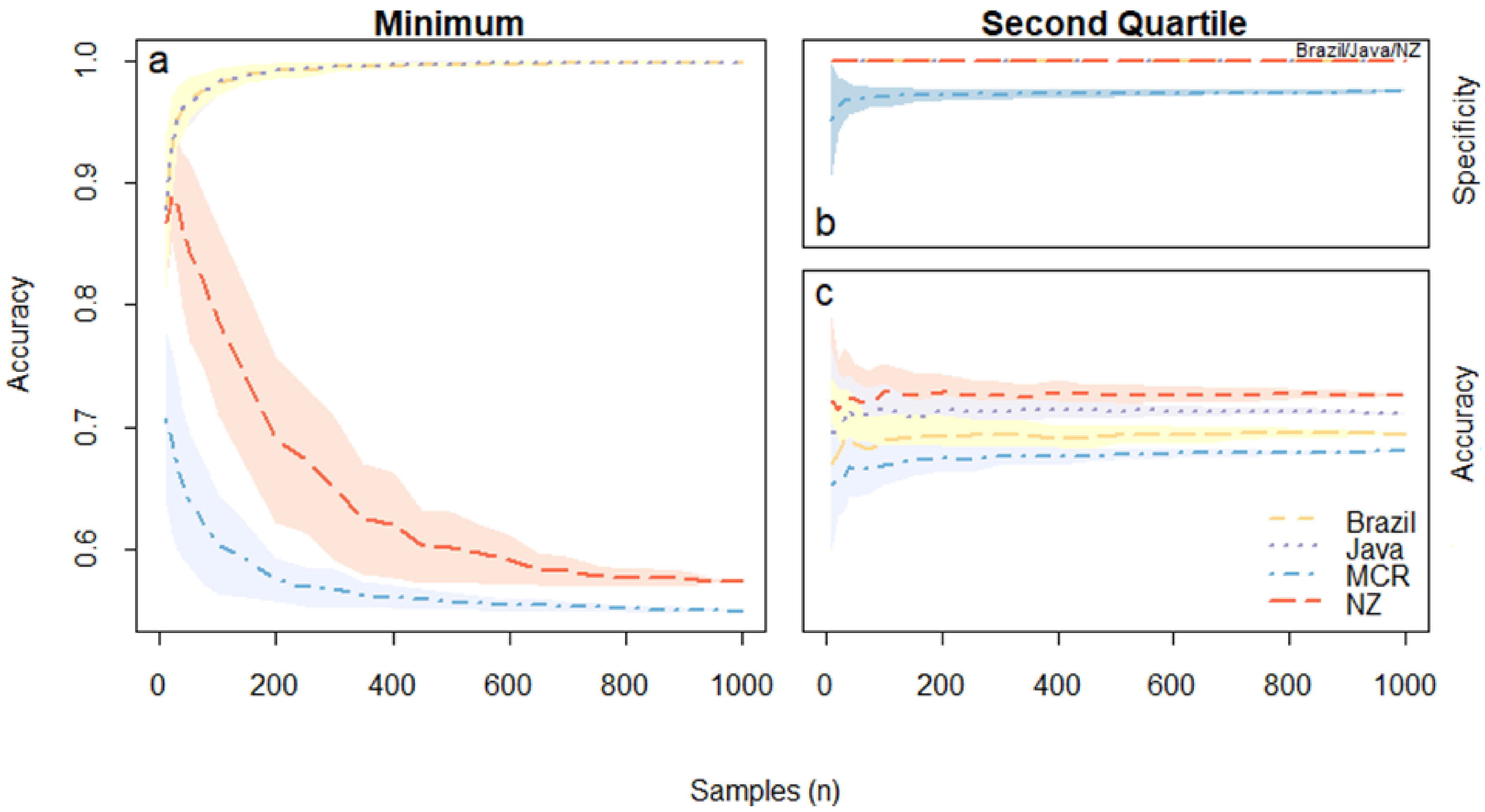
The results produced by using both frequency bands were on average significantly better than those using just the 0.6-1.2 kHz band across both Specificity and Accuracy, with the exception of Accuracy when using the Q2 threshold, although results varied somewhat by country (Table 2.1). As Accuracy is not likely to be as important a consideration as Specificity for those choosing to use a Q2 threshold, using two frequency bands was deemed the better choice, and all further results discussed here are for classification with measurements taken from both frequency bands.

Detection responses to sample size varied both by country and by the choice of threshold value, but were consistent across Specificity and Accuracy metrics. When using minimum threshold values, Accuracy showed rapid increases until an asymptote at 200 samples for Brazil and Java, but declines for Manchester and New Zealand (Figure 2.3a). Specificity reaches 100% for all samples sizes in the Brazil and Java datasets, but follows a similar, but steeper trend to Accuracy for Manchester and New Zealand (not shown in Fig 2.3). Using the Q2 threshold, Specificity is at 100% for all sample sizes for Brazil and Java and New Zealand and around 97% for Manchester (Fig 2.3b), whilst Accuracy reaches stable scores for all countries between 100 and 200 samples (Fig 2.3c).

Table 2.1. *Accuracy and Specificity scores by country, threshold choice, and number of frequency bands measured. 500 samples were used to set the thresholds. Results with significant differences (corrected p-value <0.05) between one and two bands are in bold. All differences in which two bands performed better than one band are shaded. A table of the p-values can be found in Appendix S2.2.*

Country	Mean Accuracy (%)				Mean Specificity (%)			
	Minimum threshold		Q2 Threshold		Minimum threshold		Q2 Threshold	
	1 band	2 bands	1 band	2 bands	1 band	2 bands	1 band	2 bands
Brazil	**99.69±0. 00**	**99.67±0.00**	**83.10±0. 01**	**69.36±0.01**	100±0.00	100±0.00	100±0.00	100±0.00
Java	99.76±0. 00	99.75±0.00	**87.13±0. 01**	**71.31±0.01**	**99.80±0. 00**	**100±0.00**	100±0.00	100±0.00
Manchester	**54.81±0. 01**	**55.73±0.01**	**79.39±0. 01**	**67.77±0.00**	**10.15±0. 01**	**12.60±0.01**	**91.05±0. 01**	**97.39±0.0 0**
New Zealand	**51.75±0. 03**	**60.14±0.03**	**82.65±0. 01**	**72.61±0.01**	**3.66±0.0 5**	**20.49±0.06**	**98.00±0. 00**	**100±0.00**
Mean	**76.50±0. 01**	**78.83±0.01**	**83.07±0. 01**	**70.26±0.01**	**53.40±0. 02**	**58.27±0.02**	**97.27±0. 00**	**99.35±0.0 0**

Figure 2.3. Selected Accuracy and Specificity scores by sample size (n), country and threshold selection method. Specificity scores for minimum threshold method not shown as Specificity=1 for all sample sizes in Brazil and Java data, and below 0.5 for almost all sample sizes in Manchester and New Zealand datasets. The shading represents standard deviation of 100 repetitions. NZ= New Zealand, MCR=Manchester.



Comparison between country scores showed that there were significant pairwise differences between all countries for both threshold choices in Accuracy and Specificity, except where Specificity was at 100% (Table 2.1). As expected, there was no clear threshold value choice to maximise both Specificity and Accuracy across all countries. The best Accuracy scores were achieved using Minimum threshold values, >99% for all training sample sizes over 200 for both Brazil and Java but this performed poorly for Manchester and New Zealand (Table 2.1, Fig 2.3). This suggests that in some countries, the differentiation is not enough to achieve high levels of Accuracy even when excellent Accuracy scores are achieved with the same method in other locations. Using the Q2 threshold, Accuracy was low for all countries (between 65% and 73%). Despite this, high Specificity scores can be achieved for all countries using the Q2 threshold (Table 2.1, Fig 2.3). This highlights that even in datasets where there may be poor distinction between Clear and HR data using PSD and StN indices, 35-50% of all HR files can be identified with loss of less than 5% of data containing no rain. Confusion matrices are provided in Table 2.2 for the mean scores of a sample size of 500 training files applied to the Manchester and New Zealand test datasets using second quartile thresholds

Table 2.2. *Confusion matrices with 500 samples of training data using second quartile threshold values.*

	Manchester - testing dataset			New Zealand – testing dataset	
	Second Quartile Threshold			Second Quartile Threshold	
	Actual Class				
Predicted Class		TRUE	FALSE	TRUE	FALSE
	TRUE	185	15	230	0
	FALSE	315	485	270	500
	Sensitivity=38.15%, Specificity=97.39%, Accuracy=67.77%			Sensitivity=45.22%, Specificity=100%, Accuracy=72.61%	

Table 2.3. *Matrix of the Brazilian case study. Data are a random sample of the entire audio dataset (n=6960, HR n=102) with threshold values taken from 500 randomly selected audio files from the Brazilian training dataset.*

		Brazil - 6960 randomly selected audio files			
		Minimum Threshold		Second Quartile Threshold	
		Actual Class			
Predicted Class		TRUE	FALSE	TRUE	FALSE
	TRUE	88	14	33	0
	FALSE	22	6836	69	6858
	Sensitivity=86.27%, Specificity=99.68%, Accuracy=92.98%			Sensitivity=32.35%, Specificity=100%, Accuracy=66.18%	

The results for classification of the case study using 6,960 files of the Brazilian dataset remained good, although lower than the test scores suggesting a small amount of overtraining between the test and training datasets (Table 2.3). To read in, measure and classify all 6960 files took 15 min 16 s using a Dell EliteBook laptop with a 4-core Intel Core i7-7600U CPU and 16 GB RAM running Windows 10.

2.5. Conclusions

We have shown that it is possible to fully automate rainfall identification within audio data from tropical environments using only two simple measurements at two frequency bands, and requiring only a relatively small set of files containing known rainfall to extract threshold values. We also demonstrate that by using different thresholds, minimum and second quartile, the technique can be adjusted for use even in cases where there is poor differentiation between rain presence and absence with a reasonably high level of success. This means that users of hardRain can make informed trade-offs between effort, accuracy and specificity.

The effectiveness of the method is clearly dependent on sample sizes, with standard deviations declining with increasing samples, but divergent impact on Accuracy by site and threshold selection method. Whilst it is possible to devise various stopping rules to optimise the sample number, the optimal solution will vary with the ease of obtaining training files containing rain and the objectives of individual research projects. The standard deviation of Accuracy and Specificity is relatively low for almost all measures at 200 samples (Fig.2.3), with corresponding accuracy and specificity scores close to their maximum for the tropical datasets when using minimum threshold values, and for all datasets when using second quartile values.

Using only PSD and StN as measurements to differentiate between rain presence and absence has clear advantages in minimising effort and ease of understanding. Along with Brown et al., (2019), we did not find StN to be a useful index for classification when we initially analysed our data using the printed formula in Bedoya et al., (2017). However, when we used the standard formula for standard deviation, the use of both PSD and StN was better than just PSD. In some circumstances, even the use of both indices resulted in poor differentiation. This is especially the case for datasets from temperate climates, with Manchester and New Zealand performing worse, presumably due to poorer distinction between PSD scores (Fig 2.2). This is possibly because rainfall is less intense at these locations, or because rain falling on to predominately concrete (Manchester) and more open temperate forest canopies (New Zealand), results in less amplification than in tropical forests (Java and Brazil). Despite this shortcoming, by using second quartile thresholds between 40-50% of rain data was identified even in Manchester and New Zealand, with no or only a very small percentages of rain-free data misidentified (Table 2.2).

Although not herein directly compared, our methodology is unlikely to match the AUC scores of the method proposed by Brown et al., (2019) or the accuracy and quantification of Bedoya et al., (2017). For those scholars studying rain through audio data, or requiring extremely precise cleaning, these would be better methods to use. However, our methodology provides a quick and effective classification method that can be applied to audio data, and is especially suited to tropical forests where the need for reliable acoustic data on biodiversity is greatest and rainfall is frequent. For researchers wishing to quickly remove rain files from large datasets prior to classification, this method will often represent the most time-effective way to do so. Additionally for research in which the penalty of false-negatives is far lower than that of false positives, this method of rain detection allows for informed trade-offs between Accuracy and Specificity which previous methods of rain detection do not.

2.5.1. Package description

To facilitate the use of this rain detection method, we have developed the R package 'hardRain'. The package will; i) set thresholds (based on training data consisting of short segments of known rain audio recordings), ii) apply the thresholds to audio data and identify presence of rain in each input file, or subdivisions therein, iii) cut audio segments with rain and save the remaining segments, and optionally, create a label file view in Audacity or Raven software. It can also be used to test the accuracy of the classification using known testing and training data. The package consists of four main functions (Table 2.4).

Before using the classify function it is necessary to decide which threshold values to use. If it is reasonable to make assumptions about the distinction between rain presence and absence, for instance if the data is collected in tropical rain forest, then the threshold can be selected and the results checked after. However, if it is unclear whether there will be a good distinction, accuracy can be tested using the classifyRain function with known testing and training data (i.e. labelled audio segments of heavy rain or clear) and confusion matrices and accuracy metrics produced (see example in vignette). See vignettes included in the package for further details on functionality.

Table 2.4. *Functions in the R package 'hardRain'.*

Function	**Description**	**Main inputs**
getThreshold	This function measures PSD and Signal-to-Noise Ratio on all input training files at two frequency bands (defaults to 0.6-1.2 kHz and 4.4-5.6 kHz) and calculates minimum and 2nd quartile thresholds over these.	wav filenames (and locations where these are stored) of audio segments of known rain, i.e. training data (see above for discussion on how many files are needed), but typically 200 wav files of about 15 s duration
classifyRain	This function takes the testing data, calculates the PSD and Signal-to-Noise Ratio and applies the thresholds produced by getThreshold function and classifies each input file (or subdivision thereof) for the presence / absence of rain. Optionally, if the function is used for accuracy testing, a label can be included denoting which files have presence of rain or not.	wav filenames (and locations) of testing data files may be of short duration already (typically, 15-30 s segments) or may be provided as much longer files (e.g. 2-3 hours) and split into segments within the function, using the t.step argument (division size, in seconds); thresholds from getThreshold()
cutRain	This function takes the output from classifyRain() and cuts out the segments identified as rain in the input wav files and saves the remaining contiguous audio in a new folder and writes a label file for the original length audio file, marking segments with no rain (either or both of these options are available). Optionally, the new start time of each file can be recorded in the filename.	output from classifyRain() - only when longer files are classified in subdivisions; output location for new wav files.
getMetrics	This function does not generally need to be called directly. It is the workhorse function that reads wav files, extracts PSD and Signal-to-Noise for specified frequency bands using seewave function spectro(). This function is called by getThreshold() and classifyRain() which will generally be used directly.	wav filenames (and locations); time division (in seconds) to subdivide wav input files for analysis (optional)
The package can be downloaded from: https://github.com/Cdevenish/hardRain		

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Chapter 3:

Optimising tropical forest bird surveys using passive acoustic monitoring and high temporal resolution sampling

Spix's Warbling Antbird Hypocnemis striata *and spectrogram from one of the surveys it was detected it in.*

3.1. Abstract

Estimation of avian biodiversity is a cornerstone measure of ecosystem condition, with turnover in avian community composition underpinning many studies of land-use change. Surveys conducted using autonomous recorders have been frequently found to be more efficient at estimating diversity than traditional point-count surveys. However, there has been limited research into the optimal temporal resolution for sampling – specifically the trade-off between number of samples and individual sample duration over a fixed total survey duration, despite autonomous recorders affording the possibility of repeat sampling with relative ease in comparison to traditional survey methods.

We use an acoustic dataset collected from a region of very high avian biodiversity - the eastern Brazilian Amazon - to test the effect of using high temporal resolution sampling to increase temporal coverage without increasing total survey duration. We use this dataset to assess whether a survey protocol consisting of 240 15 second samples at 29 locations, high temporal resolution (HTR) sampling, has an influence on resulting alpha and gamma diversity and detection frequency, in comparison to low temporal resolution (LTR) sampling of four 15 minute samples at the same locations.

We find repeated HTR sampling outperforms LTR sampling in every metric considered herein, with HTR sampling predicted to detect approximately 50% higher alpha diversity, and 10% higher gamma diversity. HTR sampling detects species more often, at more survey locations. LTR sampling produced almost four times as many false absences for species presence. Additionally, LTR sampling incorrectly found 70 species or 34% of the total species detected, at only a single forest type when they were in fact present in multiple forest types, whilst the use of HTR sampling reduced this to just 2 species or 0.9%. Whilst there is no difference between the proportion of uncommon species detected by the two methods, when considering species detected multiple times at multiple locations, HTR sampling detected three times more uncommon species than LTR sampling.

We conclude that HTR sampling of passive-acoustic monitoring based surveys should be considered the primary method for estimating the species richness of bird communities in tropical forests where feasible.

3.2. Introduction

Estimation of avian biodiversity is a cornerstone measure of ecosystem condition used in a wide range of ecological and conservation applications. Understanding alpha diversity in avian communities underpins many studies of land-use change in high biodiversity environments like tropical forests. However reliable detection, identification and counting of birds can be challenging in such environments (Robinson et al., 2018), where avian species richness reaches its global peak (Jenkins et al., 2013). It is well documented that tropical birds can be difficult to detect and count accurately as a consequence of their low abundance and difficulties in detecting cryptic species in structurally complex environments such that accumulating sufficient inventory completeness can be challenging (Karr, 1981; Robinson et al., 2000; Terborgh et al., 1990).

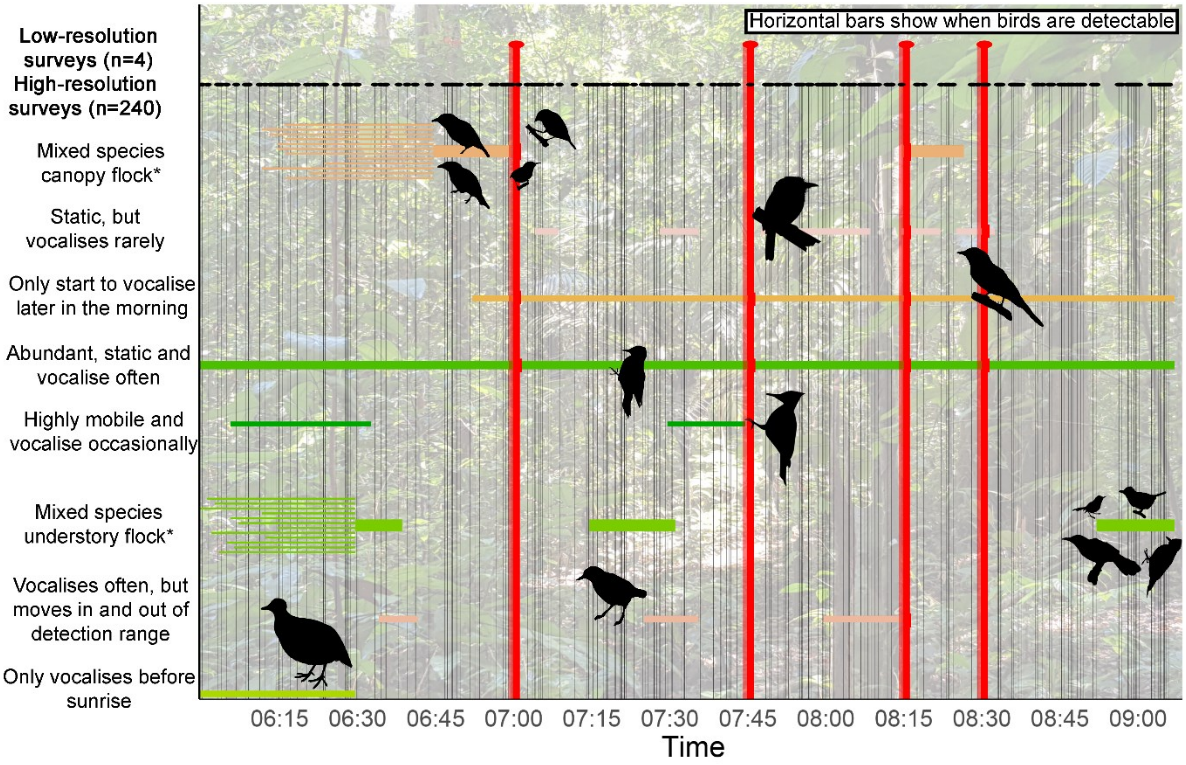
Point counts are established as a standard survey technique for obtaining measures of bird species richness, abundance and population density, particularly in forest habitats (Bibby et al., 2000). Now that affordable and reliable passive-acoustic monitoring (PAM) equipment has become available (Gibb et al., 2019), autonomously recorded surveys in which recording units are left to document soundscapes over extended periods, are emerging as a supplement or alternative to traditional field-conducted point counts (Shonfield and Bayne, 2017). A recent review found that recorder-based surveys detect an average of 11% more species than traditional point counts with field-based observers, hereafter ‘traditional surveys’, albeit often with slightly different species composition (Darras et al., 2019). This is alongside other benefits including reduced costs, avoidance of the effects of observer presence (Hutto and Mosconi, 1984), increased standardization through expert review (Campbell and Francis, 2011), the ability to archive data for future use, and the capacity to record for an extended duration - including at night when traditional surveys are rarely conducted. Whilst automated detection and classification methods are not yet widely available to analyse all of the additional data collected (Priyadarshani et al., 2018), using autonomous recorders to collect data whilst subsequently manually detecting and identifying the species with passive acoustic monitoring surveys (hereafter ‘PAM surveys’) can still obtain significant improvements over traditional methods.

An accompanying benefit of cost-effectively recording large amounts of acoustic data is the ability to greatly increase the temporal resolution of sampling. Higher temporal resolution is achieved by a high number of short duration samples from the recorded audio data whilst maintaining the same total survey duration during a fixed period, something that would be logistically impossible with traditional surveys. Higher resolution sampling with traditional point-count surveys has been shown to lead to both detection of higher species richness (Fuller and Langslow, 1984; Siegel et al., 2001) and better quality data for further modelling, reducing standard error and increasing the accuracy of density estimation (Lee and Marsden, 2008; Smith et al., 1998). In tropical forests, where hyper-diverse avian communities include a small number of commoner species and a long tail of rarer species (Robinson et al., 2000; Terborgh et al., 1990), traditional point counts often fail to accrue enough independent repeat detections to allow modelling of rarer species, leading to knowledge deficits for those species most likely to be sensitive or vulnerable to disturbance and consequently underestimating impacts of land-cover change (Robinson et al., 2018). PAM surveys allow survey protocols to focus on a high number of short-duration samples without the costs associated with multiple repeated field visits. Despite this potential benefit of PAM surveys, most comparisons with traditional surveys have been conducted either simultaneously or using identical sampling methods. As with traditional surveys, several recent studies comparing PAM surveys indicate that using a higher temporal resolution for sampling allows detection of a higher number of species compared to lower resolution samples (Klingbeil and Willig 2015, Smith et al., 2020, Wimmer et al., 2013). However, these studies were conducted predominantly in temperate forests or arid systems in regions of relatively low species richness (n=44, n=96, and n=79 species respectively), and none used a minimum sample duration of less than one minute, giving relatively low temporal resolution. Additionally, Cook and Hartley (2018) found that using 10 s duration samples increased estimation of species prevalence compared to lower temporal resolution sampling through increased independent detections. Increased detection frequency can reduce the number of false absences, something that can have a significant negative impact on the accuracy of, in particular, species distribution modelling (Gu and Swihart, 2004; Lobo et al., 2010; Phillips et al., 2009).

Estimating species richness with passive acoustic monitoring depends on two factors: availability and detectability (Kéry and Schmidt, 2008). The number of species available for detection over time (e.g. the number of species close enough to the recorder to be heard), varies as species move – for instance the number of available species would be much greater if a large mixed-species flock entered the detection space of the recorders. The detectability of each species (e.g. whether an individual of the species makes an identifiable sound during the survey) is the probability of recording the species when it is within the recording area. This is influenced by (i) species abundance, as the more individuals available for detection increases the probability of one of them vocalising, and (ii) the frequency of vocalisation, which varies by many orders of magnitude - for example, Screaming Pihas *Lipaugus vociferans* may vocalise for 77% of the time between 06:45-17:15 (Snow, 1961), whilst Variegated Antpittas *Grallaria varia* have been shown to only sing only twice in 50 days (Jirinec et al., 2018) and (iii) the distance at which a call is detectable, impacted by the amplitude and acoustic frequency of the call and a range of environmental factors (Yip et al., 2017).

In some cases, it may be possible to predict which time periods have the highest probability of detecting a higher proportion of the species pool, suggesting survey efforts should be targeted to those periods. For instance, traditional point counts are often conducted in the two hours following sunrise. However, there is a high degree of variation in the proportion of the total species pool that is both available and detectable over time, which means that having a higher number of samples over a fixed period (e.g. high temporal resolution) makes it more likely for a survey to coincide with a period in which a high proportion of the total species pool is detectable (Figure 3.1). Furthermore, high temporal resolution also supports detection of species that only vocalize within strict temporal niches, or are only detectable at certain periods. For example, forest falcons *Micrastur spp.*, only reliably vocalise before and around dawn (Fjeldså et al., 2020), when a low proportion of the total species pool is detectable. Other species may have habitual movements that make them only available for detection during narrow windows. With low temporal resolution sampling, it may be possible to sample during one or several of these availability windows if they are known; but this would reduce the capacity to sample at times with a high proportion of the species pool available. Additionally, vocalizations of rare species are likely to be largely stochastic, so having a higher number of samples spread across the survey period increases the probability of detection.

Figure 3.1. *Theoretical model of high and low temporal resolution sampling regimes over one morning in the tropics.*



*Red vertical lines represent four 1 minute samples, black vertical lines represent 1 second instantaneous samples (black vertical lines illustrated at double width). This represents a similar contrast in resolution to four 15 minute samples and 240 15 second samples over a 15 day survey season, as compared in this paper. The y-axis shows a non-exhaustive selection of behaviours that impact detection probability. *Mixed flocks shown both prior to and after formation. Bird behaviour affecting detectability is hypothetical. Bird silhouettes from www.phylopic.org.*

We used an acoustic dataset collected between June and August 2018 in eastern Amazonia in order to compare the impact of using high temporal resolution (HTR) and low temporal resolution (LTR) sampling on species detection, without increasing total survey duration. We compared the results between sampling methods to answer the following questions: does HTR sampling result in estimating higher species richness and a faster species accumulation? Does HTR sampling increase the frequency of species detection and consequently decrease the number of false absences and falsely unique occurrences? Finally, is HTR sampling more efficient at detecting species with low abundance?

3.3. Materials and Methods

3.3.1. Data collection

We collected acoustic data from 29 of the survey transects of the Sustainable Amazon Network (Gardner et al. 2013) across an area of approximately 1 million ha, located in the eastern Brazilian Amazon in the municipalities of Santarém, Belterra, and Mojuí dos Campos (latitude ~ -3.046, longitude -54.947 WGS 84), hereafter 'Santarém' in the Brazilian state of Pará. Survey points were located halfway along permanent 300 m transects. All transects were located in non-seasonally inundated 'Terra firme' forest and distributed across a human-disturbance gradient, comprising seven forest classes. To minimize spatial correlation, survey points were separated by a minimum distance of 2 km.

All recordings were made between 12th June 2018 and 16th August 2018, outside of the peak period for bird breeding (Kirwan, 2009) which commences with the onset of the rainy season in November, and across a period in which detectability and community composition should be relatively constant. Recordings at each survey point were made over one or two recording periods, with each recording period varying in length between 3 and 22 days for logistical reasons. A minimum of 13 days were surveyed at each location. Full details of recording periods for each location are given in Appendix S3.1.

We installed Frontier Labs Bioacoustic Recording Units with a 16-bit 44.1 kHz sampling rate each survey point. Recorders were placed in trees at a height of 7-10 m, with the microphone facing downward, 10-20 m from the transect to reduce the chance of recorder theft. Recording units were positioned to avoid sound being blocked by overhanging branches. Frontier Labs microphones have 80 dB signal to noise ratio and 14dBA self-noise, a fixed gain pre-amp of 20dB, a flat frequency response (±2dB) from 80Hz to 20kHz and an 80Hz high-pass filter to filter out low-frequency wind noise (Frontier Labs, 2015). All files were recorded continuously in wav format.

The continuous acoustic recordings were randomly and independently subsampled twice. In the first subsample (hereafter 'LTR samples'), survey periods were 15 minutes in duration, and four periods were extracted per survey point, totalling one hour of data from each transect. Across all survey points, there were a total of 116 LTR samples. We used 15 minute durations as it is a commonly used point-count duration in tropical forests (Robinson et al., 2018), and as previous traditional surveys from the same location have used this survey duration (e.g. Moura et al., 2013). The second subsample (hereafter 'HTR samples') again independently sampled one hour of recordings from each survey point, but this time in the form of 240 15 s periods, totalling 6,960 samples across all transects. The selection of 15 s durations for HTR sampling is primarily a trade-off between the highest possible resolution, the associated increase in effort during analysis through the increasing number of files and the number of complete versus truncated vocalisations, which can be difficult or impossible to identify without a longer recording. Further considerations include minimizing bird movement in and out of the detection space of recorders and 15 s spectrograms can easily be displayed on a standard monitor at a resolution where vocalisations can be visually recognized. All samples for both survey methods were taken in a two-and-a-half-hour period starting 30 minutes before sunrise, which has been shown to be the most effective period for estimating species richness with PAM surveys (Wimmer et al., 2013). Subsampling was not stratified within that period, but LTR samples commenced on the hour, or 15, 30 or 45 minutes past the hour, to avoid overlapping samples. Audio containing heavy rainfall was removed prior to initial sampling using the hardRain package in R (Metcalf et al., 2020).

3.3.2. Analysis

The audio samples were analysed manually, through visually inspecting spectrograms generated in Raven Pro (Center for Conservation Bioacoustics, 2019) at the default settings, and listening to the recordings. All identifiable avian vocalisations were assigned to species by a highly experienced ornithologist (NGM, for survey experience in the region see Moura et al., (2013), and Moura et al., (2016)). All vocalizations that could only be determined to family level were discarded from this study. During analysis, it was apparent that 343 of the 6,960 HTR samples fell during periods of rain intense enough to significantly inhibit bird vocalization activity and/or detection. These were removed from consideration but not replaced, leading to an uneven sample size (see Appendix S3.1). Consequently, for each survey point, we calculated both observed species richness and rarefied species richness for 45 minutes of sample effort to account for the uneven total sampling effort across methods, using the iNext package in R (Hsieh et al., 2020, v2.0.20), but patterns and results were similar to observed species richness, so only observed species richness is considered hereafter.

Species Richness

We compared alpha and gamma diversity metrics between the two survey methodologies. First, we modelled species richness at each survey point using a linear mixed effect models in the lme4 package, using sampling resolution as a fixed effect, survey point nested within forest disturbance class as a random effect, and a Gaussian error structure. We also calculated total species richness across all survey points (gamma diversity). For a repeat of this analysis including rarefied species richness, and data from traditional point-counts conducted in 2016, see Appendix S3.2. To address whether the use of HTR sampling accrued species richness at a faster rate than LTR sampling, we constructed sample-based species accumulation curves for each survey method, interpolating for 20 hours of sampling effort using the iNext package.

Detection Frequency

Next, we looked at whether HTR or LTR sampling detected species more frequently. A single detection is counted as a species presence in a sample, (e.g. incidence), not the total number of times it is detected within a sample. We summed the total number of detections of each species by sampling method (with a maximum possible of 116 for LTR samples and 6,960 for HTR samples) and compared the total number of detections for the species detected in both methods using a Wilcoxon signed ranks test. As total detections are highly dependent on the total number of samples and not necessarily reflective of improvements caused by greater temporal coverage, we also looked at the impact of detection frequency on where species were detected. We summed the number of survey points at which each species was detected and calculated the number of species falsely found to be absent per survey point. A species was determined to be falsely absent if it was undetected at a location by one temporal resolution of sampling but detected at the same location by the converse resolution.

In addition, we looked at extreme cases of false absences, in which species were detected at only a single survey point by a sampling resolution, but were actually detected at other locations by the converse method (hereafter 'false uniqueness'), something that is likely to be highly detrimental to the accuracy of habitat modelling in particular. As most analysis of this type are directed at the habitat level we analysed this at the scale of forest class, and calculate the proportion of the total species richness of each forest class that was determined to be falsely unique species. The seven forest classes are: undisturbed forest (five survey points), selectively-logged forest (four survey points), secondary forest - forest recovering from complete historical clearance *sensu* Putz and Redford, (2010) (three points), and four categories of burnt forest. The four burnt categories were categorised dependent on whether they burnt during the extensive El Niño-induced fires in 2015 and whether they have been selectively logged, with all logging occurring prior to 2015. The categories are; burned in 2015 but never logged (five points), logged and burned prior to 2015 (four points), logged and burned in 2015 (five survey points) and logged and burned both before 2015 and in 2015 (three survey points).

Sensitivity to abundance

To test if HTR sampling detected more rare species, we compared the relative abundance of species detected by both methods using chi-squared tests. We designated each species as common, fairly common, or uncommon, using the Parker et al., (1996) ecological and distributional databases, the most comprehensive and reliable database for this type of data in the region. Species marked as intermediate between two abundance classes in Parker were assumed to belong to the rarer class, categories marked as uncertain were assumed to be correct, and we combined the categories of uncommon, patchily distributed and rare. Species nomenclature was aligned to the taxonomy of the Brazilian Ornithologists Records Committee (Piacentini et al., 2015). We also tested whether HTR sampling detected each rare species more often. To ensure that any increase in detection of rare species was not caused by repeatedly detecting a single individual more often with HTR sampling, we also compared the number and proportion of species that were detected from a minimum of two transects and with >10 total detections (hereafter ‘multiple detections’).

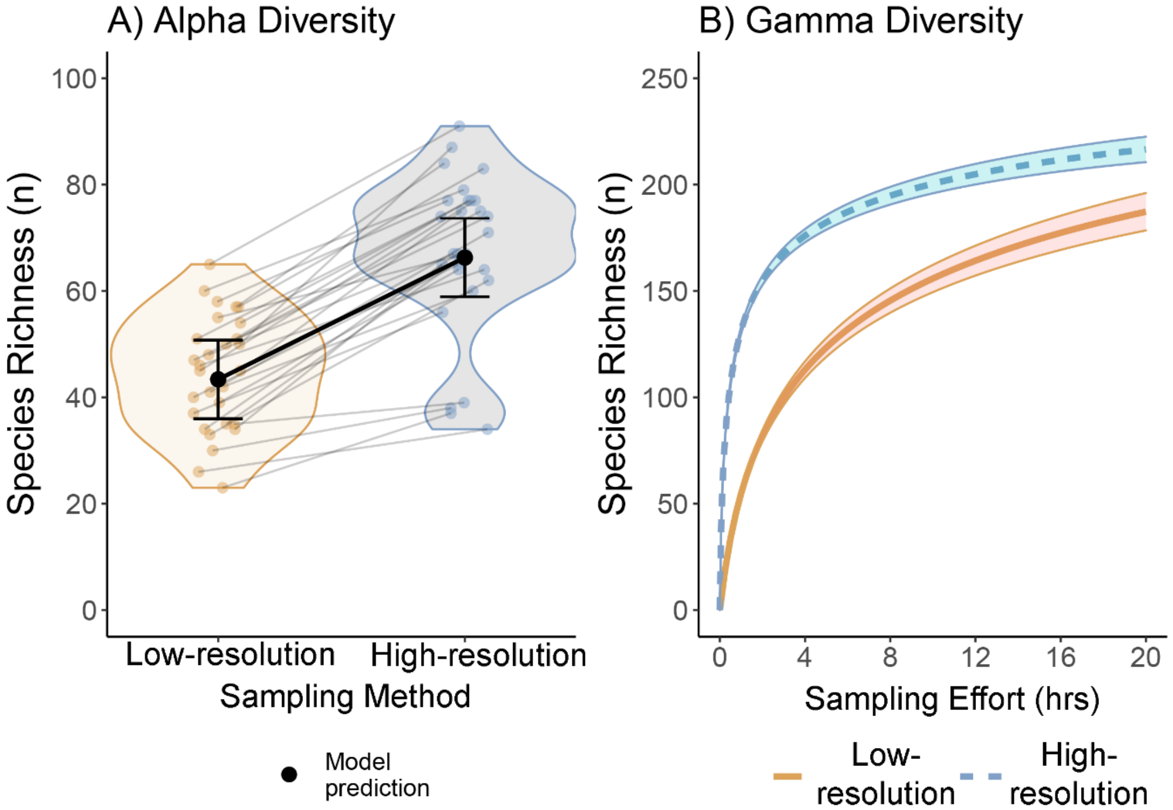
3.4. Results

3.4.1. Species Richness

We detected higher alpha and gamma diversity (Figure 3.2 A) using HTR sampling. In total, we detected 245 species; 224 species using HTR sampling with a median of 4.0±0.02 (SE) species and 204 species using LTR sampling with a median of 19.5±0.68 species per sample. The linear mixed effects model predicted that HTR sampling detects 22.9 species more per survey point than LTR, with HTR detecting 66.27±3.77 (SE) per point and LTR sampling detecting 43.37±3.77 species per point. HTR sampling detected 41 species undetected in LTR samples across the landscape, whilst LTR sampling detected 21 species not detected by HTR sampling.

We found that for sample-based rarefaction/extrapolation by sample method (Fig. 3.2 B), HTR sampling led to steep increases in species accumulation up to around four hours of sampling effort, with 176 ± 2 (SE) species detected, and then attenuated, with species accumulation continuing up to 20 hours. In contrast, LTR sampling showed a shallower curve, in which the accumulation did not slow as quickly. LTR sampling detects lower species richness at all quantities of sampling effort and were predicted to detect 187 ± 8 (SE) species after 20 hours of sampling effort, compared to 217 ± 5 species by HTR sampling. HTR sampling was predicted to take just 11 hrs 23 mins to achieve the same species total as LTR did in all surveys (204 species, 29 hrs).

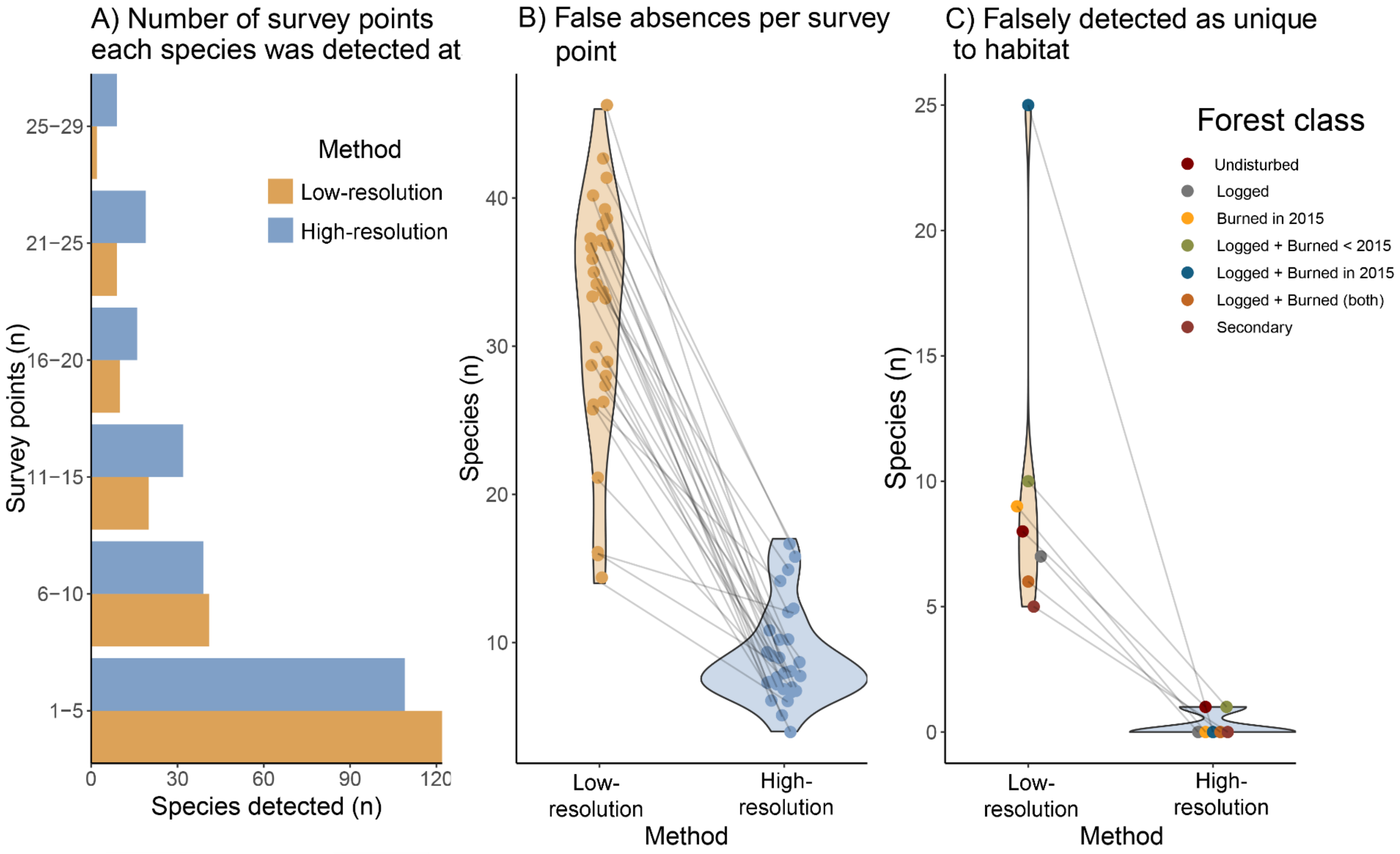
Figure 3.2. A; *Comparison of the species richness detected at each of 29 survey points employing either low temporal resolution samples, comprised of four 15-min periods, or high temporal resolution surveys of 240 15-s periods.* ***B****; Sample-based species accumulation curves for the two sampling methods, showing interpolated predictions up to 20 hours sampling effort.*



Detection Frequency

Detection frequency also significantly increased with HTR sampling. Species were detected more often, a median of 47 ± 18.9 (SE) times compared to just 7 ± 1.0 for LTR sampling (V=15865, p<0.001), and at more transects, 8 ± 0.57 to 4 ± 0.47 (V=976, p<0.001) (Fig.3.3 A). Additionally, LTR sampling detected 65% of all species fewer than ten times, and only six species were detected more than 50 times, with a maximum of 64 detections for Grey Antbird *Cercomacra cinerascens.* HTR sampling detected only 33% of all species fewer than ten times, recorded 40% of all species more than 50 times, recorded three species more than 1,000 times, and had a maximum of 1,821 detections for Bright-rumped Attila *Attila spadiceus*.

Figure 3.3. *Frequency of detection.* ***A;*** *The number of survey points each species was detected according to sampling method.* ***B;*** *The number of species falsely identified as absent per survey point.* ***C;*** *the number of species wrongly identified as unique to each forest class.*



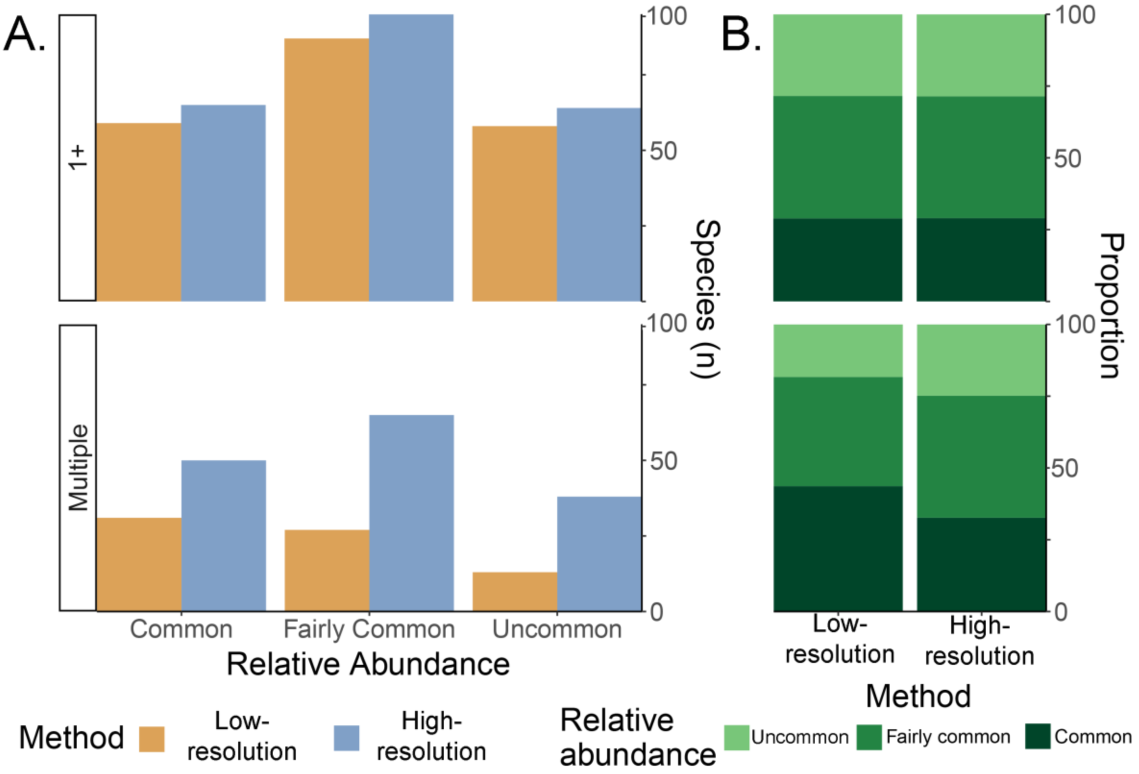
We found that the higher detection frequency had a striking effect on the accuracy of species absences with LTR sampling producing 927 false absences compared to just 263 for HTR sampling. Every survey point had fewer false absences with HTR sampling than LTR (Fig.3.3 A, Fig.3.3 B), and at one location, 50 species were detected with LTR samples, but a further 46 were missed – whilst only nine were missed with HTR samples.

This pattern was also apparent when looking at species that were only detected in a single forest class by one temporal resolution of sampling, but were actually detected in other forest classes by the converse sampling resolution. There were only two species that HTR sampling wrongly identified as unique to a forest class, compared to 70 by LTR sampling. One forest class, logged and burned in 2015, had an exceptionally high error rate using LTR samples, with 25 species or 21% of the total detected species at that class being wrongly detected as unique - something that could be highly misleading in habitat or distribution modelling.

3.4.2. Sensitivity to abundance

HTR sampling detected a mean 10% ±0.7 (SD) more species for common, fairly common and uncommon birds. However, both sampling methods detected a remarkably similar proportion of each category of relative abundance (Fig 3.4). When only considering multiple detections of species (10+ total detections and detected at two or more locations), HTR sampling detected substantially more species than LTR sampling, with the largest difference being for uncommon species for which HTR sampling detected nearly three times as many species (n = 13 and 38, respectively). Furthermore, the number of uncommon species detected as a proportion of all species detected multiple times declined for LTR sampling (28% to 18%) but stayed relatively stable for HTR (29% to 25%). When analysing only LTR sampling, the proportion of uncommon species in the total species pool declined from 28% for all species detected, to 18% when considering only multiple detections. For HTR, the detection of uncommon species remained similar, regardless of the abundance metric used (29% to 25%).

Figure 3.4. *The proportion of common, fairly common and uncommon species detected using both high and low temporal resolution sampling methods.*



3.5. Discussion

Much recent research on PAM surveys have focussed on automated methods (Stowell and Sueur, 2020). However, acoustic indices are limited by their inability to identify species, whilst machine-learning based classification methods remain limited to relatively small numbers of species, are technically challenging and time-consuming to create, and are less accurate than manual analysis methods. It is likely to be several years before off-the-shelf, readily applied classification methods are available for the world's most speciose regions (Gibb et al., 2019; Priyadarshani et al., 2018; Sugai et al., 2019). Given this, it remains of high importance to investigate and explore the benefits of PAM surveys coupled with manual analysis.

We found that HTR avian sampling using passive acoustic monitoring outperformed LTR sampling in every metric considered, often by a substantial margin. This is particularly true for species richness, where we predict HTR sampling to record just over fifty percent more species at each location, as well as finding substantially higher gamma diversity across the entire survey. Looking beyond species richness, HTR sampling is a more reliable method to obtain data for distribution and occupancy modelling. HTR sampling produce far fewer false negatives for the presence of species, and identifies far fewer species as unique to forest class, both of which can be significant hindrances in habitat and distribution modelling (Gu and Swihart, 2004; Kramer-Schadt et al., 2013). For instance, as the two logged and burnt forest classes had the two highest rates of false uniqueness, it seems likely that the two classes share a high proportion of species at low abundance that were not well detected by LTR sampling, but were by HTR. This could give a misleading impression that the time since burning, the only difference between the two classes, has a strong impact on species community, when the effect is actually an artefact of sampling. The ability to reliably repeatedly detect rare species also means that HTR sampling is more robust to low relative abundance, which can be advantageous in surveying bird communities, particularly in the tropics (Robinson and Curtis, 2020).

We have not conducted sensitivity analysis to optimise the duration of samples. However, one previous study compared survey durations of ten, five, three, two and one minute across equivalent cumulative periods and found species detection rates increased as survey durations decreased (Bayne et al., 2017). This, alongside our own results suggest that by shortening survey duration and increasing the temporal spread of samples, species accumulation will continue to increase. In fact, whilst estimates of abundance from acoustic surveys remain in their infancy due to difficulty with estimating distance from audio data (Darras et al., 2016; Yip et al., 2017), using near instantaneous survey durations could resolve the issue of movement in and out of detection range during the survey period. However, there are some inhibiting factors to suggest that extremely small durations (<10 s) may not be beneficial overall. Firstly, NGM reported issues with identification of calls with the shorter duration samples due to vocalisations being truncated at the start and end of the recordings, or absence of patterns in vocalisations that can be important cues in longer recordings. Secondly, and potentially more significantly, analysis of HTR sampling can take substantially longer. This is due to the effect of recording metadata and results for each sample, and there simply being many more samples to record with HTR sampling. At the temporal resolutions used in this study, results and metadata needed to be recorded 60 times with HTR sampling for every LTR sample. Whilst the extra time required in analysis is undoubtedly substantial, the time taken to record results and metadata is relatively small compared to the identification process, so that analysis time does not increase linearly with increasing number of samples. Furthermore the extra analysis time could be offset by the use of specialist software e.g. BORIS (Friard and Gamba, 2016), and by lower total survey duration required due to the increased species accumulation rate.

We chose to only sample from a two-hour period at dawn for two reasons. Firstly, we believe that conducting repeated point-counts in the field around dawn remains the standard bird surveying method for many ornithologists, and closely replicating this facilitates comparison for those selecting a sampling strategy to use in the future. Secondly, sampling from a single time-period within a short survey season enables very high temporal resolution sampling at a scale that will allow a strong impact on species-richness estimation, making it simple to demonstrate the concept. However, the estimation of species richness might be most effective at a ‘medium’ temporal resolution, but one generated from extending the survey period across diel or seasonal cycles, rather than increasing the duration of the sample. Several studies have found that PAM surveys incorporating dusk, night, or the whole diel cycle are more effective at estimating species richness (Araújo et al., 2020; La and Nudds, 2016; Wimmer et al., 2013). It may well be the case that the most effective method would involve variable temporal resolution, designating sampling effort according to expected species richness with the highest temporal resolution at dawn and dusk, and a smaller number of samples spread across the middle of the day and night for instance. Varying temporal resolution could just as easily be done across the seasonal cycle, with a higher temporal resolution used in the Neotropics at the onset of the rainy season when avian vocalisation and detectability peaks for instance (Kirwan, 2009; Pieretti et al., 2015), with a lower temporal resolution across the rest of the year to detect austral migrants.

When considering whether to use HTR sampling, it is necessary to consider that advantages and disadvantages of HTR sampling are intrinsically linked to those of PAM surveys, as PAM surveys are required to obtain sufficiently high temporal resolution. This means that HTR surveying will be particularly effective at locations in which a high percentage of species are detectable by vocalisation such as forest, although PAM surveys have been found to adequately reflect overall diversity even in arid regions in Australia (Smith et al., 2020).

In habitats in which PAM-based surveys are more effective than traditional survey methods, the more species detection probability varies temporally, the more HTR sampling is likely to be beneficial – most likely habitats with high avian species richness and corresponding high conservation value. In areas with high species richness, spatial and vocalisation niches are more tightly packed in a given period (Robinson et al., 2018; Terborgh et al., 1990), and a high proportion of species occur naturally at low abundance. This leads to higher variability in the proportion of species available per survey period, and higher turnover of species between surveys – so that increasing the temporal spread of sampling across a fixed period leads to increased species detection. Whilst we have tested the impact of HTR sampling in Amazonia, where the benefits of increased sampling resolution are likely to be greatest, these results are likely to be transferrable to other tropical forest landscapes, and it is probable that it will benefit other regions with high temporal variability in the proportion of species detectable. LTR sampling offers few benefits over HTR except efficiency in analysis, and therefore is unlikely to be a preferential choice for inventorying bird species except in highly homogenized landscaped occupied by relatively few common species, such as small, degraded forest fragments.

3.6. Conclusion

We believe that HTR sampling from PAM surveys should be considered the standard and primary method for sampling bird communities in tropical forests. There is strong evidence that surveys conducted on lower-resolution samples from PAM surveys outperform human observations for bird inventories (Darras et al., 2019), suggesting that autonomous surveys should be used preferentially or in combination with traditional point-count surveys. Given the additional benefits of HTR sampling, we believe that within tropical forest environments manually conducted point counts should mainly be employed as a supplement to HTR sampling. Exceptions include when autonomous recordings are not possible, for example if equipment cost is too high, when estimates of abundance are of higher priority than estimates of species richness, and when a high proportion of non-vocalising species are expected. Low temporal resolution sampling offers little benefit over either human observations or HTR sampling, except when analysis time is of high priority. Whilst a combination of traditional and autonomous survey techniques should still be considered the gold standard for conducting bird species inventories (Robinson and Curtis, 2020), if only a single survey method is to be used, repeated HTR sampling is likely to be the most effective.

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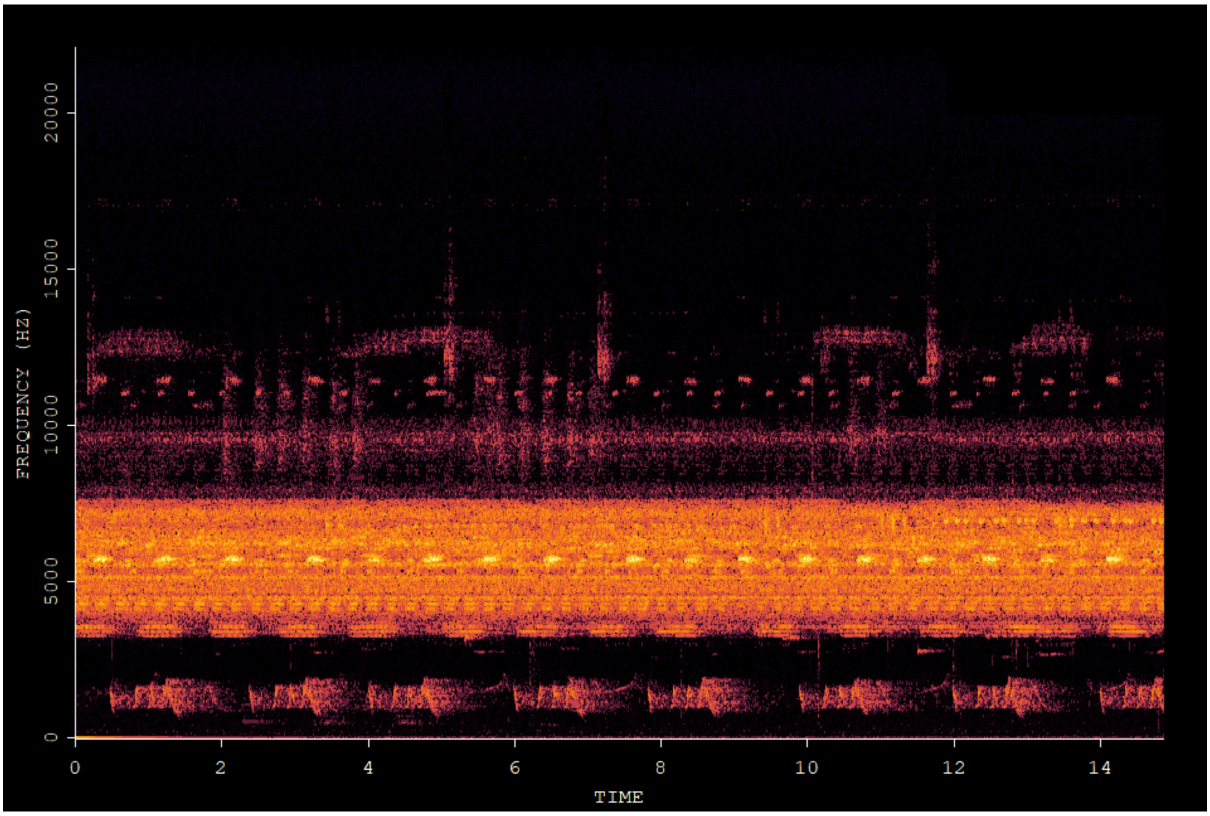
Chapter 4:

Acoustic indices perform better when applied at ecologically meaningful time and frequency scales



A spectrogram of logged forest at night

4.1. Abstract

1. Acoustic indices are increasingly employed in the analysis of soundscapes to ascertain biodiversity value. However, conflicting results and lack of consensus on best practices for their usage has hindered their application in conservation and land-use management contexts. Here we propose that the sensitivity of acoustic indices to ecological change and fidelity of acoustic indices to ecological communities are negatively impacted by signal masking. Signal masking can occur when acoustic responses of taxa sensitive to the effect of interest are masked by less-sensitive acoustic groups, or target taxa sonification is masked by non-target noise. We argue that by calculating acoustic indices at ecologically appropriate time and frequency bins, masking effects can be reduced and the efficacy of indices increased.

2. We test this on a large acoustic dataset collected in Eastern Amazonia spanning a disturbance gradient of undisturbed, logged, burned, logged-and-burned and secondary forests. We calculated values for two acoustic indices: the Acoustic Complexity Index and the Bioacoustic Index, across the entire frequency spectrum (0–22.1 kHz), and four narrower subsets of the frequency spectrum; at dawn, day, dusk and night.

3. We show that signal masking has a large impact on the sensitivity of acoustic indices to forest disturbance classes. Calculating acoustic indices at a range of narrower time–frequency bins substantially increases the classification accuracy of forest classes by random forest models. Furthermore, signal masking led to misleading correlations, including spurious inverse correlations, between biodiversity indicator metrics and acoustic index values compared to correlations derived from manual sampling of the audio data.

4. Consequently, we recommend that acoustic indices are calculated either at a range of time and frequency bins, or at a single narrow bin, predetermined by a priori ecological understanding of the soundscape.

4.2. Introduction

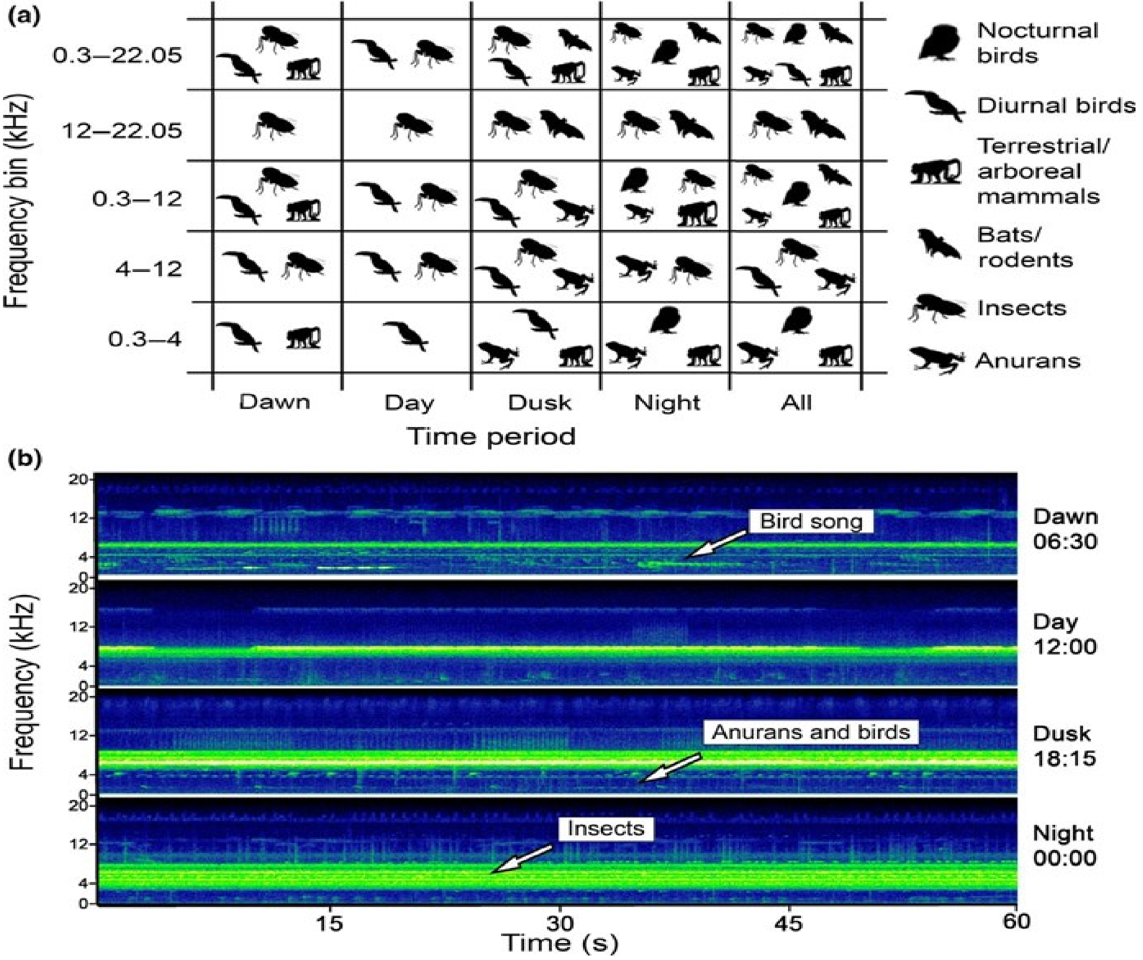
Acoustic monitoring is rapidly becoming a key tool to measure biodiversity, with strident calls for broader uptake (Burivalova et al., 2019; Deichmann et al., 2018; Wagner Ribeiro Jr. et al., 2017). Despite increasing ease of data collection, there remain significant obstacles to the analysis of acoustic data, with species-level classification limited by the expertise and effort required to train machine learning models, and the limited availability of both open-source software and large audio libraries (Gibb et al., 2019; Priyadarshani et al., 2018). Consequentially, the use of acoustic indices has grown in popularity, often used as proxies for more traditional biodiversity metrics like species richness and composition, and presented as alternative effective tools for rapid biodiversity assessments (Sueur et al., 2008). There are a wide range of acoustic indices, but most involve calculating and comparing acoustic power within temporal and frequency bins (Buxton et al., 2018; Farina, 2014; Gibb et al., 2019; Sueur et al., 2014). These are, in turn, used to assess soundscape qualities such as evenness, entropy and complexity. Acoustic indices infer community-level information from entire soundscapes; in contrast to species-level classification approaches that require time-consuming complex model-training techniques necessitating large training libraries, indices are relatively simple and readily available on a range of open-source platforms.

Despite their increasing popularity, acoustic indices are not always effective at answering key questions related to conservation or natural resource management. The first issue relates to their sensitivity to changes in environmental conditions. Acoustic indices have been shown to effectively distinguish between disparate land uses (Bradfer-Lawrence et al., 2019; Carruthers-Jones et al., 2019; Depraetere et al., 2012). However, they are less successful in distinguishing differences between similar land uses; for example between different types of forest (Bormpoudakis et al., 2013; Do Nascimento et al., 2020; Eldridge et al., 2018), or require a very large number of spatial replications to do so (Mitchell et al., 2020). The second issue relates to their fidelity as indicators of biodiversity, as they can be inconsistent predictors of traditionally used biodiversity metrics such as species richness (Eldridge et al., 2018; Fuller et al., 2015; Jorge et al., 2018; Mammides et al., 2017).

The problems of low sensitivity and inconsistent fidelity are potentially caused by signal masking—while certain vocalising taxa or taxonomic groups may respond strongly to changes in environmental condition, others may not. By measuring acoustic indices at intervals that measure across multiple taxonomic groups, sensitivity to these varied responses is lost, which may not be the case if indices were measured with multiple intervals. Similarly, fidelity to a single taxonomic group is lost by the use of broad time and frequency intervals, which may be improved by the use of narrower, tailored intervals. There are two key ways in which signal masking can occur in acoustic indices. The first, temporal masking, can occur when acoustic indices are measured over time periods that are too long, so that sounds from sensitive time periods may be confounded by a lack of change or contrasting responses in other time periods. For example, the vocal community at dawn may respond to a disturbance event very differently from the dusk community (Deichmann et al., 2017), so that measuring both together masks overall community responses. To avoid this, the analysis of acoustic indices often involves temporally limiting or splitting the data analysed into discrete periods, such as dawn and dusk (Bradfer-Lawrence et al. 2020; Deichmann et al., 2017; Eldridge et al., 2018; Fuller et al., 2015; Machado et al., 2017), selecting time periods that coincide with the peak communication time for certain groups.

The second form of signal masking, frequency masking, can occur when acoustic indices are measured at frequency bins that are too broad, so that sounds at sensitive frequencies are swamped by contrasting or null responses at other frequencies. Although the importance of frequency masking has not been explicitly considered in relation to acoustic index functioning, there is a strong a priori reason to believe it may be important, and has been postulated by others (Eldridge et al., 2018). There is a broad negative relationship between body size and the frequency at which animals vocalise (Gillooly & Ophir, 2010; Ryan & Brenowitz, 1985; Seddon, 2005; Wilkins et al., 2013), meaning that the largest species, predominantly mammals, vocalise at the lowest frequencies, while orders composed of smaller species such as orthopterans predominate at higher frequencies. In addition, neotropical bird vocalisations exhibit both temporal and frequency partitioning to avoid signal masking from cicadas and other loud insects (Aide et al., 2017; Hart et al., 2015). At its simplest, this should result in different frequency bins being dominated by sounds from different broad taxonomic groupings (Figure 4.1).

Figure 4.1. *A conceptual framework of soundscape dominance across time and frequency.*



***(a)** Conceptual framework illustrating the expected acoustic niches of different taxonomic groups in variable time–frequency bins (TFBs). The 0.3–22.05 kHz bin (top row) shows which taxonomic groups would be included without frequency partitioning, while the right-hand column shows the same without temporal partitioning. Note that the taxonomic groups are illustrative and are not applicable to every species, for example, many rodents vocalise at both low and high frequencies. **(b)** Shows four 1-min spectrograms taken from a single location in the Amazon rain forest (point 21) on an arbitrarily selected date (8 July 2018), demonstrating soundscape partitioning across temporal and frequency scales. The variation in amplitude in the intense band of insect noise between 4 and 12 kHz is particularly noticeable, as is the increase in avian vocalisation at dawn below4 kHz*

Here, we use a dataset from one of the world's most speciose ecosystems—the Brazilian Amazon—to explore how the use of time and frequency bins (henceforth TFBs) can improve the sensitivity and fidelity of acoustic indices. By calculating acoustic index values within restricted frequency bands, the potential masking effect could be reduced, and correlations with specific taxonomic groups increased. Initially, we establish whether measuring indices at broad time and frequency scales, as is standard practice, masks variation in acoustic responses across narrower TFBs. Next, we look at the impact of signal masking on the efficacy of acoustic indices as a proxy for biodiversity and test the suitability of using TFBs as a solution by asking two questions of high relevance to practitioners and policy makers. First, do TFBs improve the sensitivity of acoustic indices to changes in forest condition (e.g. disturbance)? This is key to monitoring forest recovery following disturbances such as selective logging or wildfire, analyses which underpin many applied ecology questions. Second, do TFBs improve the fidelity of acoustic indices as proxies for traditional field surveys aimed at establishing species richness and composition? These field surveys can be expensive and inefficient for a range of taxonomic groups (Gardner et al., 2008), and if acoustic indices can be shown to be a reliable replacement for traditional survey methods, such as point count bird surveys, then they may offer a significant cost saving.

4.3. Materials and Methods

4.3.1. Study area and data collection

We collected acoustic data in the eastern Brazilian Amazon in the municipalities of Santarém-Belterra-Mojuí dos Campos (latitude−3.046, longitude −54.947, hereafter Santarém) in Pará state, between 12 June 2018 and 16 August 2018. We used the permanent transects of the Sustainable Amazon Network (Gardner et al., 2013) distributed in terra firme forest habitats. We sampled 28 300-m transects distributed into five forest classes: undisturbed primary forests (n = 4), logged primary forests (n = 4), burned primary forests (n = 5), logged-and-burned primary forests (n = 12) and secondary forests— forests recovering after being completely felled (n = 3).

We installed Frontier Labs Bioacoustic Recording Units with a 16-bit 44.1 kHz sampling rate at points halfway along each transect. Recorders were placed in trees at a height of 7–10 m, with the microphone placed in a downward facing position, at a distance of 10–20 m from the transect to reduce the chance of recorder theft. Recording units were placed away from immediately overhanging dense vegetation to avoid sound being blocked and to limit geophony from leaves and branches. The microphones used have 80 dB signal to noise ratio and 14 dBA self-noise, a fixed gain pre-amp of 20 dB, a flat frequency response (±2 dB) from 80 Hz to 20 kHz and an 80 Hz high-pass filter to filter out low-frequency wind noise (Frontier Labs, 2015). All files were recorded in wav format. Recordings were made continuously (Frontier Labs software writes a new file every ~6 hr) over multiple discrete time periods of differing length at each point with discrete time periods ranged in duration between 3 and 20 days. Total recording duration and first and last recording dates are included in Appendix S4.1. The inaccessibility of some transects used in previous studies meant that a balanced survey design was impossible across the disturbance categories (Table 4.1).

Table 4.1. *Audio sampling by forest class after automated removal of recordings containing heavy rainfall.*

Forest class	***Sampled points (n)***	***Total sampling time (min)***
Primary	*4*	*90,600*
Logged primary	*4*	*89,540*
Burned primary	*5*	*139,720*
Logged-and-burned primary	*12*	*238,130*
Secondary	*3*	*60,970*

4.3.2. Data analysis

We selected two acoustic indices, the Acoustic Complexity Index and the Bioacoustic Index as they are two of the commonest indices used in ecoacoustic studies. However the Acoustic Complexity Index is commonly applied across broad frequency ranges, and the Bioacoustic Index (BI) is typically applied at restricted frequency ranges, making an ideal comparison for this study as in combination, they are likely to be representative of how many acoustic indices will be affected by the use of narrower time and frequency bins. The Acoustic Complexity Index is intended to quantify biotic sound while being robust to non-target noise (Duarte et al., 2015; Fairbrass et al., 2017; Pieretti et al., c), and is commonly applied across broad frequency bins. Acoustic Complexity Index measures the irregularity in amplitude across time samples by frequency bin, relative to the total amplitude of the frequency bin. The Acoustic Complexity Index has been found to significantly correlate with species richness for some taxa (Bertucci et al., 2016; BradferLawrence et al., 2020; Eldridge et al., 2018; Mitchell et al., 2020), while in others it showed little or no correlation (Fuller et al., 2015; Mammides et al., 2017; Moreno-Gómez et al., 2019) although this may be due to limitations in methodology and small sample sizes. In contrast, the BI is generally applied to narrower frequency bins, and is intended to provide relative abundance of avian community within a frequency range that contains most bird sound (Boelman et al., 2007). It measures the disparity between the quietest and loudest 1 kHz frequency bins. Again, the BI has been found to be a good predictor of diversity in some studies (Eldridge et al., 2018; Gasc et al., 2017; Hilje et al., 2017; Mitchell et al., 2020) while others have found it to be poor (Fuller et al., 2015; Moreno-Gómez et al., 2019), although concerns about the limitations of the methodologies used in these studies apply here too. We expect both indices to increase with increasing species richness and species abundance, and for correlations between both abundance and richness with the indices to be strongest in the frequency and time bins that are most dominated by the target taxa (Table 4.2), particularly diurnal bird species at dawn between 0.3 and 12 kHz and nocturnal taxa at night between 0.3 and 4 kHz.

We calculated the indices using the soundecology package (Villanueva-Rivera et al., 2011, v1.3.3) in R (R Core Team, 2019) which includes minimum and maximum frequency limits for both the Acoustic Complexity Index and BI, allowing easy and consistent index calculation at a range of frequency bins. To limit microphone self-noise, the lowest frequency included in analysis was 300 Hz. We then calculated the mean index value per 10-min interval of data collected for each acoustic index and each of the 20 TFBs (Figure 4.1a), having first screened out recording periods containing heavy rainfall (n = 527) using the hardrain package (Metcalf, Lees, et al., 2020, v0.1.1) in R Studio.

We selected TFBs with the objective of capturing periods of time and frequency bands that are most taxonomically homogenous. TFBs were not quantitatively optimised, but rather subjective approximations that aimed to effectively capture broad taxonomic groupings in tropical forest landscapes. Temporal limits were determined by patterns in animal communication in the diel cycle, to encapsulate dawn, dusk, daytime and night-time periods (Pieretti et al., 2015; Rodriguez et al., 2014); commonly used sampling periods in acoustic recording (Sugai et al., 2019). 'Dawn' was assigned to the period from 30 min prior to sunrise and for the following 2 hr, while 'Dusk' was the 2-hr period ending at 30 min after sunset. 'Day' and 'Night' are the respective intervening periods. Frequency limits were determined by a review of the literature and our own experience of manually analysing 100s of hours of acoustic data from the region. The taxonomic groupings we hypothesise dominate each TFB are illustrated in Figure 4.1a. Table 4.2 contains some of the TFBs likely to contain particularly high activity from particularly homogeneous groupings. 0.3-22.1 kHz frequency bin (hereafter 'baseline') was used as baseline data, representative of how most terrestrial acoustic indices are currently calculated across the spectrum of human hearing or the common sampling rate of 44.1 kHz. However, it is worth noting that the BI is commonly calculated with a narrower frequency bin than the baseline, typically from 2 to 8 or 11 Khz (Boelman et al., 2007; Bradfer-Lawrence et al., 2019; Villanueva-Rivera et al., 2011). We have used the same baseline as the Acoustic Complexity Index for ease of comparison, and because the mechanisms causing masking between ecologically relevant and non-relevant frequency bins are the same regardless of absolute frequency. Of course, macro frequency bands will never solely encompass single taxonomic groups, and boundaries will always be somewhat arbitrary due to variations in acoustic communication at species, temporal and even individual levels.

Table 4.2. Selected time–frequency bins and the taxonomic groups expected to dominate each sample

Frequency band (kHz)	Time period	Taxonomic group	References
0.3–4	Night	Terrestrial/arboreal mammals, anuran and birds	Chek et al. (2003) and Lima et al. (2019)
4–12	Day	Hemiptera/orthoptera	Hart et al. (2015) and Schmidt et al., 2013
4–12	Night	Hemiptera/orthoptera	Hart et al. (2015) and Schmidt et al. (2013)
0.3–12	Dawn	Diurnal/crepuscular birds	Tobias et al. (2014)
12–22.1	Dusk	Insects, bats and frogs	Lima et al. (2019) and Schmidt et al. (2013)
12–22.1	Night	Insects	Schmidt et al. (2013)

4.3.3. Signal masking

To investigate whether the soundscape responds differently to human-driven disturbance across time and frequency, we looked at the variation in response of each disturbance class for each TFB. Having removed periods with extreme outlying index values, we took a random sample of acoustic index values for each acoustic index and TFB from each forest class (n = 500), giving a total sample size of n = 2,500 per TFB/index. For each TFB and acoustic index we conducted a Kruskal–Wallis (Kruskal & Wallis, 1952) test between the five forest classes, and calculated the effect size (ε2). When significant differences between the classes were found, we used a Dunn's test (Dunn, 1964) to establish how many of the ten forest class pairs were significantly different from each other.

4.3.4. The sensitivity of acoustic indices to habitat

To assess whether the use of TFBs increased acoustic index sensitivity to forest classes, we built distributed random forest models from the h2o r package (LeDell et al., 2020, v3.30.0.1), varying the number of TFBs used as predictors. Firstly, we tested if the use of TFBs improved classification accuracy between the two most ecologically distinct sampled habitats; undisturbed primary forest and secondary forest (Moura et al., 2013). To do so, we built two binomial random forest models, the first using training data only from the baseline frequency bin across all time periods, the second using training data from all frequency bins and time periods. Next, models were trained and tested on data from all five forest classes, which previous studies (e.g. Moura et al., 2013) suggest would provide a more challenging classification problem.

We used each combination of index and TFB as a separate predictor. The training datasets required subsampling to obtain predictors of equal length, as not all time periods were of the same duration, and forest classes had unequal survey effort. We used the same subsample as above (see Section 2.3), so that each TFB predictor had 2,500 samples, with 500 samples from each forest class. This resulted in a greatly reduced dataset for training the models with 100,000 acoustic indices values compared to 1,277,560 in the original dataset. Prior to model training, the dataset was split with 75% of observations used for training and 25% as a test dataset. Model parameters were kept constant across all models (Appendix S4.2). We used balanced accuracy (Fielding & Bell, 1997), F1 scores (Chinchor, 1992) and Matthew's Correlation Coefficient (Guilford, 1954) as accuracy metrics (Appendix S4.5A), which were calculated per forest class based on predictions of the test dataset and are presented here as an unweighted mean across all forest classes included in the respective model.

4.3.5. Fidelity of acoustic indices to taxonomic measures of biodiversity

We assessed correlations between acoustic index scores and biodiversity indicator metrics, to see how representative the indices were of commonly used indicators of diversity. Data on the presence/absence of three sets of species were generated from two subsets of the audio data. Each audio subset consisted of 28 hr of sound recordings, in the form of two hundred and forty 15-s recordings from each point. The first dataset was restricted to the dawn period (hereafter dawn birds), in which all identifiable avian vocalisations were assigned to species by an ornithologist (Nárgila Gomes De Moura) with extensive field experience of point counts in the same sites (e.g. Moura et al., 2013). This method of species detection is likely to produce comparable results to traditional point count surveys as several papers have shown that experienced observers reviewing recordings and spectrograms can be more or equally effective at detecting species than field-based surveys (Darras et al., 2019; Shonfield & Bayne, 2017). The second set of data was restricted to the nocturnal period (hereafter nocturnal birds), and again all identifiable avian vocalisations were assigned to species by an experienced ornithologist (OCM). The third set was generated from the nocturnal data subset again (hereafter nocturnal taxa), but comprises all biophony below 4 kHz, identified (by OCM) where possible or sonotyped if not. It is worth noting that all of the bird species identified at night vocalised below 4 kHz, so that the nocturnal bird set is wholly a subset of the nocturnal taxa set.

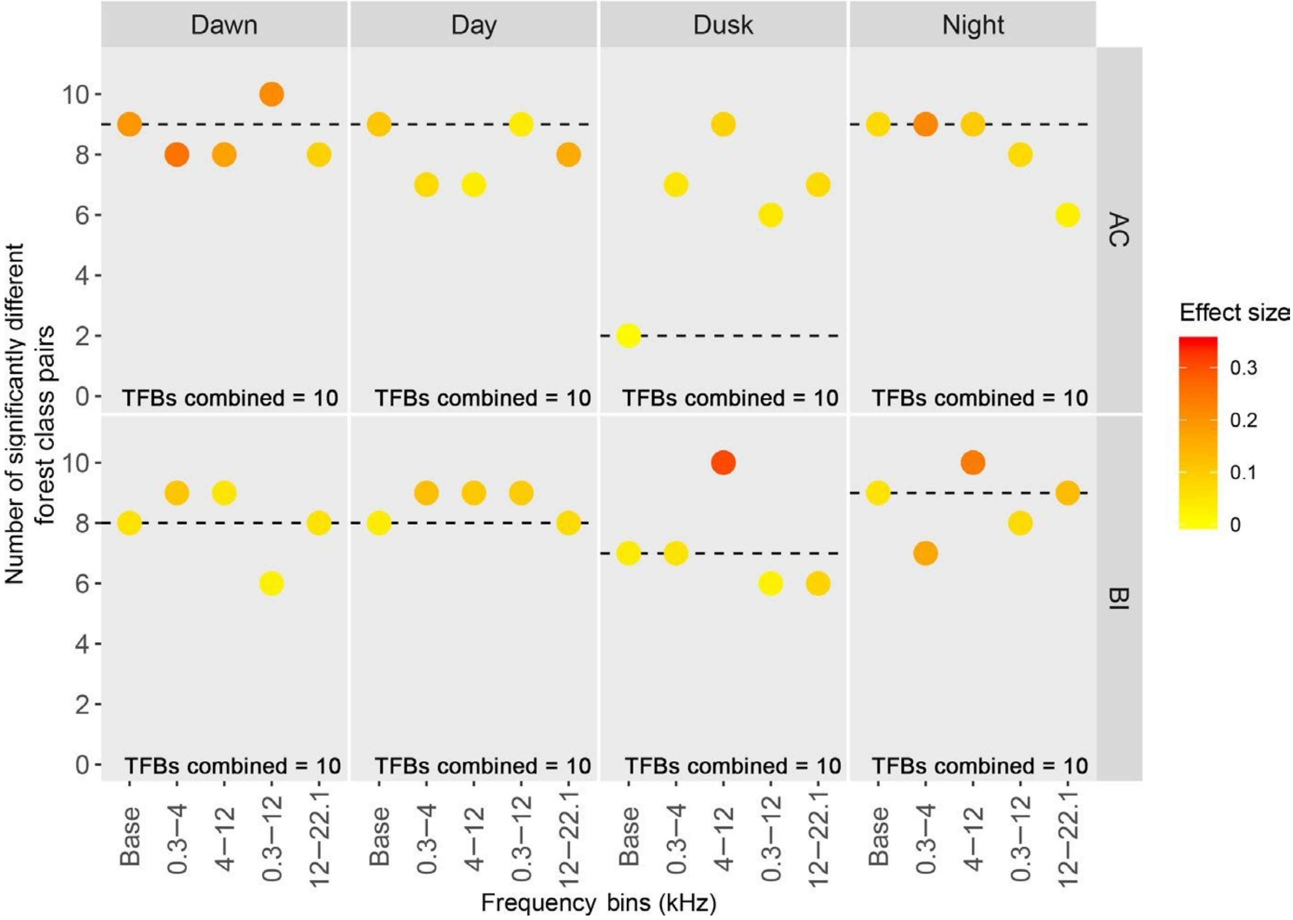
For each of these matrices (i.e. dawn birds, nocturnal birds and nocturnal taxa), five metrics were calculated; total number of encounters (the sum of the number of 15-s recordings each species was present in), species richness, Shannon diversity, Pielou's evenness and the first axis from a non-metric multidimensional scaling ordination (hereafter MDS1) using the Jaccard method from the vegan package (Oksanen et al., 2019). Total encounters were included as a proxy for the abundance of sounds, to test if indices responded more strongly to more sources of noise, regardless of composition. Estimated species richness from the dawn matrix was calculated for each point at 98.5% coverage based on rarefaction/extrapolation using the iNEXT package (Hsieh et al., 2020, v2.0.20), as some of the survey files were removed as they contained periods of heavy rain which affected the number of vocalising species. Observed species richness was used for metrics from the nocturnal matrix, as the data were pre-screened for rain. Shannon diversity, Pielou's evenness and species richness were included as standard measures of ecological diversity (Oksanen et al., 2019). MDS1 was included to reflect turnover mediated by disturbance, as high values correspond with less disturbed habitats, while lower values have communities associated with more disturbed habitats. Correlations between these metrics are available in Appendix S4.3. Median values of each acoustic index were calculated for each point and TFB, and Spearman's rank order correlations ($\alpha = 0.05$) were calculated between these and the biodiversity metrics. Significant differences between each correlation and the respective baseline correlation were calculated using Zou's confidence interval test (Zou, 2007) in the cocor package (Diedenhofen & Musch, 2015, v.1.1–3).

4.4. Results

4.4.1. Sensitivity: Forest disturbance

The Kruskal–Wallis and Dunn's test revealed strong evidence that acoustic masking affects the sensitivity of acoustic indices, both temporally and by frequency. All of the Kruskal–Wallis tests were significant ($p < 0.05$), showing that acoustic indices are sensitive to at least some disturbance events regardless of frequency band or time period. There were significant differences between all 10 forest class pairs in every time period and with both indices when considering all frequency-restricted TFBs together. In contrast, there were no time periods with significant differences between all forest class pairs when using only the baseline TFBs, but Acoustic Complexity did have significant differences between nine forest class pairs in three time periods, and BI once. Twelve TFBs showed significant difference ($p < 0.05$) between more forest classes than the corresponding baseline, and 21 TFBs had higher effect sizes than the corresponding baseline, suggesting that in many cases stronger responses to disturbance events at narrower frequency bins are masked by the use of broad frequency bins (Figure 4.2). No baseline TFB achieved perfect separation between all 10 forest class pairs but this was achieved by three of the non-baseline TFBs. Furthermore, Acoustic Complexity Index at dusk and the baseline frequency bin produced the lowest number of significantly different forest class pairs, just two, suggesting that using only the broadest frequency bin can result in relatively poor differentiation between forest disturbance classes. No one frequency bin or time period had a consistently larger effect size, or consistently differentiated between more forest classes. There were several occasions in which effect size increased in comparison to the baseline while the number of different forest classes decreased (e.g. Acoustic Complexity Index at dawn, 0.3–4 kHz, BI at night, 0.3–4 kHz). This suggests that the soundscape at this frequency bin is showing a particularly strong response to disturbance in one or more of the forest classes (in Appendix S4.1).

Figure 4.2. *The difference between index values for the five forest classes at 20 time–frequency bins (TFBs) and the Acoustic Complexity Index and Biodiversity Index.*

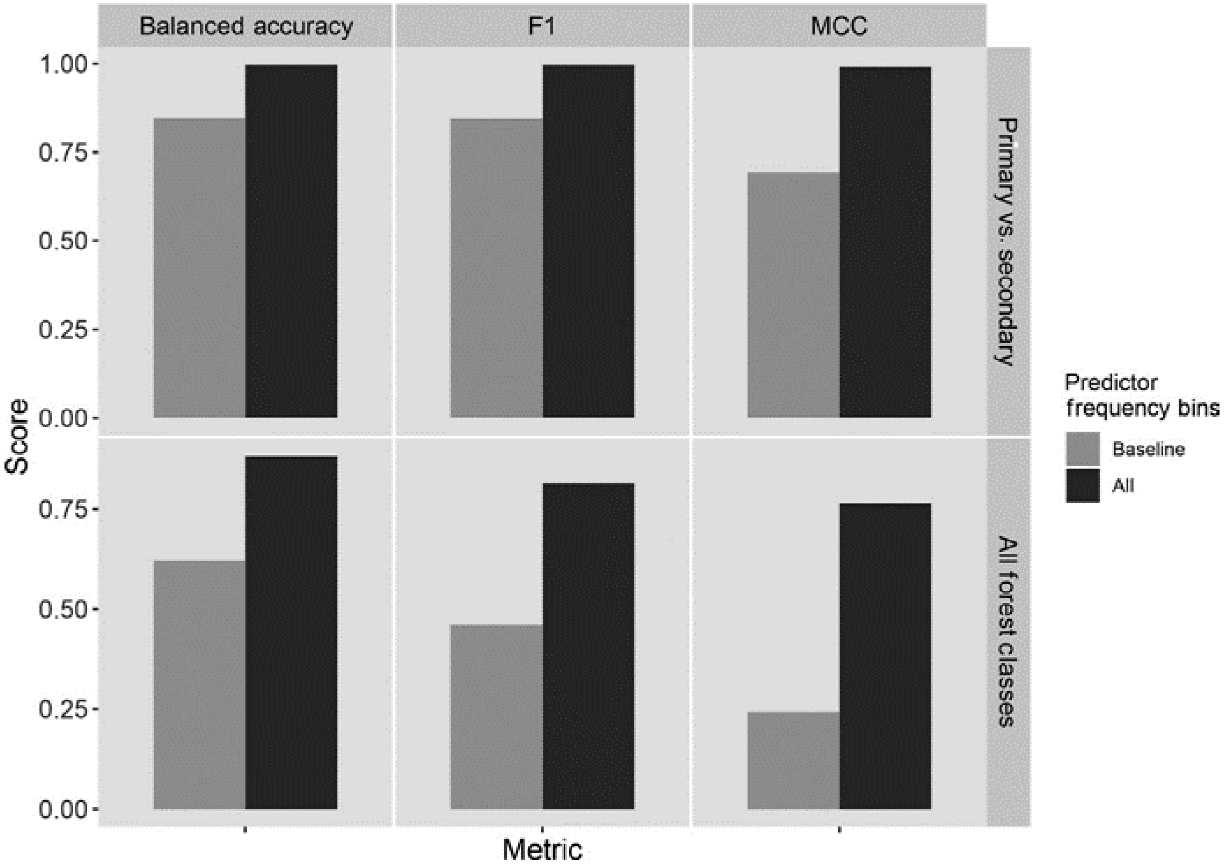


All TFBs (points) detected significant differences ($p < 0.05$) between forest classes. The number of significantly different ($p < 0.05$) forest class pairs were calculated for all TFBs using a Dunn's test. Colour scale represents the effect size (ε2). Frequency bins above the dotted line have more significantly different forest class pairs than the corresponding baseline frequency bin, while frequency bins which are redder in colour than the corresponding baseline show a greater effect size. The number of significantly different forest class pairs detected by all TFBs except the baseline is shown at the bottom of each panel. This additional sensitivity to disturbance would be masked if acoustic indices were only calculated at broad (e.g. baseline) frequency bins.

4.4.2. Sensitivity: Forest class differentiation

The random forest models generated using all of the TFBs as predictors were able to classify forest classes with a high degree of accuracy, with 99.6% balanced accuracy between secondary and undisturbed forest and 88.2% between the five forest classes (Figure 4.3). The models using all TFBs as predictors outperformed the corresponding baseline models in both tests, but as expected the baseline models performed particularly poorly when classifying between all five forest classes, achieving just 62.1%. The confusion matrix for the random forest model using all TFBs across all five classes suggest that acoustic indices do respond to soundscapes in ecologically meaningful ways, as both burned forest classes had comparatively high error between them, as did the two most disturbed classes, logged and burned versus secondary forest (Appendix S4.5B).

Figure 4.3. *Random Forest accuracy metrics for classification of forest classes.*



*Left-hand bars (light grey) show accuracy scores from models using acoustic index values only from baseline (0.3–22.1 kHz) frequency bins, while right-hand bars (dark grey) show accuracy scores from models using index values from all frequency bins. The **top row** shows models trained and tested on the two most ecologically distinct forest classes, primary and secondary forest, the **bottom row** shows models trained on all five forest classes. The accuracy scores are unbalanced mean scores across all classes included for balanced accuracy, F1 and Matthew's correlation coefficient (MCC). Models using all time–frequency bins as predictors consistently perform better than models only using the baseline frequency bin.*

4.4.3. Fidelity: Biodiversity correlations

Correlations with traditional biodiversity metrics revealed complex patterns, underpinned by strong variation across index, frequency bins and time periods. For simplicity, we have focussed on time periods in which acoustic index values most directly reflect variation in manually reviewed datasets—dawn and day time for the dawn bird dataset, and night for the nocturnal datasets (Figure 4.4). The two strongest correlations, were at night between BI and diurnal avian MDS1 at 4–12 kHz (rs = 0.74) and dusk at 0.3–12 kHz (rs = 0.72).

The correlation scores provide strong evidence that the use of TFBs increase the fidelity of correlations. We found that correlation directions of the frequency/bins differed from the corresponding baseline frequency bin for at least one of the metrics in every time period in both indices. The strongest examples of this were between BI at dawn with dawn birds, which saw predominantly significant positive correlations at frequency bands at which dawn birds vocalise, but negative correlations in the baseline and 12–22.1 kHz frequency bins. We also found 28 instances in which correlations were significantly different to the corresponding baseline frequency bin.

Overall, the Acoustic Complexity Index was inconsistently correlated with biodiversity indicator metrics with predominantly negative and significant correlations with diversity metrics at dawn, but mostly positive correlations during the day and at night for most frequency bands, with far fewer significant correlations. In contrast, the BI showed predominantly positive correlations with most diversity metrics except MDS1 across all three time periods and all three frequency bins only including sound below 12 kHz. For the community metrics most likely to be useful to ecologists, species richness and Shannon diversity, there were 19 significant correlations. However, where we found significant correlations with these metrics, there were still strong reasons for doubting the fidelity of acoustic indices as proxies. At dawn, correlations for both indices were weaker than the respective correlations with total encounters or MDS1, suggesting the indices were more sensitive to the number of individual sounds or the overall community. At night, nocturnal birds and taxa correlations with the BI showed conflicting patterns with correlations at frequency bins more likely to be relevant to the relevant taxonomic group, suggesting a strong masking effect by vocalisations of non-target taxa. The exception to this is the correlation between dawn birds and BI during the day at 0.3–4 kHz, which shows strong correlations with species richness and Shannon diversity (rs = 0.44 and 0.40), a similar correlation with total encounters (rs = 0.40) and no significant correlation with MDS1.

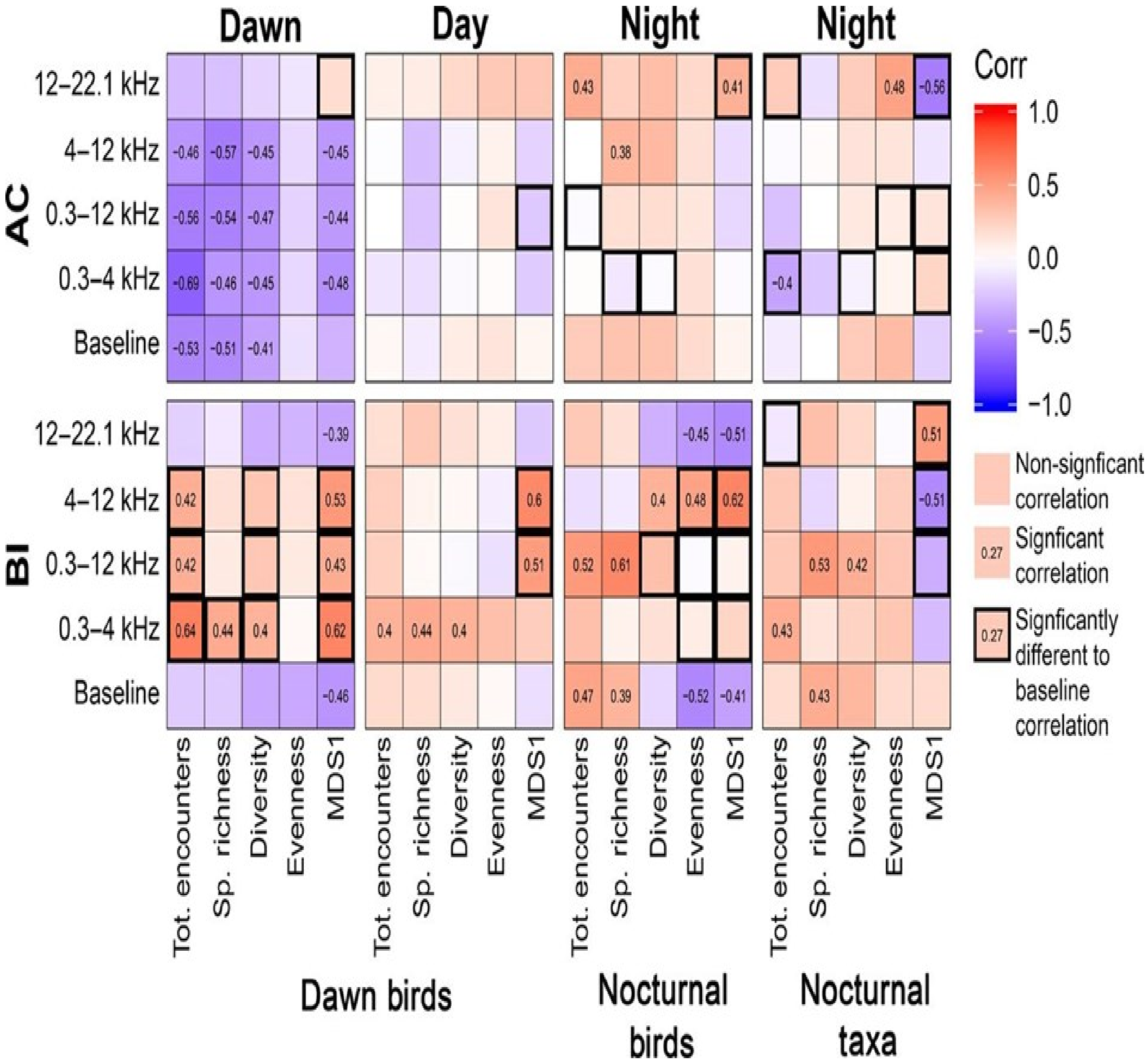


Figure 4.4. *Spearman's rank correlation coefficients between acoustic indices (Acoustic Complexity Index, Bioacoustic Index) at five frequency bins and three time periods, and biodiversity indicator metrics. Biodiversity indicator metrics are derived from dawn birds, nocturnal birds and all nocturnal taxa vocalising between 0.3 and 4 kHz, obtained through manual identification of species in a subset of the acoustic data. Total encounters (Tot. Encounters) was included as a proxy for the abundance of sounds. Species richness (Sp. Richness), Shannon diversity (Diversity) and Pielou's evenness (Evenness) are included as standard measures of ecological diversity. The first axis of a non-metric multidimensional scaling ordination (MDS1) is included to reflect turnover mediated by disturbance. Non-significant correlations are shown in coloured empty squares, significant (p < 0.05) correlations are shown in squares containing their correlation coefficient (rs) and correlations significantly different to the corresponding baseline correlation (Zou's confidence interval test) have black borders. Colour scale indicates the direction and strength of the correlation.*

4.5. Discussion

We found that calculating acoustic indices at narrower TFBs results in large increases in the sensitivity of acoustic indices to the soundscape response of different forest classes. Calculating acoustic indices across a single broad frequency bin, as is commonplace in the ecoacoustic literature (Buxton et al., 2018; Gibb et al., 2019; Sueur et al., 2014) can mask varied responses across time periods and frequency bins, reducing the sensitivity of acoustic indices. Furthermore, when acoustic indices are used as proxies for biodiversity indicator metrics, masking can have a serious impact on the fidelity of the correlations. Correlating broad frequency bins with biodiversity metrics generated from taxa whose vocalisations do not occur across the entire frequency range is likely to be highly misleading. It not only misrepresents the magnitude of correlations, but potentially results in spurious inverse correlations caused by the responses of acoustically dominant species or patterns from acoustic space that are not biologically relevant.

The sensitivity gains of this new methodology are particularly apparent when using acoustic indices to differentiate between environments with classification accuracy greatly increased. Accuracy scores are as good or better than many in the literature (Bormpoudakis et al., 2013; Bradfer-Lawrence et al., 2019; Do Nascimento et al., 2020; Eldridge et al., 2018), especially considering that model hyperparameters are not optimised, fewer acoustic indices were used, and that the forest classes considered here are all of the same land cover (tropical forest) and within the same landscape. In addition, these results have been achieved while using only approximately one sixth of the training data compared to the models using only a single baseline frequency band, suggesting that by using TFBs, large efficiency savings can be made in terms of data collection. We therefore recommend that acoustic indices are calculated across a range of frequency bins and temporal periods in any study using acoustic index values to characterise and identify land use.

The impact of signal masking and the benefits of using narrower time–frequency bins to avoid it are equally apparent when correlating acoustic indices with biodiversity metrics. However, despite the increased fidelity of the correlations, the use of single acoustic indices as direct proxies for biodiversity indicator metrics is still problematic.

While we found the predicted positive correlations between diversity, richness and the BI at the most relevant TFBs, we found a negative correlation between the Acoustic Complexity Index at dawn with bird species richness and abundance. This contrasts with other similar studies in comparable habitats that found positive relationships (Bradfer-Lawrence et al., 2020; Eldridge et al., 2018; Mitchell et al., 2018). However, Mitchell et al. (2020) found high Acoustic Complexity values in oil palm plantations where diversity was low, and noted that the significant relationships they found were within habitat types, but not across different habitats. Furthermore, the complex mechanisms determining abundance and species richness in tropical forests remain poorly understood, particularly in relation to the impacts of disturbance (Barlow et al., 2016, Terborgh et al., 1990). It is possible that idiosyncratic responses of single or a few taxa to disturbance could create such a negative correlation (Moura et al., 2016), especially if the taxa are acoustically dominant. In general, the strongest correlations we found were with total encounters and MDS1—metrics that would only be of ecological interest if the underpinning species were well-understood, requiring extensive manual surveys and undermining the purpose of acoustic indices. Despite this, the strong positive correlation between BI and dawn bird species richness and diversity in the day at 0.3–4 kHz is interesting. It is plausible that this time–frequency bin contains the least vocalisation from non-target taxa, insects sonify predominantly around >4 kHz and after the dawn chorusing of acoustically dominant vertebrates, particularly red-handed howler monkey Alouatta belzebul (Sekulic, 1982). Furthermore, it is after the end of the bird dawn chorus, during which it is possible that intense vocal activity of a few species may mask underlying richness and diversity.

We have deliberately chosen to use subjective frequency bins determined by a priori knowledge of acoustic space use in our study system, to demonstrate both the wide applicability of this method, and that frequency bin selection need not be onerous to generate substantial benefits. However, choosing narrower or different frequency bins and time periods based on prior quantification of acoustic space use could provide substantial further benefits in understanding the effects of signal masking on correlations. Several existing methods exist to do so, either comprehensively through the multiscalar fractal approach (Monacchi & Farina, 2019), or more broadly using measures of acoustic space use or biophonic density (Aide et al., 2017; Eldridge et al., 2018). Quantifying TFB dominance by even broad acoustic clades could be highly informative and could provide quantifiable data on the relative effect size of the impact of disturbance types on those clades. Additionally, variation in the granularity of TFBs may well-reveal further unknown ecological patterns. While we have focused primarily on masking in the frequency domain, and across the diel cycle in the temporal domain, it is entirely plausible that analysis of acoustic indices at both greater and finer temporal scales, and broad frequency ranges, could reveal other patterns. For instance, within dawn choruses where we already know bird species can hold very specific temporal niches in the tropics (Fjeldså et al., 2020), or across seasonal scales such as the winter midday chorus in temperate forests (Farina & Ceraulo, 2017).

We found that acoustic indices are sensitive to soundscapes modified by habitat disturbance and can therefore be highly costeffective tools for assessing forest condition and monitoring changes in conservation value in response to management interventions or other environmental changes. Acoustic indices are however highly susceptible to signal masking, where divergent responses across temporal and frequency spectrums are masked by calculating indices at inappropriate scales. We therefore recommend that acoustic indices are calculated either at a range of time and frequency bins when used to characterise a landscape, or a narrow bin predetermined by a priori ecological understanding of the soundscape when used as a proxy for the biodiversity of a specific taxonomic group.

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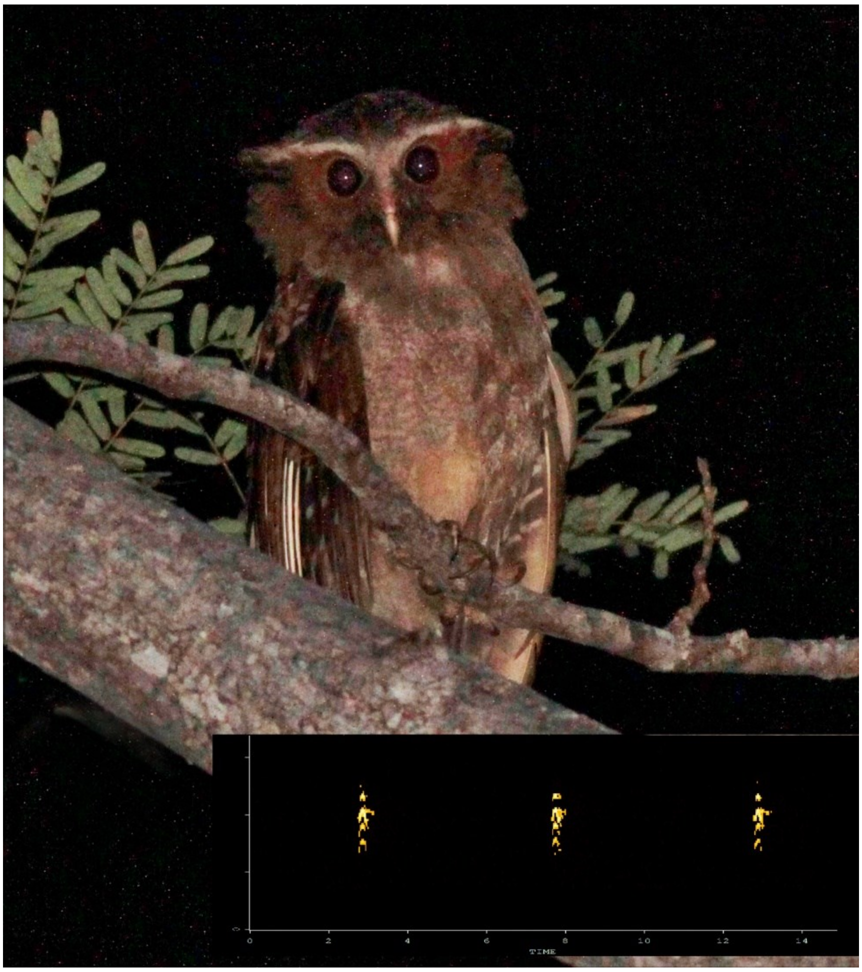
Chapter 5:

The impacts of anthropogenic forest disturbance on nocturnal Amazonian avifauna: a two-step method for acoustic classification of a nocturnal bird community and reduction of spatially heterogeneous error using passive acoustic monitoring in disturbed forest landscapes.



Crested Owl Lophostrix cristata *and a spectrogram of its call from a correctly classified audio file.*

5.1. Abstract

Amazonian forests are threatened by anthropogenic disturbance with selective logging and forest fire, affecting large areas of primary rainforest. Avian responses to disturbance can be variable across species, and the impact of forest disturbance on the regions nocturnal bird species is unknown. We use passive acoustic monitoring (PAM) techniques to study the nocturnal avian community in eastern Amazonia across a degradation gradient.

PAM can be an effective method for monitoring nocturnal species as it allows the collection of large audio datasets, removes logistical constraints in the data collection process, and avoids altering species behaviour. However, analysis of large acoustic datasets is challenging, and fully automated machine-learning processes rarely used. Here, we develop a new two-stage method to fully automate the classification process for ten nocturnal species using random – the first to classify detected sound events to species level, the second to correct for spatially heterogenous error in classification.

We find that the open-source acoustic classification toolbox Tadarida is able to detect and classify sound events with accuracy comparable to other published methods. However, we also show that even for species with good classification accuracy, spatial heterogeneity of false positive errors can be large. Our second contextual classification stage resolves this issue, providing reliable and accurate data from which to make ecological inferences.

None of the target species were most commonly detected in undisturbed forest. For the seven species detected often enough to allow for modelling, four had significantly higher incidence in forest with some type of anthropogenic disturbance and three showed no significant difference between forest classes. There was no significant difference in species richness between undisturbed forest and forest that had been disturbed. The nocturnal avian species considered in this study appear to be robust to at least some degree of disturbance, and may even benefit from increased forest openness associated with some types of disturbance. However, given the intensification of disturbance in the region, it is necessary to study the longer-term impact of repeated wildfires and of more severe forms of disturbance than considered here before drawing conservation conclusions.

5.2. Introduction

Tropical forests face intense anthropogenic pressure from deforestation, fragmentation and disturbance acting in synergy with climate change. Approximately one third of the world’s remaining tropical forest is found in Brazil, and after falling year on year from 2004 until 2012, deforestation rates in the Brazilian Amazon have now started increasing again with an estimated 11,088 km2 of forest cleared in 2020 alone (Silva Junior et al., 2020; TerraBrasilis, 2020). Declines in species richness and shifts in community composition are most acute following habitat conversion to non-forest land-uses and associated fragmentation of remaining forests (Barlow et al., 2007; Lees and Peres, 2006; Moura et al., 2016; Neate-Clegg and Şekercioğlu, 2020; Stouffer, 2020). However, forest disturbance through logging, fires and edge effects is more widespread, and has affected an area greater than that deforested in the Brazilian Amazon to date (Bullock et al., 2020; Matricardi et al., 2020).

Forest disturbance alters species composition by changing forest structure (Barlow et al., 2006, 2002; Burivalova et al., 2015; Haugaasen et al., 2003; Johns, 1991; Thiollay, 1997), doubling the loss of conservation value compared to deforestation alone (Barlow et al., 2016). Yet there is considerable variation in the way species or taxa respond to disturbance (Barlow et al., 2007; Gardner et al., 2009; Lawton et al., 1998; Moura et al., 2016). Within well-studied taxa such as birds, small-bodied and insectivorous species tend to fare worse (Burivalova et al., 2015; Sekercioglu et al., 2002) but it is often necessary to study individual families and even species in order to accurately predict responses to disturbance (Gardner et al., 2008). Furthermore, some tropical birds remain understudied; nocturnal bird species (here *Strigidae, Nyctibidae* and *Caprimulgidae* following Sberze et al., 2010*)* are foremost amongst these, and particularly in Amazonia there is much uncertainty about how they respond to forest disturbance. For example a widely-used classification based on expert-knowledge lists many as having medium or high sensitivity to anthropogenic disturbance (Parker et al., 1996), and a limited number of studies have found differences in occurrence and abundance by forest type (Lloyd, 2003), forest structure (Barros and Cintra, 2009; Esclarski and Cintra, 2014), altitude (Walter et al., 2017) and habitat fragmentation (Claudino et al., 2018; Walter et al., 2017). However, this contrasts with a study from central Amazonian that suggests a low degree of sensitivity: primary and secondary forest showed similar species richness of nocturnal species, and of six focal species only White-winged Potoo *Nyctibius leucopterus* avoided secondary growth (Sberze et al., 2010). These contrasting findings indicate a need for further work to understand the response to disturbance of nocturnal Amazonian birds which occupy a unique diel activity niche, and elevated trophic positions which may mean they have disproportionately important ecological roles (Sberze et al., 2010), and as predominantly sedentary species at low elevation, are potentially particularly vulnerable to climate change (Sekercioglu, 2010).

Surveying tropical forests present a range of logistical challenges and safety concerns even by day, with nocturnal fieldwork being especially challenging. Almost all studies of nocturnal birds in tropical forests have been conducted using traditional field survey methods such as walked line transects, which limit the number of spatial and temporal survey repetitions (Lloyd, 2003; Sberze et al., 2010).Such traditional surveys often fail to detect species when playback is not used (Barros and Cintra, 2009), a method which can significantly alter behaviour and space use by drawing birds long-distances towards the acoustic lure (Zuberogoitia et al., 2020). Passive acoustic monitoring (hereafter PAM) techniques resolve many of these issues, by allowing surveying to be conducted without affecting behaviour, and over a long enough duration that false negatives can be reduced (Darras et al., 2019; Gibb et al., 2019). PAM, coupled with automated classification algorithms, has been successfully used in North America to provide novel insights into the behaviour and ecological niches of nocturnal species (e.g. Knight et al., 2017; Ruff et al., 2020; Shonfield et al., 2018). The only Amazonian study using such methods that we are aware of - Ovaskainen et al., (2018) was conducted at the same study site as Sberze et al., (2010) and reconfirmed their findings. However, no PAM study in the Amazon has assessed nocturnal species responses to some of the most spatially extensive disturbance types (logging and fire) that may eventually impact much of the basin’s remaining forests under pessimistic scenarios of climate and land use change (Asner et al., 1999; Fonseca et al., 2019; Matricardi et al., 2020, 2013).

Despite the advances promised by PAM, automated classification approaches available through user-friendly software platforms (e.g. those listed in Table 4 of Priyadarshani et al., (2018)) have often required a large amount of post-classification validation, which can be very time-consuming (Campos-Cerqueira and Aide, 2016; Knight et al., 2017; Metcalf et al., 2019). Furthermore, when false positives are not equally distributed across survey points, they can skew ecological interpretations, an issue that has only recently been highlighted in the ecological literature (Balantic and Donovan, 2019; Chambert et al., 2018a, 2018b; Clement, 2016; Louvrier et al., 2019; Stolen et al., 2019; Wright et al., 2020), and has yet to be addressed in avian PAM monitoring. For instance, classification error could be high at ecotones where replacement species with similar vocalizations may overlap, potentially introducing classifier bias.

Here, we address two key knowledge gaps relating to nocturnal species and automated detection. First, we test a method using two-step random forest classification, to produce an initial classification with high accuracy and then to correct for heterogeneity of false positives. Secondly, we assess the responses of ten focal nocturnal species (four species of owl, three potoos and three nightjars) in a human-modified landscape.

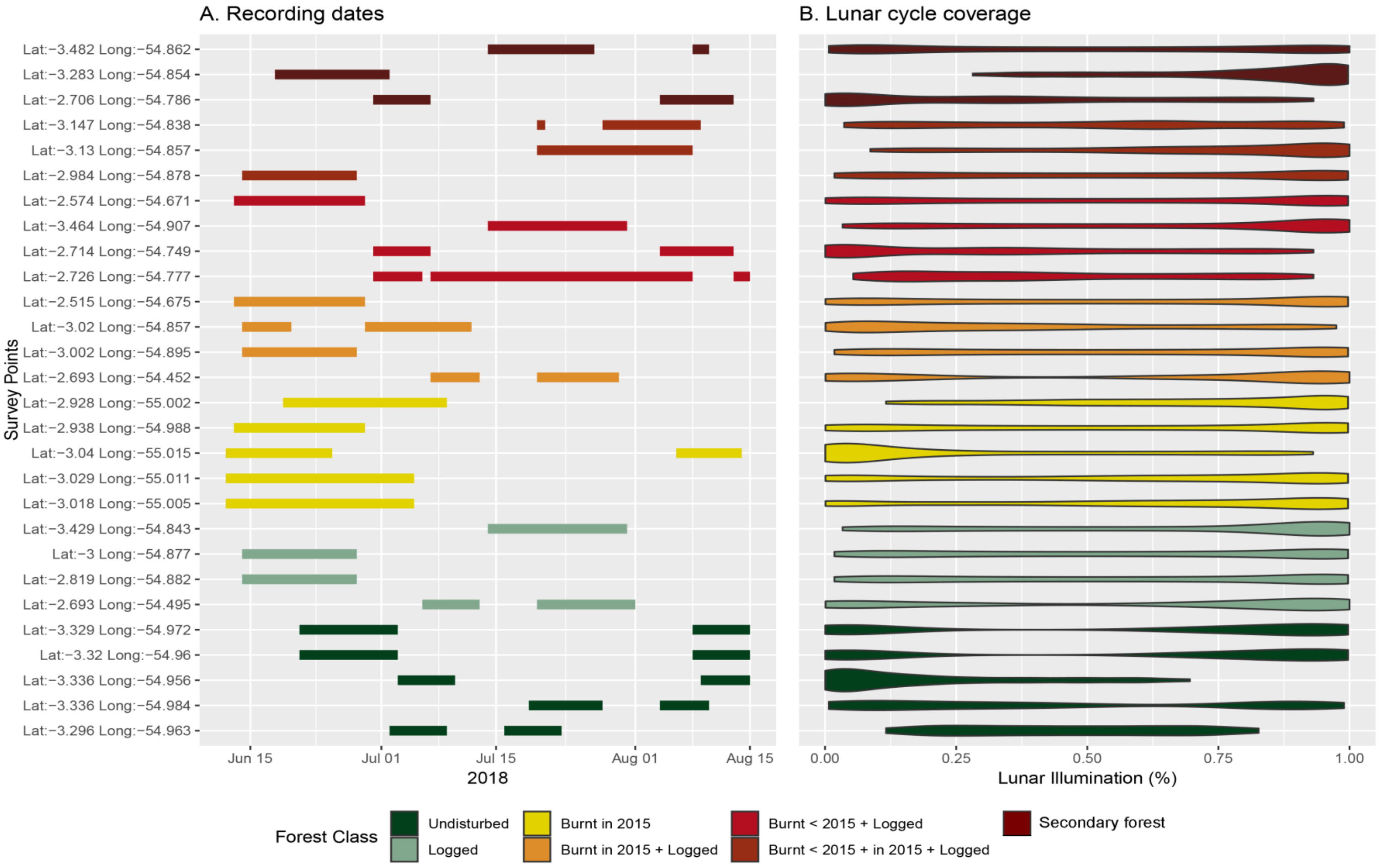
5.3. Materials and Methods

5.3.1. Study site and data collection

Our study area covers approximately 10,000 km^2 of the eastern Brazilian Amazon in the municipalities of Santarém, Belterra, and Mojuí dos Campos (latitude ~ -3.046, longitude -54.947 WGS 84), hereafter ‘Santarém’ in the Brazilian state of Pará. We collected acoustic data from survey points halfway along 29 survey transects maintained by the Sustainable Amazon Network (Gardner et al., 2013; RAS, 2020). Transects have a minimum separation of 2 km to minimize spatial dependence, and are located in terra firme rain forest across an anthropogenic disturbance gradient comprising seven classes; undisturbed primary forests (n=5), primary forests that has been selectively logged (n=4), primary forest which have been logged and burnt prior to 2015 (n=4), primary forest burnt in 2015-2016 (n=5), logged primary forest burnt in 2015-2016 (n=5), and logged primary forest burnt prior to 2015 and burnt again in 2015-2016 (n=3) and secondary forest (n=3) here defined as forests recovering from historical clear-cutting following Putz and Redford, (2010).

We collected acoustic and ecological variables at each transect. All recordings forming the main acoustic dataset were made between 12 June and 16 August 2018 using Frontier Labs Bioacoustic Recording Units (Frontier Labs, 2015). Recordings at each survey point were made over one or two recording periods to allow the best possible lunar coverage that logistical limitations would allow, with each recording period varying in length between 3 and 22 days. A minimum of 13 days were surveyed at each location. Full details of recording periods, equipment and protocols for each location are given in Figure 5.1 and Appendix S5.1.

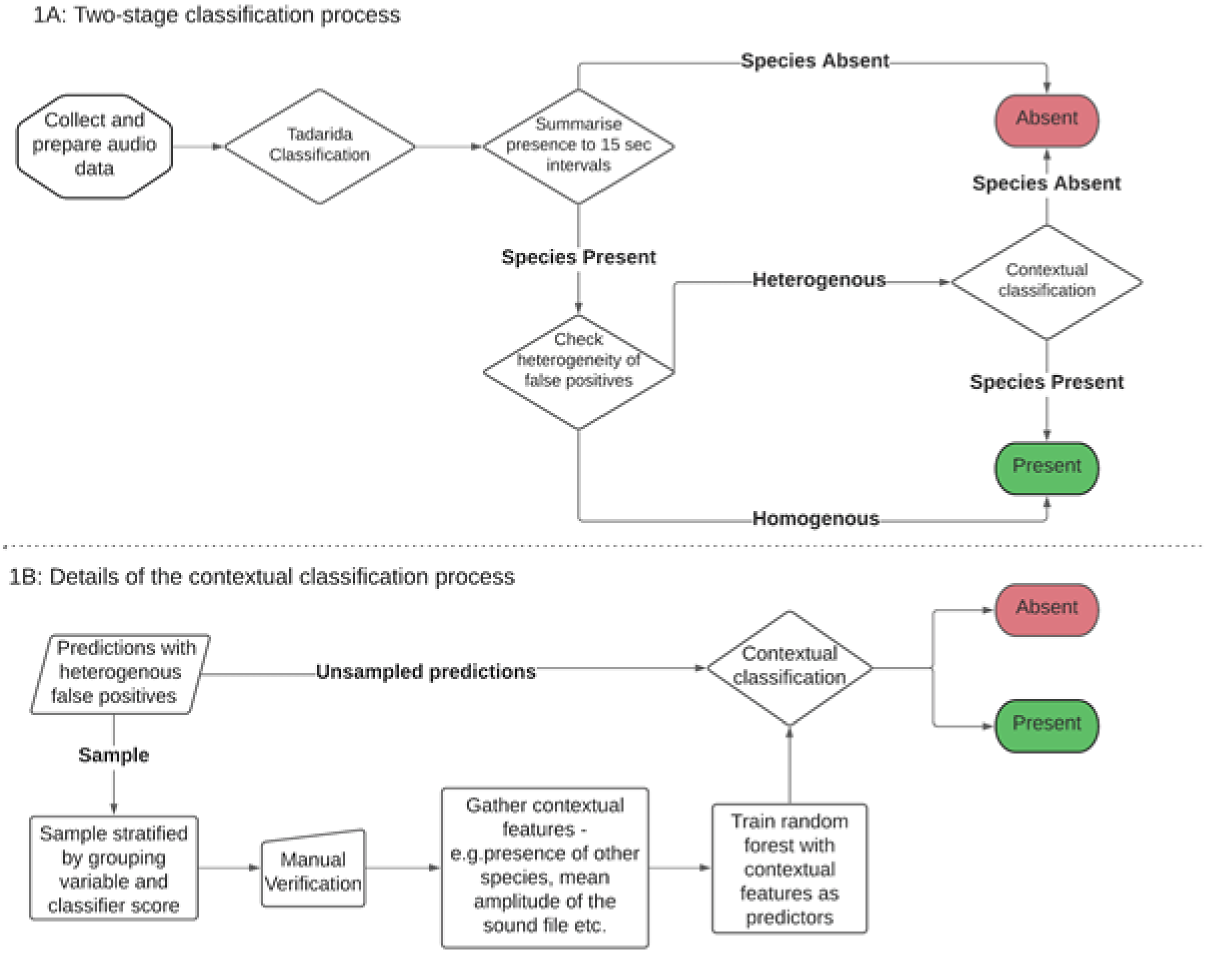
Figure 5.1. *A. Recording periods per transect. B. Violin plot of the survey coverage of the lunar cycle by transect. The thickness of the bars represent proportion of coverage. Lunar illumination is from zero (no moon) to one (full moon).*



Automated classification

Tadarida (Bas et al., 2017) is an open-source toolbox requiring limited post-classification validation that has been shown to be effective at classifying various European species of insects and mammals (Barré et al., 2019; Newson et al., 2017). Tadarida first detects sound events using an hysteresis function, extracts 269 acoustic features (e.g. minimum and maximum frequency, peak frequency, duration) and facilitates labelling of features for use as training data in a random forest classifier (see Bas et al., 2017 for full details). We used Tadarida to build a classifier in R (R Core Team, 2020) for 59 common sonotypes identified in our training data set, comprising birds, amphibians, reptiles, mammals and several other sources of noise. We used labelled data from our own training set, as well as recordings from online archives (Amphibian Survival Alliance, www.amphibians.org; Emmons et al., 1997; Macaulay Library, www.macaulaylibrary.org; Marantz et al., 2006; xeno-canto, https://www.xeno-canto.org) and augmented recordings by adding rain noise to manipulate the signal-to-noise-ratio. Details of the training dataset and labelling process are in Appendix S5.2. Once the classifier was built, we extracted the out-of-bag scores to assess performance. Out-of-bag scores were stratified by survey point and date for recordings from our own monitoring and by unique recording for recordings from online databases, in order to limit over-training. Tadarida produces a confidence score for every class in the training data (n=59) for every sound event classified, so for accuracy metrics we treated the class with the maximum score as the predicted class. We calculated commonly used accuracy metrics for classification; Precision, Recall, area-under-the-curve (AUC) for Precision/Recall and Reciever Operating Curves, Balanced Accuracy and F1 Score, in standard manner following Fielding and Bell (1997), using the ‘caret’ package (Kuhn, 2020).

Figure 5.2. *Workflow for two-stage classification.*



We intended to use every nocturnal species that we detected from the families *Strigidae, Nyctibidae* and *Caprimulgidae*, however it was apparent from early trials that we were unable to find enough training data for the calls of Tropical Screech-owl *Megascops choliba,* Long-tailed Potoo *Nyctibius aethereus* or Blackish Nightjar *Nyctipolus nigrescens* for the classifier to accurately classify these species, so they were not considered as target species. Black-banded Owl *Strix huhula* vocalisations were common in the data, but appeared to show huge variation in all call types, forming a continuum of calls that at the extremes we struggled to distinguish from a range of species including *M. usta, N. aethereus* and Mottled Owl *Strix virgata*, despite consulting a range of regional experts. An additional consequence was that *S. virgata* was suspected to be present but not confirmed in the dataset. Consequently, we were left with ten target species; Southern Tawny-bellied Screech-owl *Megascops usta,* Crested Owl *Lophostrix cristata,* Spectacled Owl *Pulsatrix perspicillata,* Amazonian Pygmy-owl *Glaucidium hardyi,* Great Potoo *Nyctibius* *grandis,* Common Potoo *Nytibius griseus,* White-winged Potoo *Nyctibius leucopterus,* Ocellated Poorwill *Nyctihprynus ocellatus,* Silky-tailed Nightjar *Antrostomus sericocaudatus* and Common Pauraque *Nyctidromus albicollis*. Of these, *N. griseus* and *N. albicollis* are commonly associated with open areas or clearings and tolerant of anthropogenic disturbance (Guilherme and Lima, 2020; Kirwan, 2009; Voudouris, 2020), whilst the others are considered forest species (Adams, 2020; Cleere and Kirwan, 2020; Cohn-Haft, 2020; Holt et al., 2020a, 2020b, 2020c; Schulenberg, 2020; Wilkinson, 2020) with medium or high sensitivity to anthropogenic disturbance (Parker III et al., 1996). To overcome the issue of multiclass classification in which only a small number of the classes were of interest, we calculated binary confusion matrices and classification scores for each of the ten target species. We then used the Tadarida random forest to classify all of the detected sound events from the entire dataset for all 59 classes, and summarised species presence of our ten target species by 15 s sound file.

5.3.2. Contextual Classification

To assess if heterogeneity of false positive error occurred in the Tadarida classification results we took a random sample of files (n=2900) in which Tadarida had classified the target species as present. We stratified the sample, taking 100 sound files from each survey location, further stratified into quintiles of confidence score from zero to 100. When there were not enough samples within a quintile, which occurred mostly at high confidence ranges, additional samples were taken randomly. We manually checked for vocalisations of the target species in each sampled file and calculated the specificity of the classifier for each species at each survey location. We used the variance of the specificity across locations to assess how severe heterogeneity of false positive error was. For the purposes of consistency in this study, we treated all species as having heterogeneous false positive error and built contextual classifiers for each species.

To rectify heterogeneity of error, we used the manually assessed samples as training data for a contextual classifier. We hypothesized that providing the classifier with more ecological context across differing timescales, the accuracy would improve. We therefore built individual contextual classifiers for each of our ten target species. As we were primarily concerned with rectifying problems with precision, we designed the contextual classifier to operate only on those 15 s files already classified by Tadarida as having a target species present. From each manually checked 15 s file, we calculated a series of variables to be used to train a new random forest. This included some environmental data about each 15 s file - the 'rainQ2' and 'rain_min' prediction of rainfall from the hardRain package (Metcalf et al., 2020) and root mean square of the sound envelope utilising the seewave package (Sueur et al., 2008) as measures of background noise levels, as well as time and date. We also used Tadarida scores as predictors - the maximum Tadarida confidence score of the target species, and for every class in the Tadarida classifier the minimum, maximum, mean, 90th and 95th quantile and summed confidence score, the ratio of classified sound events to the target species, and the three species most commonly detected in the file. In addition, we calculated the same confidence score variables for over both ten minute and one hour periods centred on the manually assessed file. For the latter, we also calculated the 98th percentile of the classifier score for each class. This gave us a feature set of 716 predictors for each target species.

We used this feature set to build a distributed random forest classifier in the H2O package (LeDell et al., 2020), first splitting the data into training (70%) and test (30%) datasets. Although random forests can handle a large number of predictor variables well, as an additional precaution against overtraining we initially built a model using the whole feature set, used the H2O variable importance function to ascertain relative variable importance, and rebuilt a final model with variables of an importance greater than 0.05. We then ran the contextual classifier on the test dataset. We used the confidence scores from the test dataset to determine an optimum threshold (Appendix S5.3) to prevent false positive occurrences whilst minimizing heterogeneity of error. We applied the same threshold selection process to the Tadarida confidence scores to test if the contextual classifier improved classification performance.

Every 15 second file in which the Tadarida classifier had predicted the presence of a target species was then reclassified with a contextual classifier. All files in which the confidence score was above the selected optimal threshold were designated as having the target species present, whilst those with confidence scores below the threshold were re-designated as absent. As the classification process prioritised precision over recall, presences were summarized to ten-minute intervals, also reducing temporal autocorrelation. Finally, we calculated the proportion of ten minute intervals each species was present in per night, having first removed all intervals that contained 15 s or more of heavy rain.

5.3.3. Impacts of Forest Disturbance

We calculated detected species richness of target species at each survey point, both with all detections and only sites with five or more detections to account for false presences introduced by the automated detection process. We tested for differences in species richness between forest classes using a Kruskal-Wallis test (Kruskal and Wallis, 1952). To understand the factors affecting species presence we built hierarchical mixed models using the glmmTMB package (version 1.0.2.1, Brooks et al., 2017) for each of our target species. We used the proportion of ten minute intervals in which the target species were detected as a response variable for logistic regression (link = log). Forest class and lunar illumination were used as predictors, and survey point as a random effect to control for spatial auto-correlation. Lunar illumination was calculated at midnight of each night surveyed using the lunar package in R (Lazaridis, 2014). We used the number of ten-minute intervals in each night as model weights.

As the data contains a high proportion of absences (zeroes), and a variety of probability distribution families can be used for proportional response data, we trialled five error structures (binomial, beta-binomial, negative binomial, poisson and hurdle models) and four zero-inflation parameters, following Brooks et al., (2017) to determine the most appropriate. We excluded three species from further analysis; *N. griseus, N. leucopterus* and *N. ocellatus* as we were unable to find a model with a good fit, potentially due to the low number of detections and high number of survey points at which they were completely absent. The best model for five species used a betabinomial error structure, with a single zero inflation parameter applied to all observations. As this error structure was second best for the remaining two species, and by less than two AIC units (Burnham and Anderson 2002), we used it for all species. Full AIC tables are in Appendix S5.4, and model diagnostic plots for the selected models in Appendix S5.5. Finally, we contrasted the effect of forest classes using multiple comparisons of group means with the Tukey test in the multcomp package (Hothorn et al., 2008).

5.4. Results

5.4.1. Acoustic Classification

The Tadarida classifier produced out-of-bag classification results with a mean balanced accuracy of 0.938 across all species, seven species had a balanced accuracy of 0.95 or greater (Table 5.1), whilst only *N. leucopterus* performed relatively poorly at 0.76. More importantly at a stage at which no threshold had been applied, recall was above 0.9 for all target species except *N. leucopterus.* Full out-of-bag accuracy metrics for target and non-target species are available in Appendices 6 and 7. Precision/recall curves are shown in the top row of Figure 5.3. However, out-of-bag results should be treated with caution as they contain many files from online archives, which may have better or worse classification results than the files from our own recordings.

Table 5.1. *Stratified out-of-bag accuracy metrics for ten target species from the Tadarida classifier (n=314,344).*

Species	**Precision**	**Recall**	**P/R AUC**	**ROC AUC**	**Balanced Accuracy**	**F1**
Megascops usta	0.383	0.969	0.869	0.981	0.959	0.549
Lophostrix cristata	0.407	0.978	0.955	0.988	0.973	0.574
Pulsatrix perspicillata	0.447	1	0.896	1	0.99	0.618
Glaucidium hardyi	0.372	0.944	0.866	0.968	0.95	0.533
Nyctibius grandis	0.425	0.892	0.881	0.942	0.925	0.576
Nyctibius griseus	0.771	0.942	0.958	0.967	0.94	0.848
Nyctibius leucopterus	0.318	0.541	0.416	0.763	0.76	0.4
Nyctiphrynus ocellatus	0.527	0.99	0.978	0.995	0.988	0.688
Antrostomus sericocaudatus	0.321	0.991	0.948	0.993	0.957	0.485
Nyctidromus albicollis	0.171	0.935	0.456	0.945	0.942	0.289

The manually-checked verification files (Table 5.2) showed high variance in precision for some species, with the precision variance of the three nightjar species particularly variable in accuracy across locations with *N. ocellatus* having a specificity variance of 0.49. In contrast, owls did not seem so impacted, with *P. perspicillata* the highest with 0.15, but both *M. usta* and *L. cristata* having very low variance of 0.09. All species showed at least one location with precision of 0, which is to be expected, as using scores prior to thresholding is likely to result in only false positives at some sites if the target species do not occur at all of the survey points.

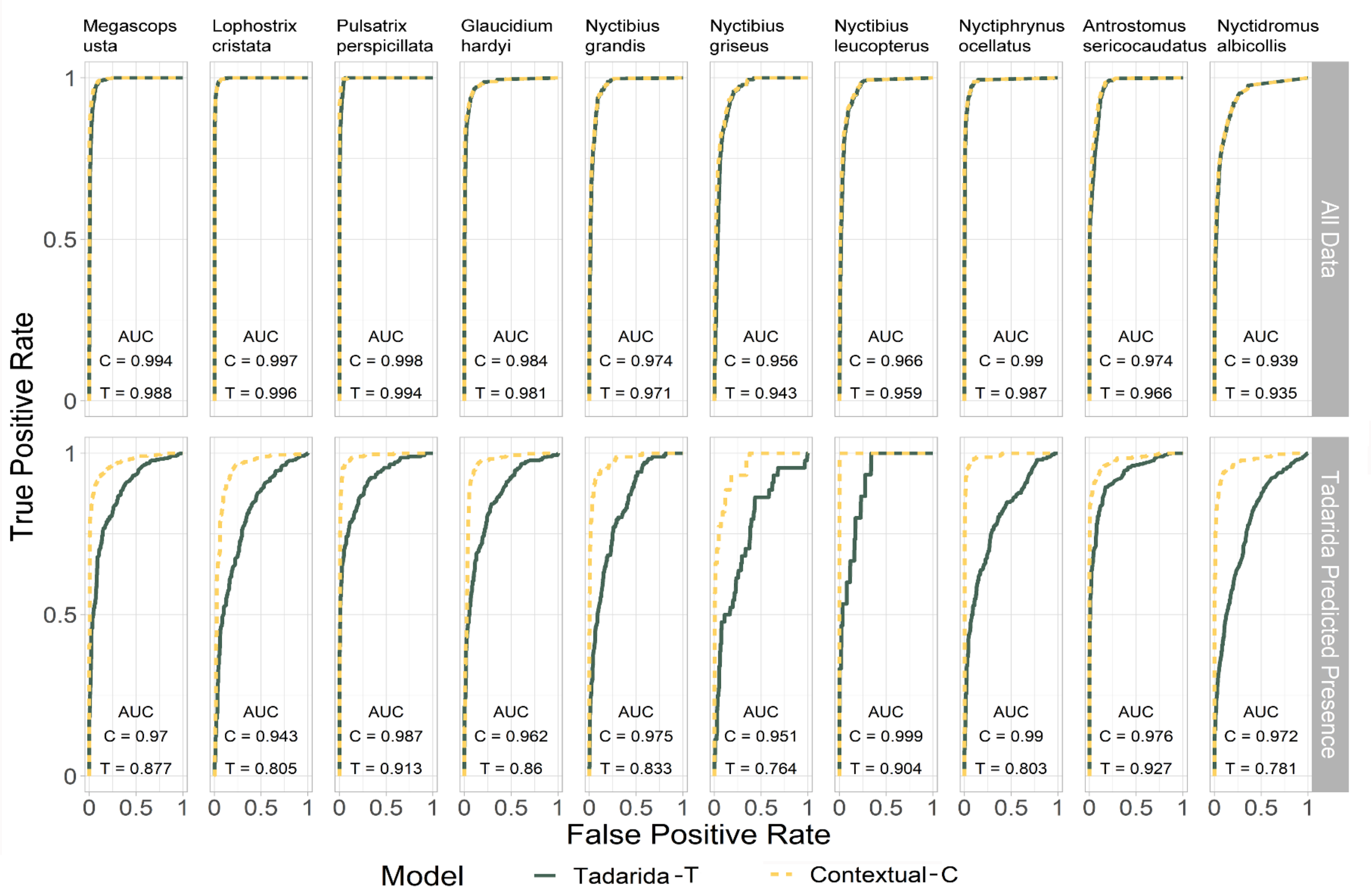
The contextual classifiers without the use of a threshold performed better than the Tadarida classifier for every species (Figure 5.3, bottom row), and with a mean ROC area under the curve (AUC) of 0.972±0.02 (SD), an average increase of 0.13 on the Tadarida results on the same data. It should be noted that all results given for the contextual classifier and the Tadarida classifier pertaining to the test dataset of the manually checked stratified sample are taken from files in which the initial Tadarida classifier has already predicted species presence – so exclude the false negatives from the original Tadarida classification. Across all candidate thresholds, the contextual classifiers had a mean variance of precision of 0.017 ±0.027 (SD) compared to 0.109±0.103(SD) for the Tadarida classifier

Table 5.2. *Variance of precision across survey locations.*

Species		*Megascops usta*	*Lophostrix cristata*	*Pulsatrix perspicillata*	*Glaucidium hardyi*	*Nyctibius grandis*	*Nyctibius griseus*	*Nyctibius leucopterus*	*Nyctiphrynus ocellatus*	*Antrostomus sericocaudatus*	*Nyctidromus albicollis*
Precision	**Minimum**	0	0	0	0	0	0	0	0	0	0
	Maximum	0.814	0.954	0.68	0.935	0.571	0.524	0.408	0.925	0.871	0.842
	Mean*	0.497	0.684	0.296	0.557	0.169	0.055	0.017	0.186	0.364	0.147
	Variance	0.092	0.089	0.148	0.14	0.183	0.241	0.345	0.491	0.291	0.366

*Mean precision is not balanced by the number of detections at each location.

Figure 5.3. Top row: *Precision/Recall curves created from out-of-bag scores per 15 s file for the Tadarida classification model, treating each target species as a binary classification.* ***Bottom row:*** *A comparison of receiver-operating-characteristic (ROC) curves for the Tadarida classifier and Contextual classifier, using a manually checked stratified sample of files in which the Tadarida classifier had predicted the presence of a target species.*



After optimal thresholds are applied, the contextual classifier has very low variance of precision (Table 5.3), with a mean of just 0.006 ±0.016 (SD). *L. cristata* had the lowest variance with the Tadarida classifier, but has the highest variance with the contextual classifier although it is still almost half the Tadarida score at 0.051. Penalising false positives and variance of precision heavily whilst optimising thresholds has come at some cost to overall accuracy, with the ROC AUC declining to a mean of 0.881±0.086. However, six species still had AUC scores of over 0.9 and only *N. griseus* had a score that could be considered poor at 0.648, driven by low recall of just 0.295. When adjusted for the estimated number of calls missed by the initial Tadarida classification, just *N. griseus* and *N. leucopterus* had recall below 0.5.

Table 5.3. *Accuracy metrics for contextual classifiers with optimal confidence score thresholds, when applied to a manually checked stratified sample of files in which the Tadarida classifier had predicted the presence of the target species.*

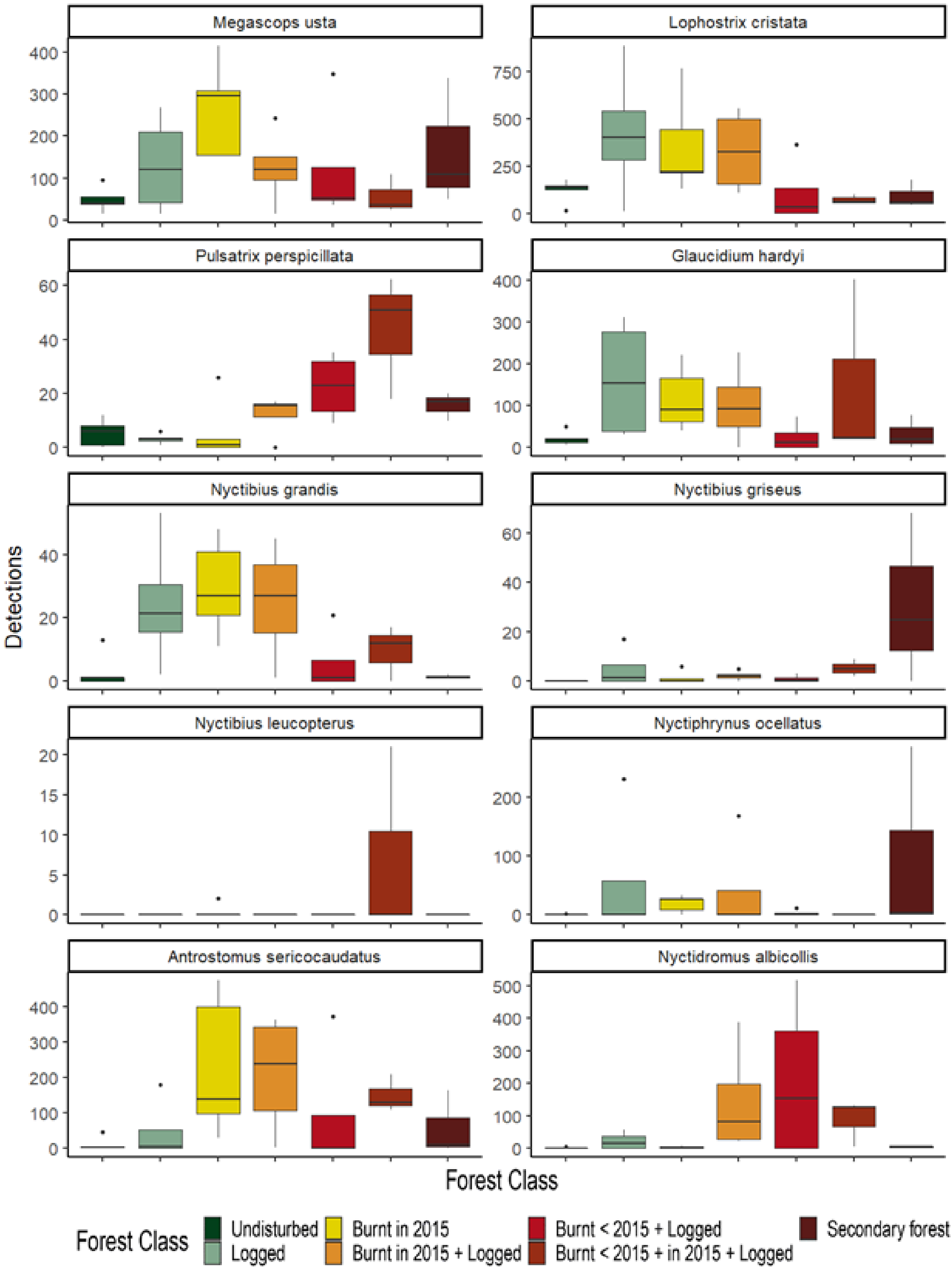
Species	Megascops usta	Lophostrix cristata	Pulsatrix perspicillata	Glaucidium hardyi	Nyctibius grandis	Nyctibius griseus	Nyctibius leucopterus	Nyctiphrynus ocellatus	Antrostomus sericocaudatus	Nyctidromus albicollis
Recall	0.86	0.872	0.876	0.881	0.69	0.295	0.867	0.848	0.838	0.813
Variance of Recall	0.034	0.007	0.075	0.014	0.115	0.311	0.001	0.024	0.098	0.18
Precision	0.972	0.956	0.97	0.961	0.967	1	0.929	0.99	0.991	0.925
Variance of Precision	0.002	0.051	0.003	0.002	0.002	0	0	0	0	0.004
F1	0.913	0.912	0.921	0.919	0.805	0.456	0.897	0.914	0.908	0.865
ROC AUC	0.916	0.889	0.931	0.916	0.842	0.648	0.933	0.923	0.916	0.898
Balanced Accuracy	0.914	0.882	0.949	0.91	0.933	0.964	0.996	0.954	0.923	0.947
Recall - Adjusted	0.833	0.853	0.876	0.832	0.615	0.278	0.469	0.84	0.831	0.76

Accuracy metrics per Field and Bell (1997) except Variance of Recall and Precision.

5.4.2. Impacts of Forest Disturbance

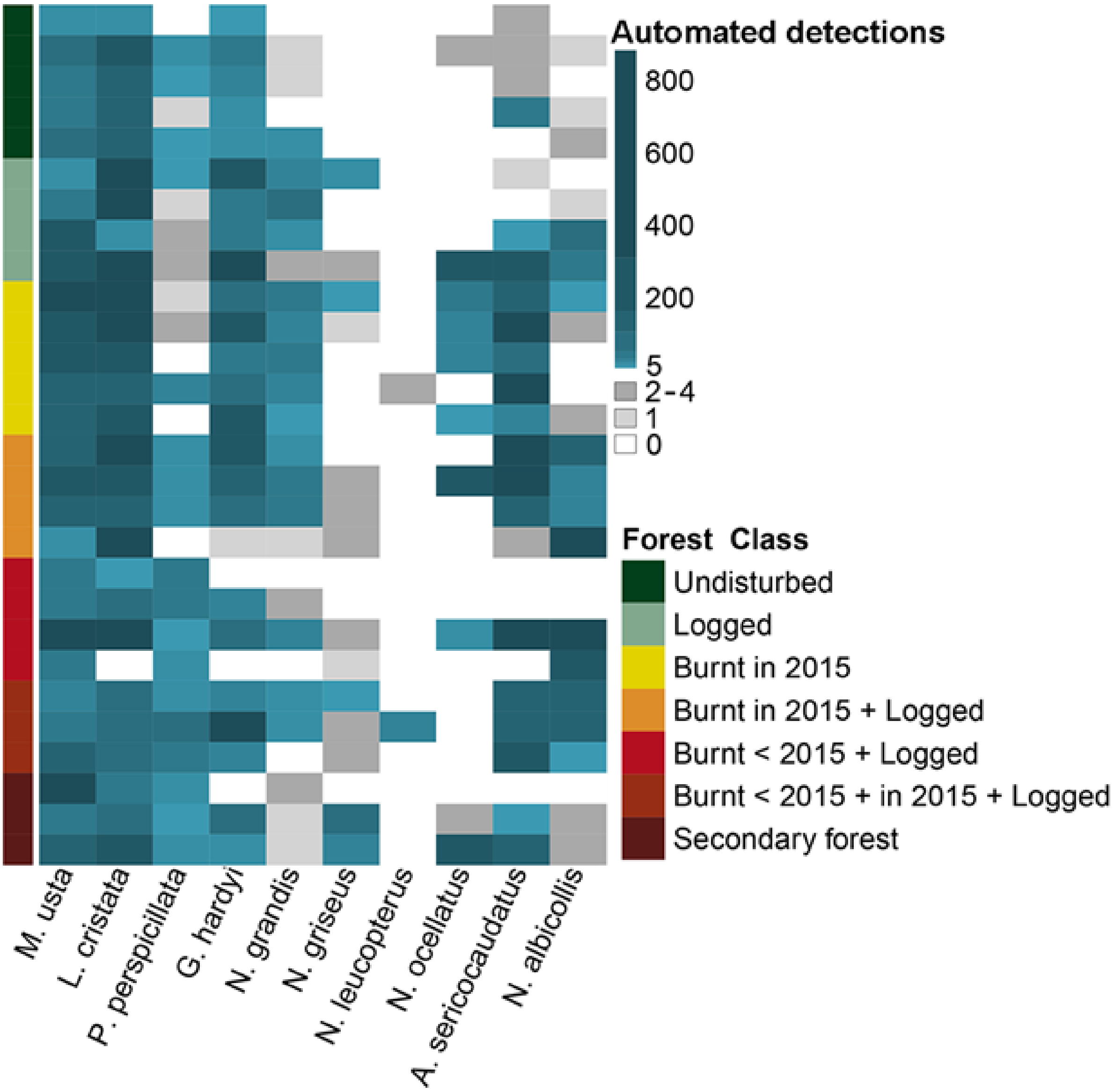
There was wide variation in how often each species was detected (Fig 5.4). *L. cristata* was detected the most often, present in 6,366 ten-minute intervals - 24% of the total number of intervals. *M. usta,* and *A. sericocaudatus* were both detected in 3,746 and 3,217 intervals respectively and *G. hardyi* 2,403. All the other species were detected in fewer than 1,000 intervals and *N. leucopterus* was the only species with fewer than 100 detections, with just 23 detections at only two survey points.

Figure 5.4. *Classifier detections by forest class. Note the variable y-axis scale to emphasize the number of detections by forest class, rather than rate of detection between species.*



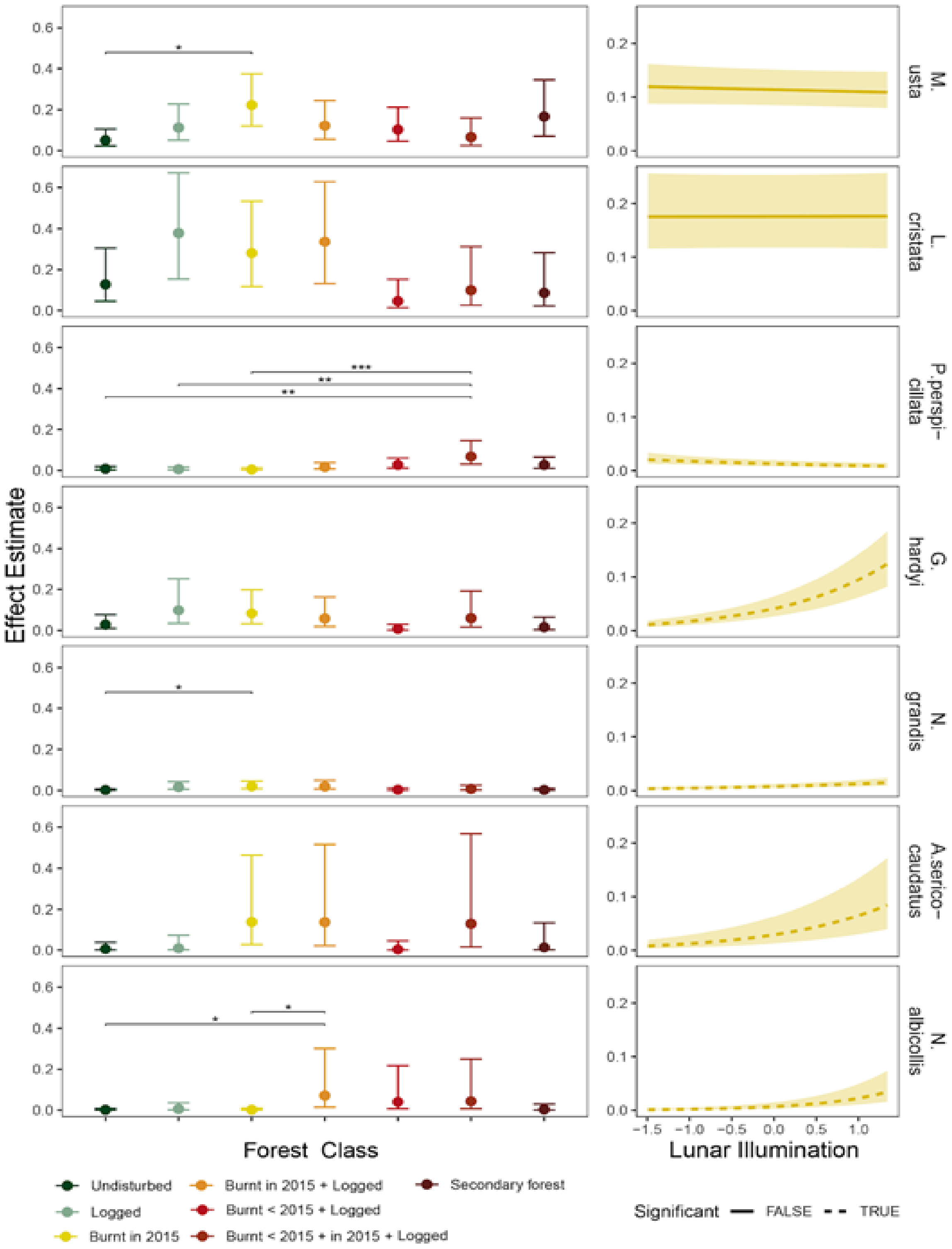
There were no significant differences in species richness between the forest classes, when calculated with all detections and when presence at survey points with fewer than five detections was discounted to limit the risk of false presence (Fig.5.5). Of all the forest classes, undisturbed forest had the second lowest richness of focal species, with a mean of just 6±1.4 (SD) species present. *N. griseus* and *N. leucopterus* were never recorded in undisturbed forest, whilst *N. ocellatus* was recorded at a single undisturbed survey point, and *N. albicollis* recorded only very rarely (Fig.5.3). Forest that was burnt both in and prior to 2015 and was also logged had the highest species richness with a mean of 8±1.0 (SD), and only *N. ocellatus* was undetected in this forest class. Forest that was burnt prior to 2015 and logged had the lowest mean species richness, 5.3±2.6, with two of the four survey points in the forest class recording just three species, with *M .usta* and *P. perspicillata* common between them. Nor did undisturbed forest have the highest encounter rate for any species (Fig 5.3., Appendix S5.8). *L. cristata* and *G. hardyi* were most common in logged forest, *N. ocellatus* was most commonly encountered in secondary forest and the remaining species were most common in forest classes that had been burnt at least once.

Figure 5.5. *Community matrix of bird species by survey point. Intensity of colour represents the number of detections by the contextual classifier. Survey points with few detections are shown in grey as there is a higher chance of false presence.*



All of the species we studied were more commonly detected in forest that had undergone some form of disturbance than in nominally undisturbed forest, although we did not find any universal patterns in the focal species response to disturbance. Of the species we were able to model, two were most commonly detected in logged forest, two in recently burnt forest, two in recently burnt and logged forest and one in forest that had been burnt before 2015, in 2015 and had been logged (Fig. 5.6). Of the three species we were unable to model, the raw detections suggested that two were commonest in secondary forest and one in forest that had been burnt before 2015, in 2015 and had been logged (Fig. 5.4). Four species showed a significant and positive response to lunar illumination which was particularly strong for *G. hardyi* and *A. sericocaudatus*. *P. perspicillata* was detected significantly less often with higher lunar illumination and two owl species *M. usta* and *L. cristata* did not show a significant response to illumination. Although we were unable to fit models for *N. griseus* and *N. leucopterus,* a similar very strong positive trend was apparent in the detections for these species too, particularly in the latter species in which calls were only detected on nights with >90% lunar illumination.

Figure 5.6. *Estimates of fixed effects on the encounter rate for seven focal species. Forest classes shown to have significantly different means using multiple comparisons of group means with the Tukey test are marked with horizontal bars.*



5.5. Discussion

5.5.1. Classification accuracy

In combination, Tadarida and the contextual classifier produce classification accuracy metrics comparable to many published results (Aide et al., 2013; Bravo et al., 2017; Cardona et al., 2021; Goyette et al., 2011; Ovaskainen et al., 2018; Pérez-Granados and Schuchmann, 2020a; Ruff et al., 2020), although is not as accurate as some of the cutting-edge deep-learning techniques (Kahl et al., 2020; Zhong et al., 2020). The Tadarida classification had an unweighted mean balanced accuracy of 94% and unweighted mean recall of 92% for the target species. The specificity of Tadarida was particularly low compared to comparable classification approaches, but this is at least in part because we have applied a threshold to the confidence scores at the stage Tadarida accuracy scores are calculated. Importantly, we found that even species showing excellent scores in standard accuracy metrics such as ROC AUC, precision/recall AUC and balanced accuracy, could exhibit up to 49% variance in classification precision across survey points.

This heterogeneity of error is rarely tested for in ecoacoustic studies using automated classification (Wright et al., 2020) and could potentially confound ecological interpretation. Although we did not explicitly test to see if this effect diminished with increasing classification confidence score (i.e. whether it could be resolved by simply applying a threshold value to the classification scores), our own informal assessments suggested that the problem remained even with stringent thresholds applied. There is no reason to think that this problem should be particularly unique to this dataset, or even to random forest classifications, as the underlying causal factors are likely ecological in nature, for instance in this case likely caused by replacement species such as *A. sericocaudatus* and *N. albicollis* meeting at ecotones. We therefore strongly recommend that future studies explicitly test for, and take measures to reduce variance in error across survey locations. By introducing a second contextual classification stage and the second confidence score thresholds, we were able to reduce the variance hugely, with no species having a variance of precision above 0.05, whilst increasing precision to an unweighted mean of 97% and maintaining a balanced accuracy of 94%.

We have not, however, presented accuracy metrics in a standard way, such as those described in Knight et al. (2017), instead relying on out-of-bag scores for the Tadarida classifier. Out-of-bag scores can be very reliable (Breiman, 2001, 1996; Janitza and Hornung, 2018), especially when stratified to match the training data as they are here (Mitchell, 2011). However, in this case ~87% of the training data comes from audio we have augmented, or is from online databases, meaning that the classifier may have different accuracy when it is applied to data solely taken from our PAM recorders. We considered reporting out-of-bag accuracy statistics only from the data from our own recorders and without augmentation, but for a number of species this is heavily biased by the very small sample size - the reason we used the additional data in the first place. Fortunately, we can gain a better insight into the classification performance on PAM collected data through the manually-checked data for the contextual classifier. These data not only shows the vital importance of accounting for spatial variation on error, but also provides a prediction of the classification specificity based entirely on manual validation of data taken from our own PAM recordings.

5.5.2. Vocal activity rate and recall

The manual validation and contextual classifier only applies to files Tadarida has already identified as having a target species presence in, which means that the vast majority of our estimation of the true negative and false negative rate is dependent on out-of-bag scores without further manual verification. This means that there is considerably more uncertainty surrounding our estimated recall rates than the estimated specificity rates. However, summarising presence over ten-minute periods should rectify this issue to a large extent, as recall over a ten-minute period becomes dependent on the classification recall rate of 15 s recordings and species call rate. For example if *N. grandis* calls in more than one 15 s recording within a ten-minute period it should be detected given the adjusted recall of 0.615.

To our knowledge there is very little published data on the call rates of these species, with the exception of (Pérez-Granados and Schuchmann, 2020b), which implies *N. albicollis* call often. Our own experience both in the field and in manually labelling the training data is that when vocalizing, the majority of the species vocalize in bouts of many calls over an extended duration. This entails that overestimation of recall of 15 s files is less problematic as even a very low recall should have enough opportunities to detect at least one vocalisation. The observations of Wilkinson (2009) that *A. sericocaudatus* usually only called only once or twice per evening in the breeding season during a study in Peru were not found to be the case here. Extended periods of repeated calling in quick succession was the norm, and single or double calls in isolation were never noted during the labelling process. An example spectrogram of this behaviour and accompanying audio file is provided in Appendix S5.9. We also found a single nest of *A. sericocaudatus* near the trail to one of our survey points (ML 308449521, eBird checklist S47118789), so think it unlikely that this difference in vocalisation rate was caused by being at different stages in the breeding cycle.

The potoos however were far less prone to calling in quick succession, an observation also found for *N. grandis* and *N. griseus* in the Pantanal (Pérez-Granados and Schuchmann, 2020a), meaning that firstly it was far harder to find enough calls to train an accurate classifier and secondly the impact of low recall is far greater. The low detection rate and subsequent poor model performance of *N. leucopterus* and *N. griseus* are perhaps suggestive that the true recall rate for these species is low enough that it is impacting detection at even the 10 minute interval scale. Conversely, when we examine our results, it suggests that precision is likely greatly underestimated for many species, with 85 survey point absences recorded, with every species being absent from at least one transect, except *M. usta* - which given the minimum of 23,760 files per survey point to classify, is suggestive of a much higher specificity rate than that estimated. Manual examination of enough ten-minute intervals to provide accurate estimates of classifier performance would be so time-consuming as to render the automated classification redundant however, and we believe that in combination the metrics provided here are enough to provide confidence in the ecological veracity of our findings.

5.5.3. Measuring encounter rates

In the absence of being able to estimate density, which remains highly challenging with large datasets in multi-species studies with PAM (Pérez-Granados and Traba, 2021), occupancy-type metrics based on the presence/absence of species are commonly used, and have been adopted in several studies using PAM-derived data (Abrahams and Geary, 2020; Campos-Cerqueira et al., 2021; Campos-Cerqueira and Aide, 2016; Duchac et al., 2020). Whilst variability in detection rates can affect the significance of species response to environmental factors, studies have shown that controlling for detection variability through study design can be as effective (Banks-Leite et al., 2014), especially in studies such as this one whose primary purpose is assessing the effect of environmental factors on species presence, as opposed to estimating occupancy. We believe we have adequately controlled for most variability in detection, distributing survey periods as equally as logistically possible across the lunar cycle (Fig. 5.1), removing periods of extreme weather and including lunar illumination as a fixed effect in the hierarchical logistic regression models, as well as including survey point as a random effect in the model.

We found lunar illumination to have a significant effect on encounter rate for five of our target species, unlike previous multi-taxa studies which found lunar illumination to not have a strong impact on vocalisation (Ovaskainen et al., 2018). This is supported by other studies that also found positive relationships between *M. usta/watsonii, L. cristata, G. hardyi, N. griseus, N. grandis* and *N. albicollis* call rates and lunar illumination (Pérez-Granados and Schuchmann, 2020a, Pérez-Granados and Schuchmann, 2020b, Rodriguez-Bravos, 2017). Only *P. perspicillata* showed a negative response to lunar illumination, matching the responses found elsewhere for that species (Rodriguez-Bravos, 2017). Our findings suggest that optimal surveying for Neotropical avian forest communities should prioritise surveying during the full moon, but would need to include some periods with low illumination to maximise detection probability for all species.

In addition, we have controlled for variation in false positive heterogeneity, something that has rarely been undertaken in occupancy modelling when using automated detection processes (Stolen et al., 2019), meaning that we are confident that the relative differences in encounter rates represent real ecological preferences in habitat use. However, we were unable to control for potential variation in detection distance across forest classes as measuring detection distance is not straightforward across long timescales and multiple species (Darras et al., 2016), and whilst detection distance can strongly influence detection, it is rarely well quantified in large-scale PAM studies. It is not apparent that there are systematic biases in detection distance, and it is not clear what the influence of forest disturbance on detection distance might be, as although there is likely to be higher density understorey blocking sound transmission, the more open canopy may also lead to increased geophony, particularly wind noise.

5.5.4. Impacts of Forest Disturbance

Whilst there were no significant differences in species richness and few in encounter rate, there are some common trends across taxonomic groups that provide valuable insight into the impacts of forest disturbance on nocturnal Amazonian species. Although the differences in species richness were not significant, they follow a pattern of richness suggestive of nocturnal species not being highly sensitive to disturbance, with richness highest in areas with disturbance that can support both most interior forest and some edge or even non-forest species. Unlike diurnal birds in the region (Moura et al., 2016), we did not find any nocturnal species that were highly sensitive to disturbance, indicated by their absence in areas with any level of disturbance, perhaps suggesting that dietary and environmental niches are broader in nocturnal species. However, we cannot rule out that we simply did not include the most disturbance sensitive species in the classifier as they were too rare to be detectable during the manual labelling of training data. Of the species known to be present in the region it is only Long-tailed Potoo *N. aethereus* that this seems plausible for, but we detected this species in burnt forest during the manual labelling process.

The encounter rates also suggest that many nocturnal species are more common in areas with some disturbance. All species were detected by the classifiers in undisturbed forest by the automated classification except *N. griseus* which was not expected in undisturbed habitat, and *N. leucopterus*, which we found to be present at an undisturbed survey point during the manual data labelling process. *N. ocellatus* and *N. albicollis* had very few detections in undisturbed primary forest, and we did not find the latter in undisturbed forest whilst manually labelling training data, suggesting that neither species is regularly found in undisturbed forest. However, all ten species, including the eight species thought to be intolerant to disturbance (Parker III et al., 1996) had higher encounter rates (or raw detections when not modelled) in human-modified forest. This suggests that many nocturnal Amazonian species occur at naturally low densities in undisturbed primary forest, possibly because they are adapted to naturally occurring forest edges such as streams and tree-falls, or because they are limited by food and nest-site availability. These species may then increase in density with forest disturbance and fragmentation, which increases the density of forest edge, of nest site availability through increased standing deadwood and tree snags, or through increased prey availability as generalist small mammal species can become hyper-abundant in human-modified and fragmented forest (Bernard et al., 2009; da Fonseca and Robinson, 1990). This is supported by a study from Indonesian Borneo (Burivalova et al., 2019), which found whilst diurnal soundscape saturation decreased with disturbance, nocturnal soundscape saturation increased. The authors hypothesized it may be caused by an increase in owls, better suited to finding prey in open forests, which appears to be similar to our own findings. We also found an increase in nightjar and potoo species too, perhaps indicating that at least some species of insect prey also increase.

This is most apparent in the significantly higher encounter rates of *M. usta* and *N. grandis* in forest burnt in 2015 compared to undisturbed forest. This pattern is mirrored in the encounter rates of the two species in the other forest classes that could be considered to have intermediate disturbance - logged or burnt only once, although they were not significant. The encounter rates of three other species that were considered to be intolerant to forest disturbance; *L. cristata, G. hardyi,* and *A. sericocaudatus* also showed the same pattern. Although none of the differences were significant, all five of these species exhibited declining encounter rates in at least some of the more severely disturbed forest classes, perhaps indicating that intense disturbance can cause decline. However, all five species were present in the most human-modified forest classes with the exception of *N. grandis* in secondary forest, indicating that these species can continue to persist at least at low levels in heavily disturbed forest and occupy regenerating secondary forests. *N. ocellatus* showed a similar pattern in number of raw detections as opposed to encounter rate, although with a high number of detections in secondary forest, perhaps indicating a preference for dense understory.

There are also three species that have their highest encounter rates or number of detections in more severely human-modified forest; logged and burnt, logged and burnt before and after 2015 and secondary forest. Two of these species, *N. griseus* and *N. albicollis,* are well known for their preference for forest edge habitats and tolerance of anthropogenic disturbance. *N. griseus* detections supported the finding of Sberze et al (2010), showing a strong preference for secondary forest. *N. albicollis,* on the other hand*,* had the highest encounter rates in logged forest that was also burnt in 2015, significantly higher than in undisturbed forest or forest that was burnt in 2015 but hadn’t been logged - and did not show a significant difference between undisturbed and secondary forest*.* The third species, *P. perspicillata* showed a strong preference for forest that had been logged and burnt before and after 2015, with significantly higher encounter rates than in undisturbed, logged or forest burnt in 2015, providing qualitative evidence that this species is more tolerant of disturbance than *L. cristata* (Holt et al., 2020c). The final target species, *N. leucopterus*, lived up to its reputation for elusiveness (Cohn-Haft, 1993), and the automated classification only detected it from two survey points. That neither of these were in undisturbed forest indicates that it is not highly sensitive to forest disturbance. In keeping with Sberze et al., (2010), we did not detect it in secondary forest.

5.5.5. Temporal trends

Although we have treated forest disturbance as discrete classes, in reality forest disturbance in the Amazon is both a gradient and dynamic, with logging and fragmentation increasing vulnerability to fire, and forest once burnt is far more susceptible to being burnt repeatedly. This means that initial indications that species may benefit from disturbance should be treated with caution, as the benefits may be short-lived as disturbance intensifies and forest degrades. Furthermore, even if additional disturbance events can be prevented, human-modified forest remains dynamic as initial dense understory growth is replaced over time by increasingly enclosed canopy. However, the timescales and processes involved in forest recovery in human-modified forest remain poorly understood (Liebsch et al., 2008, Nunes et al., 2021, Sist et al., 2007, Stouffer et al., 2020), as do the impacts this will have on the nocturnal avian community. This highlights the importance of long-term monitoring of forest disturbance in the Amazon, something ecoacoustics is well suited to.

5.6. Conclusions

The use of PAM and automated classification of acoustic data facilitates the collection and analysis of acoustic big data to ascertain patterns of distribution of nocturnal Amazonian species, far in excess of anything logistically feasible using traditional survey methods. We have shown the open-source machine-learning toolbox Tadarida to be useful in producing precise predictions of the presence of vocalisations of a range of bird species, even in acoustically complex environments such as tropical rainforests. However, we have also shown that even ostensibly accurate classifications with balanced accuracy >95% can still exhibit high amounts of variance in error rates, potentially confounding ecological insight if the factors underlying the variance correlate with the ecological factors being studied, as they do here. Contrary to our expectations we found that incidence rates of all species were higher or no different in anthropogenically disturbed forest than in undisturbed forest, albeit with highly variable responses between species and across disturbance types. The perennial challenge remains however in dealing with the rarest species which we were unable to model and which may be more sensitive to disturbance than other members of the assemblage.

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Chapter 6:

Discussion

Discussion

The Brazilian Amazon is a vast, dynamic and complex system, that requires precise, effective and efficient methods to reveal the complexities of biodiversity loss in the region. Failure to engage with this task will have global ramifications for the current anthropogenic extinction crisis (Ceballos et al., 2015). Three years ago 15 pre-eminent scientists argued that ecoacoustic studies could play a vital role in achieving that understanding in tropical forests, suggesting that *"failure to collect acoustic data now in tropical ecosystems would represent a failure to future generations of tropical researchers and the citizens that benefit from ecological research"* (Deichmann et al., 2018).

In the following years, ecoacoustics as a discipline has risen to meet that challenge, and passive acoustic monitoring (PAM) has proven to have wide applicability for biodiversity monitoring in tropical forests (Bradfer-Lawrence et al., 2020; Burivalova et al., 2019, 2018a; Campos-Cerqueira et al., 2021; Campos-Cerqueira et al., 2020; Darras et al., 2019; de Camargo et al., 2019; LeBien et al., 2020; Pérez-Granados and Schuchmann, 2020; Sugai et al., 2019). Despite its increasing influence, ecoacoustics remains on the cusp of maturity as a discipline (Stowell and Sueur, 2020). Much of the literature is dominated by methods papers still resolving fundamental knowledge gaps in how to apply ecoacoustic techniques (e.g. Bradfer-Lawrence et al., 2019; Mitchell 2020, Yip et al., 2019), although the number of applied papers are increasing, particularly studies using semi-automated classification (Priyadarshani et al, 2018, Gibb et al., 2019). Aspects of the field are advanced, in particular the hardware requirements for effective passive acoustic monitoring have been well addressed (Darras et al., 2021; Hill et al., 2018; Sethi et al., 2018) and increasingly automated classification with deep learning appears ready for applied usage (Ruff et al., 2020; Zhong et al., 2020). However, many other facets are under-developed. In particular there remains a lack of clarity around the theoretical underpinnings and practical applications of acoustic indices, and a surprisingly limited amount of research into how manual analysis of acoustic data can be optimised with passive acoustic monitoring.

6.1. Developments in ecoacoustic analysis

In **Chapter One**, I discuss how ecoacoustics can be applied to monitoring biodiversity in Amazonia, and the recent advancements made in the field. I summarize a range of studies that show ecoacoustic workflows have great potential in helping to gain a better understanding of the complex impacts of forest disturbance on biodiversity in the region. I also highlight a range of knowledge gaps that prevent wider adoption of PAM and ecoacoustic workflows, and argue that many of the limiting factors related to hardware have been overcome, or are likely to be in the near future – but that greater research is needed in creating simple, effective and replicable analysis workflows.

In **Chapter Two** I present a method and accompanying R package to fully automate rainfall identification in audio data. The method provides a quick and effective classification and is especially suited to tropical forests where the need is greatest. I demonstrate that through the use of minimum and second quartile thresholds, the method can be adjusted for use even in cases where there is poor differentiation between rain presence and absence with a reasonably high level of success. This allows users of hardRain to make informed trade-offs between effort, accuracy and specificity. Whilst the method may not be as accurate as other more technical approaches (Brown et al., 2019), for researchers wishing to quickly remove rain files from large datasets prior to ecoacoustic analysis, this method will often represent the most time-effective way to do so.

In **Chapter Three**, I test subsampling methods for the manual analysis of acoustic data, the most technically accessible method of analysis to inventory biodiversity using ecoacoustics. Up to 2018, 58% of all ecoacoustic studies were still analysed manually, with the majority of studies in recent years also using autonomous recorders (Sugai et al., 2019). Autonomous recorders allow users to adopt a range of study designs and subsampling approaches that are not practically possible with more traditional monitoring approaches (Darras et al., 2019; Prince et al., 2019), yet there is little understanding of the potential benefits or trade-offs. This is particularly important as the use of fully or even semi- automated classification methods for inventorying bird species in highly biodiverse regions remains distant. The most species-rich bird communities yet to be sampled with semi-automated classification

(Campos-Cerqueira and Aide, 2021) and fully automated methods (de Camargo et al., 2019) involve 50 and 60 species respectively, approximately a quarter of the 245 species inventoried in my study. Given the discrepancy between the capabilities of current classification methods and the complexity of ecological reality, better understanding of how manual analysis can be optimised should be a priority for the ecoacoustic field. I find that subsampling 240 fifteen second samples at each point for a total duration of one hour outperforms the use of four 15 minute samples, detecting approximately 50% higher alpha diversity, and 10% higher gamma diversity. The low temporal resolution sampling is almost four times more likely to miss species presence at a site. These are substantial benefits, and I believe this subsampling approach should be adopted as the standard and primary method for sampling bird communities in tropical forests, until automated classification methods for entire communities are widely available.

In **Chapter Four**, I test the performance of acoustic indices for measuring biodiversity in complex acoustic environments, particularly whether the sensitivity and fidelity of acoustic indices are negatively impacted by signal masking. Soundscape analysis with acoustic indices offers great potential if habitats can be accurately characterised and reliable proxies for biodiversity metrics obtained, as they are easily calculated with a minimum of effort (Eldridge et al., 2018). I show that signal masking has a large impact on the sensitivity of acoustic indices to forest disturbance classes. Calculating acoustic indices at a range of narrower time–frequency bins substantially increases the classification accuracy of forest classes by random forest models. Furthermore, signal masking leads to misleading correlations, including spurious inverse correlations, between biodiversity indicator metrics and acoustic index values compared to correlations derived from manual sampling of the audio data. Consequently, I recommend that acoustic indices are calculated either at a range of time and frequency bins, or at a single narrow bin, predetermined by a priori ecological understanding of the soundscape.

In **Chapter Five** I use automated classification of acoustic data to generate a presence/absence dataset of the nocturnal bird community in the study region, and then examine the impact of disturbance on these little-studied species. I find that Random Forest classification techniques, in particular those developed by the Tadarida toolbox, are able to accurately classify a range of taxa even in highly complex acoustic environments like tropical rainforest. Automated classification is already one of the most developed aspects of ecoacoustics (Stowell and Sueur, 2020), but use of these methods to produce accurate data suitable for ecological inference remains rare, so this study represents valuable evidence as the field advances - from theoretical and methodological research to application for ecological and conservation research. While a range of classification algorithms exist - with the most recent methods reporting higher accuracy than our own, there is limited research into the impact of context-specific error structures produced in this manner, or best methods to prepare and analyse data from classifiers for ecological inference and prediction. Here, I provide important insights into how small inaccuracies in classification-derived data such as heterogeneity of false positives, can have a disproportionate effect on ecological inference and provide a new, relatively straightforward method to resolve biases in accuracy.

Having corrected for heterogeneity of error, I use the classification data to model the impact of forest disturbance on the regional nocturnal bird community, the first study of its kind to consider the two commonest forms of disturbance in Amazonia, logging and fire. I show that all of the species studied were more commonly detected in forest that had undergone some form of disturbance than in nominally undisturbed forest, although there were no universal patterns in the focal species response to disturbance. This suggests that the nocturnal avian community is not highly sensitive to disturbance, although further research is needed to understand species-specific resilience to forms and intensity of disturbance at a wider spatial scale.

6.2. Future Research

6.2.1. Signal Processing

Acoustic pre-processing and noise reduction, including the detection and removal of rainfall, can play an important role in the effectiveness of acoustic analysis. In many ways, this aspect of analysis is quite advanced as there is considerable overlap in methods that have high levels of industry investment and development such as speech recognition (Stowell et al., 2016). However, as with much of the development of ecoacoustic analysis methods, there are few guidelines or studies targeted at ecologists rather than computer scientists as the primary end users, thus limiting the potential applied impact. In particular, much of the research on noise reduction is aimed at the use of automated classification with deep learning techniques, and quantification of the impacts of proposed methods on ecological conclusions are rare. Exceptions to this include some studies related to cicada chorusing and rainfall (Brown et al., 2019; Sánchez-Giraldo et al., 2020), and a brief summary of noise reduction techniques in relation to automated detection of bird calls (Priyadarshani et al., 2018). A thorough review of pre-processing and noise reduction techniques aimed at ecologists would be a highly useful addition to the ecoacoustic literature. Further studies that include explicit considerations linking analysis methods to pre-processing methods would also be useful, as pre-processing that may be appropriate for classification may be inappropriate for acoustic indices. In addition, software or R/Python packages facilitating the use of a collection of the most appropriate pre-processing techniques for ecoacoustic analysis would be highly desirable, although several packages currently offer one or two methods with limited documentation as to expected impact (e.g. ‘rmnoise’ in Seewave, Sueur et al., 2008).

6.2.2. Manual Analysis

There are still many questions that remain unanswered regarding optimisation of the use of passive acoustic monitoring for inventorying biodiversity. Whilst I focus on a comparison of two methods after data collection and within a set survey period, there are still questions about optimal recorder array number and layout, detection distance and subsequent trade-offs with recording duration and analysis time (Sugai et al., 2020). As these questions are related to the spatio-temporal structuring of species richness, a repeat of the famous Cocha Cashu study on the structure and organisation of bird communities (Terborgh et al., 1990) but using autonomous recording units would likely be highly revealing in this regard. Studies using automated classification for a fraction of total avian biodiversity in a region have shown that spatial turnover can far outweigh temporal turnover for instance (de Camargo et al., 2019). Furthermore, better understanding of the spatio-temporal dynamics of species richness, and importantly the variation of species availability for detection, can allow for better optimisation of sampling across diel and seasonal cycles (Pieretti et al., 2015). For instance using a higher temporal resolution during peak periods and targeted sampling at periods or locations with highly distinct species composition could result in higher, and more accurate, estimations of species richness.

6.2.3. Acoustic Indices

There has been a considerable amount of research conducted on the appropriate methods/methodology for the use of acoustic indices. Independent studies have addressed the impact of temporal (Bradfer-Lawrence et al., 2019) and spatial scale (Mitchell et al., 2020) at which recordings are taken on the effectiveness of indices, complemented by our own findings on the appropriate temporal and frequency scales at which to apply indices. It is quite apparent from a range of studies, including our own, that soundscapes vary considerably between habitats and across habitat quality gradients. These differences can be used to compare acoustic communities relative to each other, (Campos-Cerqueira and Aide, 2017; Furumo and Aide, 2019), and to classify habitat types (Bradfer-Lawrence et al., 2019; Do Nascimento et al., 2020). Despite this, questions remain as to the cost-effectiveness of using acoustic indices to classify land cover types, as remote sensing techniques or in-situ inventories of forest structure may produce better results (e.g. MapBiomas www.mapbiomas.org, Terra Class, www.terraclass.gov.br, Gardner et al., 2013).

Using indices as proxies for biodiversity metrics, or to make direct inferences about species richness or community turnover also remains problematic. Whilst it is clear that it is possible to achieve even quite strong correlations with traditionally measured biodiversity metrics (e.g. Bradfer-Lawrence et al., 2020; Hilje et al., 2017), and whilst the methods I have developed can certainly make those correlations both stronger and more reliable, it is not entirely apparent how to interpret those correlations. For instance, what does a 60% correlation with species richness and/or a 50% correlation with total number of sound events actually tell us about species communities that respond to habitat changes and disturbance in highly idiosyncratic ways? In fact, acoustic indices may be most useful in identifying the taxonomic groups most likely to be impacted by habitat changes (Rappaport et al., 2021), by comparing relative acoustic communities, and identifying acoustic niches that are most different to reference sites. Here, relatively straightforward indices, such as acoustic space use and soundscape saturation (e.g. Aide et al., 2017; Burivalova et al., 2019) may be the most useful.

In order to better understand the acoustic events driving variation in acoustic indices' responses to ecological change, two aspects of further research should be prioritised. The first is the impact of species abundance, something that is rarely considered or quantified in acoustic soundscape studies. Secondly, further investigation into the theoretical underpinnings of acoustic indices and ecological reality are required. Acoustic indices are predicated on two theoretical paradigms (Sueur and Farina, 2015), the acoustic niche hypothesis, which suggests that sound producing organisms each occupy their own time and frequency niche in which to vocalise (Krause, 1993), and the acoustic adaptation hypothesis that postulates that the acoustic properties of habitats shape animal sounds (Morton, 1975), resulting in habitats having unique acoustic signatures. It has been argued that intact ecosystems have saturated soundscapes, whilst defaunation leads to gaps, or missing niches, in the soundscape. These gaps are detectable by acoustic indices and are interpretable as relating to biodiversity richness and intactness (Sueur et al., 2014), an approach that has been widely adopted (Burivalova et al., 2018; Moreno-Gómez et al., 2019; Rappaport et al., 2021; Zhao et al., 2017). Yet more direct studies of ecological responses to forest disturbance and degradation show that whilst species richness often declines overall, generalist species are often able occupy degraded areas where they were previously absent (Moura et al., 2016; Solar et al., 2015; Tabarelli et al., 2012). Generalist species, by their nature, often occupy less speciose habitats, so it would be reasonable to assume that they may occupy wider acoustic niches. Therefore, increases in these species may create a more complete, or even over-saturated soundscape than explained by species richness or intactness alone. Currently, the turnover of species whose vocalisations may have evolved to occupy different acoustic niches is rarely considered in soundscape ecology.

6.2.4. Automated classification

Automated classification of biophony, and bird calls in particular, receives a relatively high degree of research attention, including frequent artificial intelligence competitions (Kahl et al., 2020). In general however, much of the research is focussed on applying new algorithms to more species, and achieving higher accuracy scores. Whilst accuracy is hugely important, it can come at the cost of efficiency and utility, and a lack of research into the impact of various types of error in ecological classification means we know very little about what ‘good enough’ might look like. I presented classification methods that are less accurate than some of those already published, but I believe remain highly of high utility to those methods already published through ease of use (Chapter 2) or were able to make an accurate and significant contribution to our knowledge of tropical ecology (Chapter 5).

For ecology and conservation research purposes many of the existing deep learning algorithms already produce accuracy scores good enough, and across enough species, to produce meaningful insights, but are unavailable to practitioners in the best position to use them. More focus should be given to making deep-learning algorithms easily available and adaptable, without requirements for high levels of technical expertise. The only deep-learning algorithm currently available without a coding interface is BirdNET (www.birdnet.cornell.edu), which does not easily facilitate the analysis of large quantities of data, whilst other software platforms, Kaleidoscope Pro (www.wildlifeacoustics.com/products/kaleidoscope-pro), the BTO Acoustic Pipeline (www.bto.org/our-science/projects/bto-acoustic-pipeline) and RFCx Arbimon (www.arbimon.rfcx.org) currently use machine-learning not deep learning for their classification processes.

Furthermore, the amount of fastidiously labelled training data required for building both machine and deep-learning algorithms is a major hindrance for their uptake (Gibb et al., 2019), yet there has been limited sensitivity analysis conducted to ascertain the impacts of reducing quantities of training data, using soft labelling, or of data augmentation methods, especially in an ecological context. Research in to algorithm development for bird classification is increasingly using ‘real world’ data, which is ultimately beneficial to the applicability of the methods. This is done either through the use of PAM derived datasets (Ruff et al., 2020; Zhong et al., 2020) and clustering (Ruff et al., 2020)or template-based detection to generate the training data (Ovaskainen et al., 2018; Zhong et al., 2020), or through the use of large online databases such as xeno-canto (Kahl et al., 2020). Online databases such as xeno-canto (www.xeno-canto.org) and the Macaulay Library (www.macaulaylibrary.org) offer large quantities of soft-labelled data offering a possible solution to the requirement for high quantities of training data. However, these datasets often have recordings that contain multiple species and noise sources, and have much higher signal-to-noise ratio than PAM recordings. Further research is needed into the best methods of applying the training data acquired from online datasets to algorithms that will ultimately be used on PAM recordings.

6.3. The Role of Ecological Knowledge and Fieldwork

Finally, I wanted to highlight the role of ecological knowledge in ecoacoustics, as a theme that occurs across this body of research and which has only clarified with the benefit of hindsight. When working with autonomous recording units and artificial intelligence techniques, it has been informally suggested to me many times, although rarely written about, that these methods will eventually replace human surveyors and human knowledge. I believe that this thesis is evidence to the contrary. Whilst passive acoustic monitoring and ecoacoustic workflows have the capacity to greatly reduce the amount of human effort required, every chapter has required or benefitted from in-depth knowledge of the ecosystems the processes are being applied to, and subtle understanding of the problems to be addressed that can only be contributed by a human.

The genesis of Chapter 3 lies in the memory of a morning spent observing the dawn chorus from a canopy tower in our study site - listening to forest-falcons *Micrastur spp.* and tinamous *Tinamus spp.,* give way to woodcreepers *Dendrocolaptinae spp.*, toucans *Ramphastos spp.,* and finally Screaming Pihas *Lipaugus vociferans*, whilst watching mixed-species canopy flocks move in and out of the estimated range of a hypothetical recording unit. This resulted in a hypothesis that higher temporal resolution sampling would result in the detection of higher species richness. Similarly, in Chapter 4, it is our own understanding of acoustic partitioning across longer timescales, obtained through hours in the field and active listening that helped define the boundaries used in measuring of acoustic indices. Measuring acoustic indices within those boundaries results in higher sensitivity to changes in the soundscape and increased fidelity to changes in biodiversity. For Chapters 2 and 5, our understanding of the ecological systems within which the classifiers were being applied allowed us to make informed trade-offs between accuracy and utility. In particular, in Chapter 5, understanding the temporal scale at which presence data are useful, and knowing that many of the species call repeatedly allowed us to apply very high thresholds, reducing greatly reducing false positives at the expense of recall. There is a paradox here that will require careful redress by the ecoacoustic field; as workflows improve there is likely to be less and less requirement for time spent in the field, but an increased need for the knowledge derived from time in the field to interpret the data and improve methods.

6.4. Conclusion

I have used passive acoustic monitoring at an Amazonian deforestation hotspot to acquire an extensive acoustic data across a representative gradient of forest quality. I use this dataset to address key knowledge gaps and methodological limitations in ecoacoustic workflows. Finally, I demonstrate that ecoacoustic workflows can be used to examine species-specific ecological responses in understudied taxa, revealing that much of the nocturnal bird community is tolerant to at least some degree of disturbance. It is clear that ecoacoustics can be a vital tool in understanding, monitoring and reducing biodiversity loss in the Amazon, as very few technologies offer the operational capacity to monitor at such varied spatiotemporal scales, and analytical capacity at such a range of taxonomic resolution.

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Appendices

S2.1 Survey metadata for the audio data used in Chapter 2.

Country	Transect	Transect name	Latitude	Longitude	Duration (hrs)	Start date	End Date	Type	Notes
Brazil	1	B112 T12	-2.693	-54.452	456	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	2	B112 T8	-2.693	-54.495	432	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	3	B125 T9	-2.804	-54.568	336	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	4	B129 T10	-2.726	-54.777	348	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	5	B129 T11	-2.706	-54.786	384	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24

									hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	6	B129 T5	-2.714	-54.749	384	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	7	B160 T10	-2.819	-54.882	336	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	8	B260 T1	-3.002	-54.895	336	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	9	B260 T4	-3.02	-54.857	432	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	10	B260 T5	-2.984	-54.878	336	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	11	B260 T6	-3	-54.877	336	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	12	B261 T10	-3.018	-55.005	552	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24

									hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	13	B261 T8	-3.029	-55.011	552	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	14	B261 T9	-3.04	-55.015	504	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	15	B307 T3	-3.13	-54.857	456	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	16	B307 T7	-3.147	-54.838	480	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	17	B357 T4	-3.283	-54.854	336	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	18	B363 T3	-3.296	-54.963	336	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	19	B363 T5	-3.337	-54.984	384	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24

									hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	20	B363 T6	-3.336	-54.956	324	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	21	B363 T7	-3.32	-54.96	456	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	22	B363 T8	-3.329	-54.972	456	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	23	B399 T7	-3.429	-54.843	408	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	24	B399 T8	-3.482	-54.862	360	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	25	B399 T10	-3.464	-54.907	408	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	26	B69 T11	-2.574	-54.671	384	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24

									hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	27	B69 T8	-2.515	-54.675	384	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	28	Bextra T2	-0.938	-54.988	384	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Brazil	29	Bextra T3	-2.928	-55.002	480	11/06/2018	16/08/2018	Continuous	Collected in continuous blocks throughout this period. Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Java	Cikuray	Carik	107.8545526	-7.331443748	120	02/12/2018	06/12/2018	Continuous	Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Java		Pemancar	107.8703651	-7.318098911	144	18/11/2018	23/11/2018	Continuous	Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Java	Limbung	Mekarwangi	107.8182765	-7.496942254	120	10/12/2018	14/12/2018	Continuous	Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Java	Masigit	Pasir Cadaspanjang	107.3824806	-7.125237426	120	12/03/2019	16/03/2019	Continuous	Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Java	Patuha	Cimanggu	107.3934156	-7.155668666	144	22/02/2019	27/02/2019	Continuous	Total duration calculated by multiplying number of days deployed by 24 hrs, so

									overestimated for days in which recorders were only partially deployed.
Java		Kawah Putih	107.4103361	-7.161622925	120	03/03/2019	07/03/2019	Continuous	Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Java	Slamet	Guci	109.1906051	-7.222455922	144	12/10/2018	17/10/2018	Continuous	Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Java		Kaliwadas1	109.1779753	-7.252378917	120	01/10/2018	05/10/2018	Continuous	Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Java		Kaliwadas2	109.1727316	-7.260066417	96	05/10/2018	08/10/2018	Continuous	Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Java		Ketenger1	109.2030743	-7.300964231	120	08/09/2018	12/09/2018	Continuous	Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Java		Ketenger2	109.2065445	-7.28306092	264	15/09/2018	25/09/2018	Continuous	Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
Java		Ketenger3	109.2026861	-7.268372385	120	21/09/2018	25/09/2018	Continuous	Total duration calculated by multiplying number of days deployed by 24 hrs, so overestimated for days in which recorders were only partially deployed.
New Zealand		Rotokare Scenic Reserve	-39.448259	-174.41464	3968	18/04/2017	19/05/2017	08:00-10:00, 15:00-17:00	
Manchester		Ancoats	53.485	-2.228	484	30/10/2018	19/11/2018	Continuous	
Manchester		Ancoats	53.485	-2.228	120	24/04/2019	30/04/2019	Continuous	

S2.2. P-values for Table 2.1

P values									
	Accuracy					Specificity			
	Minimum threshold			SQ Threshold		Minimum threshold		SQ Threshold	
Country	1 Band	2 bands		1 Band	2 bands	1 Band	2 bands	1 Band	2 bands
Brazil	0.000627			3.90E-18		NA		NA	
Java	0.582768			3.74E-18		2.58E-23		NA	
Manchester	2.74E-18			3.78E-18		3.51E-18		3.43E-18	
New Zealand	3.69E-18			3.81E-18		3.80E-18		3.26E-21	
Mean	4.74E-39			2.71E-67		3.13E-51		3.03E-35	

S3.1: Survey locations, effort and protocols

Point	Transect name	Latitude	Longitude	First recording period	Second recording period	Duration (mins)	Habitat type (primary forest unless stated)	Short-duration surveys (n)	Standard-duration surveys (n)
1	B112 T12	-2.693	-54.452	06/07/2018-13/07/2018	20-07/2018-30/07/2018	22992	Logged and burned in 2015	231	4
2	B112 T8	-2.693	-54.495	06/07/2018-13/07/2018	20-07/2018-31/07/2018	26397	Logged	231	4
3	B125 T9	-2.804	-54.568	02/08/2018-16/08/2018	NA	19716	Logged and burned in 2015	239	4
4	B129 T10	-2.726	-54.777	30/06/2018-07/07/2018	04/08/08-16/08/2018	17862	Logged and burned < 2015	232	4
5	B129 T11	-2.706	-54.786	30/06/2018-07/07/2018	04/08/08-13/08/2018	21970	Secondary	214	4
6	B129 T5	-2.714	-54.749	30/06/2018-07/07/2018	04/08/08-13/08/2018	21700	Logged and burned < 2015	238	4
7	B160 T10	-2.819	-54.882	14/06/2010-28/06/2018	NA	19333	Logged	192	4
8	B260 T1	-3.002	-54.895	14/06/2010-28/06/2018	NA	19145	Logged and burned in 2015	231	4

9	B260 T4	-3.02	-54.857	14/06/2018-20/06/2018	29/06/2018-12/07/2018	25897	Logged and burned in 2015	224	4
10	B260 T5	-2.984	-54.878	14/06/2018-28/06/2018	NA	19081	Logged and burned – both	230	4
11	B260 T6	-3.00	-54.877	14/06/2018-28/06/2018	NA	19113	Logged	219	4
12	B261 T10	-3.018	-55.005	12/06/2018-05/07/2018	NA	30769	Burned in 2015	222	4
13	B261 T8	-3.029	-55.011	12/06/2018-05/07/2018	NA	31468	Burned in 2015	227	4
14	B261 T9	-3.04	-55.015	12/06/2018-16/06/2018	06/08/2018-13/08/2018	28212	Burned in 2015	218	4
15	B307 T3	-3.13	-54.857	20/07/2018-08/08/2018	NA	27146	Logged and burned – both	239	4
16	B307 T7	-3.147	-54.838	20/07/2018-21/07/2018	28/07/2018-09/08/2018	18932	Logged and burned – both	240	4
17	B357 T4	-3.283	-54.854	18/06/2018-02/07/2018	NA	19371	Secondary	210	4
18	B363 T3	-3.296	-54.963	02/07/2018-09/07/2018	16/07/2018-23/07/2018	18958	Undisturbed	239	4
19	B363 T5	-3.336	-54.984	04/08/2018	10/08/2018	17827	Undisturbed	230	4

20	B363 T6	-3.336	-54.956	03/07/2018-10/07/2018	08/08/2018-15/08/2018	18958	Undisturbed	240	4
21	B363 T7	-3.32	-54.96	21/06/2018-03/07/2018	08/08/2018-15/08/2018	26246	Undisturbed	239	4
22	B363 T8	-3.329	-54.972	21/06/2018-03/07/2018	08/08/2018-15/08/2018	26119	Undisturbed	239	4
23	B399 T7	-3.429	-54.843	14/07/2018-31/07/2018	NA	22085	Logged	240	4
24	B399 T8	-3.482	-54.862	14/07/2018-27/07/2018	08/08/2018-10/08/2018	25334	Secondary	240	4
25	B399 T10	-3.464	-54.907	14/07/2018-31/07/2018	NA	21897	Logged and burned < 2015	237	4
26	B69 T11	-2.574	-54.671	13/06/2018-29/06/2018	NA	25989	Logged and burned < 2015	199	4
27	B69 T8	-2.515	-54.675	13/06/2018-29/06/2018	NA	26103	Logged and burned in 2015	225	4
28	BExtra T2	-2.938	-54.988	13/06/2018-29/06/2018	NA	25687	Burned in 2015	219	4
29	BExtra T3	-2.928	-55.002	19/06/2018-09/07/2018	NA	32277	Burned in 2015	233	4

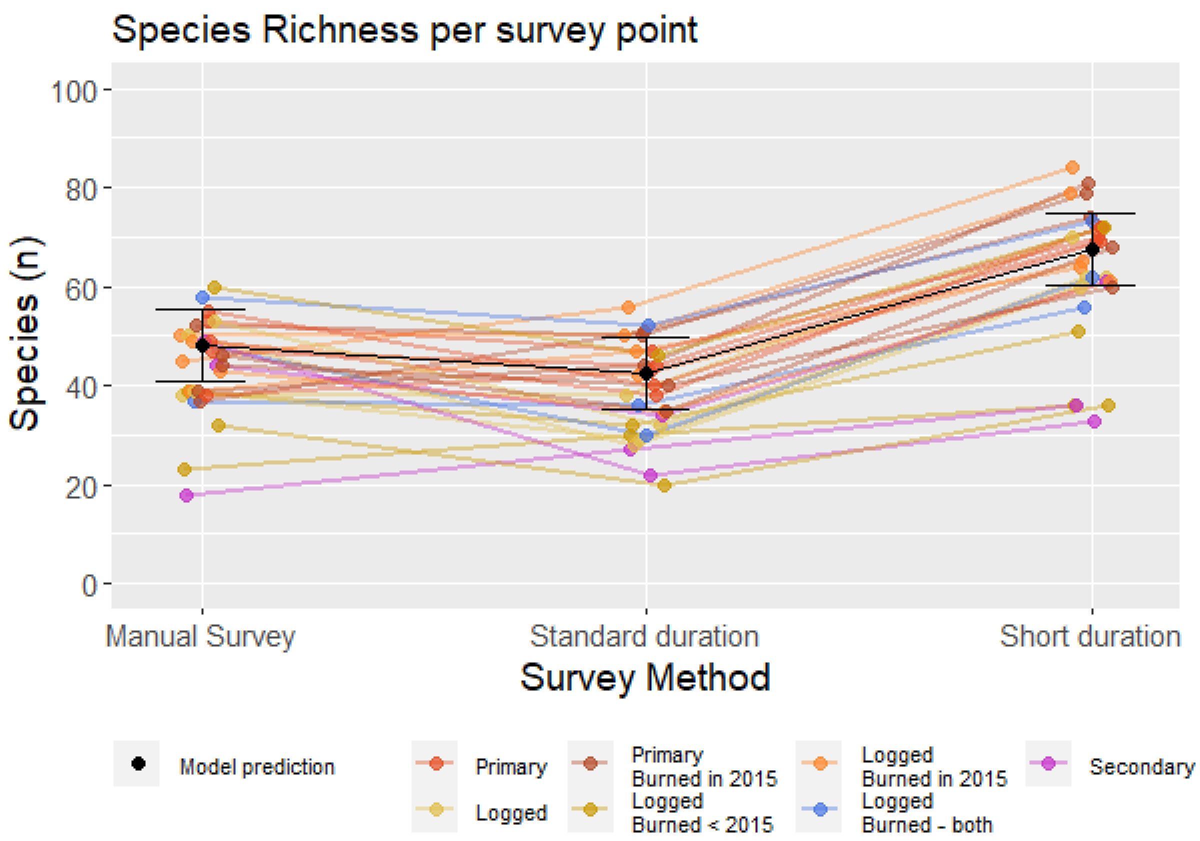
Transect name: B=catchment number, T= transect number as detailed in Gardner et al.,(2013)

We installed Frontier Labs Bioacoustic Recording Units with a 16 bit 44.1 kHz sampling rate at points halfway along each transect. Recorders were placed in trees at a height of 7-10 m, with the microphone placed in a downward facing position, at a distance of 10-20 m from the transect to reduce the chance of recorder theft. Recording units were placed away from immediately overhanging dense vegetation to avoid sound being blocked and to limit geophony from leaves and branches. The microphones used have 80 dB signal to noise ratio and 14dBA self-noise, a fixed gain pre-amp of 20dB, a flat frequency response (±2dB) from 80Hz to 20kHz and an 80Hz high-pass filter to filter out low-frequency wind noise (Frontier Labs, 2015). All files were recorded in wav format. Recordings were made continuously (Frontier Labs software writes a new file every ~6 hrs).

S3.2: Manual surveys

We compared this acoustic data with traditional point count surveys conducted at the same sites by three experienced observers (Alexander C. Lees, NGM and Sidnei Dantas, see Moura et al., (2013), Moura et al., (2016), Henriques et al., (2003)) between 15-26th November 2016. Surveys lasted 15 minutes each, and were conducted between 05:45 and 09:45, and two surveys were conducted from each of 0 m, 150 m and 300 m along the transect, so that each transect was surveyed six times in total. The detection method was noted for each species per survey as either visual or auditory. In all other respects, the surveys followed the protocols set out in previous published surveys at the site (Lees et al., 2013). There are distinct differences between the traditional surveys and the recorded surveys; being conducted at the start of the rainy season when birds are expected to be most vocally active and hence easily detected, across a greater spatial scale (three points, at 0m, 150 m and 300m along each transect), for 90 minutes rather than 60 at each transect, and over a slightly longer survey window each morning. Furthermore, ten of the transects were fire-damaged during El Nino events in 2015, and therefore have significantly different vegetation structure between 2016 and now owing to two years worth of post-fire regeneration (Berenguer et al., 2018), whilst the structure of the other transects remains similar.

We modelled the resulting species richness scores using linear mixed effects models in the lme4 package, using survey method and presence of fire in 2015 as fixed effects and transect nested within disturbance class as a random effect.



Traditional surveys detected a total of 255 species, higher than either of the other methods. However, traditional surveys detected 48±3.7 (SE) species per transect, which is 5.4±1.85 more than standard-duration surveys, but 19.4±1.85 species less than short-duration surveys.

Whilst we statistically account for the differences in survey method where possible using rarefied species richness data (Oksanen et al., 2019), we believe that the traditional surveys are detecting higher species richness than had they been conducted in the same season of 2018 using identical protocols as the autonomously recorded surveys – particularly given the results of Darras et al., (2019). However, we have included the comparison here as we believe it is useful to readers to place the results of the comparison between short and long duration surveys with autonomous audio recordings in the context of the regional species pool likely to be detected by traditional point counts. It further emphasises the efficacy of short-duration surveys that despite the considerable biases in favour of the traditional surveys, short-duration recorded surveys still recorded substantially higher species richness.

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S4.1: Survey locations and effort

Point	Transect name	Latitude	Longitude	First recording date	Last recording date	Duration (mins)	Habitat type pre 2015 (primary
1	B112 T12	-2.693	-54.452	06/07/2018	30/07/2018	22992	Logged and burned
2	B112 T8	-2.693	-54.495	06/07/2018	31/07/2018	26397	Logged
3	B125 T9	-2.804	-54.568	02/08/2018	16/08/2018	19716	Logged and burned
4	B129 T10	-2.726	-54.777	30/06/2018	16/08/2018	17862	Logged and burned
5	B129 T11	-2.706	-54.786	30/06/2018	13/08/2018	21970	Secondary
6	B129 T5	-2.714	-54.749	30/06/2018	13/08/2018	21700	Logged and burned
7	B160 T10	-2.819	-54.882	14/06/2010	28/06/2018	19333	Logged
8	B260 T1	-3.002	-54.895	14/06/2018	28/06/2018	19145	Logged and burned
9	B260 T4	-3.02	-54.857	14/06/2018	12/07/2018	25897	Logged and burned
10	B260 T5	-2.984	-54.878	14/06/2018	28/06/2018	19081	Logged and burned
11	B260 T6	-3.00	-54.877	14/06/2018	28/06/2018	19113	Logged
12	B261 T10	-3.018	-55.005	12/06/2018	05/07/2018	30769	Burned
13	B261 T8	-3.029	-55.011	12/06/2018	05/07/2018	31468	Burned
14	B261 T9	-3.04	-55.015	12/06/2018	13/08/2018	28212	Burned
15	B307 T3	-3.13	-54.857	20/07/2018	03/08/2018	27146	Logged and burned
16	B307 T7	-3.147	-54.838	20/07/2018	03/08/2018	18932	Logged and burned
17	B357 T4	-3.283	-54.854	18/06/2018	02/07/2018	19371	Secondary
18	B363 T3	-3.296	-54.963	02/07/2018	23/07/2018	18958	Unburned
19	B363 T6	-3.336	-54.956	03/07/2018	15/08/2018	18958	Unburned

20	B363 T7	-3.32	-54.96	21/06/2018	15/08/2018	26246	Unburned
21	B363 T8	-3.329	-54.972	21/06/2018	15/08/2018	26119	Unburned
22	B399 T7	-3.429	-54.843	14/07/2018	31/07/2018	22085	Logged
23	B399 T8	-3.482	-54.862	14/07/2018	10/08/2018	25334	Secondary
24	B399 T10	-3.464	-54.907	14/07/2018	31/07/2018	21897	Logged and burned
25	B69 T11	-2.574	-54.671	13/06/2018	29/06/2018	25989	Logged and burned
26	B69 T8	-2.515	-54.675	13/06/2018	29/06/2018	26103	Logged and burned
27	Bextra T2	-2.938	-54.988	13/06/2018	29/06/2018	25687	Burned
28	Bextra T3	-2.928	-55.002	19/06/2018	09/07/2018	32277	Burned

Transect name: B=catchment number, T= transect number as detailed in Gardner et al.,(2013)

S4.2: H2O RandomForest Hyperparameters

h2o.randomForest(x, y, data, classification = TRUE, ntree = 50, depth = 20,

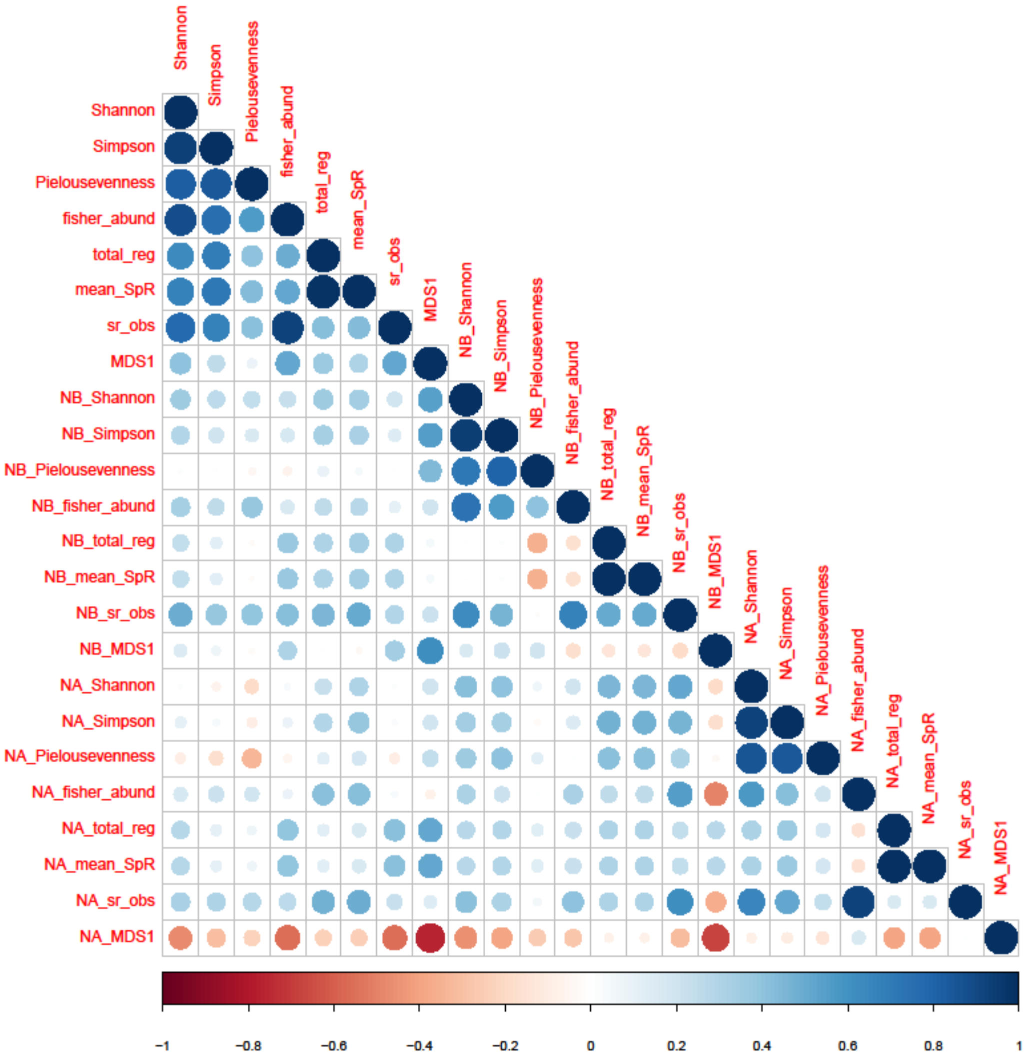
sample.rate = 2/3, classwt = NULL, nbins = 100, importance = FALSE,

validation, nodesize = 1, balance.classes = FALSE, max.after.balance.size = 5,

use_non_local = TRUE, version = 2, ntrees=200, mtries=5, score_each_iteration = T,

seed = 1000000)

S4.3: Correlations between biodiversity metrics



NB=nocturnal birds, NA= Nocturnal all taxa, no label = Dawn birds

S4.4: Results table for Kruskal Wallis tests

Acoustic Index	Time period	Frequency bin	Effect size	No. of significantly different habitat pairs
AC	Dawn	0.3-12	0.211	8
AC	Day	0.3-12	0.0384	7
AC	Dusk	0.3-12	0.0448	6
AC	Night	0.3-12	0.0706	8
AC	Dawn	0.3-4	0.251	8
AC	Day	0.3-4	0.0702	6
AC	Dusk	0.3-4	0.0484	7

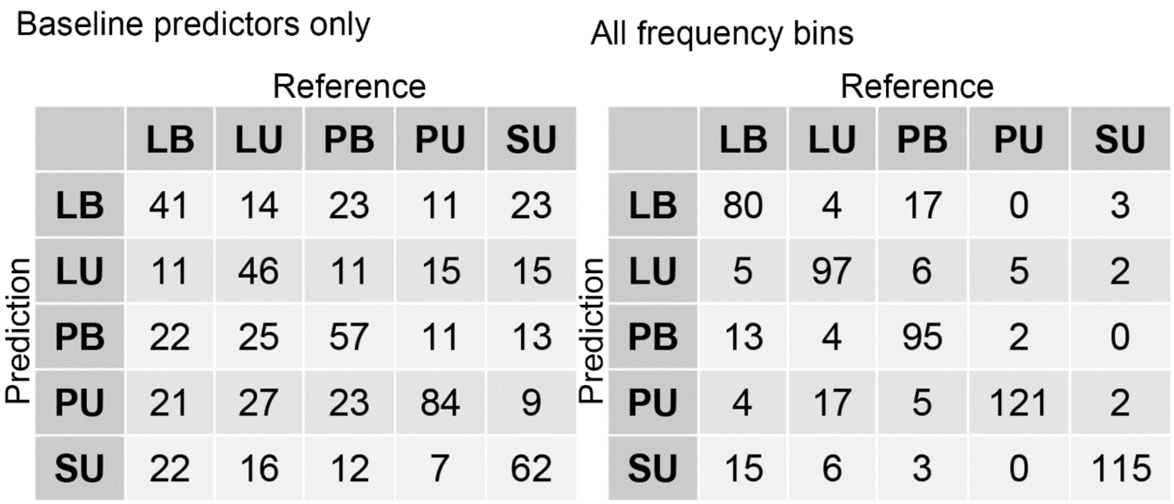
AC	Night	0.3-4	0.219	8
AC	Dawn	12-22.1	0.0869	8
AC	Day	12-22.1	0.157	8
AC	Dusk	12-22.1	0.0695	7
AC	Night	12-22.1	0.0295	6
AC	Dawn	04-12.0	0.173	7
AC	Day	04-12.0	0.0345	6
AC	Dusk	04-12.0	0.0855	8
AC	Night	04-12.0	0.0996	9
AC	Dawn	Base	0.193	9
AC	Day	Base	0.105	9
AC	Dusk	Base	0.00894	2
AC	Night	Base	0.0707	9
BI	Dawn	0.3-12	0.0266	6
BI	Day	0.3-12	0.0982	9
BI	Dusk	0.3-12	0.0248	6
BI	Night	0.3-12	0.0682	8
BI	Dawn	0.3-4	0.106	7
BI	Day	0.3-4	0.119	9
BI	Dusk	0.3-4	0.0514	7
BI	Night	0.3-4	0.166	7
BI	Dawn	12-22.1	0.0537	8
BI	Day	12-22.1	0.0672	7
BI	Dusk	12-22.1	0.0815	6
BI	Night	12-22.1	0.125	9
BI	Dawn	04-12.0	0.0492	8
BI	Day	04-12.0	0.103	8
BI	Dusk	04-12.0	0.305	7
BI	Night	04-12.0	0.237	10
BI	Dawn	Base	0.0547	7
BI	Day	Base	0.0372	7
BI	Dusk	Base	0.0392	6
BI	Night	Base	0.0524	8

S4.5A. Random forest accuracy metrics for classification of forest classes:

Forest Class	**Frequency bins used as training data**	**Metric**	**Score**
Primary vs Secondary	Baseline	Balanced Accuracy	0.859475
Primary vs Secondary	All	Balanced Accuracy	0.995726

All	Baseline	Balanced Accuracy	0.636062
All	All	Balanced Accuracy	0.891751
Primary vs Secondary	Baseline	F1	0.860385
Primary vs Secondary	All	F1	0.995909
All	Baseline	F1	0.47718
All	All	F1	0.829385
Primary vs Secondary	Baseline	MCC	0.722627
Primary vs Secondary	All	MCC	0.99185
All	Baseline	MCC	0.2716
All	All	MCC	0.784214

S4.5B. Confusion matrices for random forest models between all 5 habitat classes.



Baseline predictors only

Reference

Prediction	LB	LU	PB	PU	SU
LB	41	14	23	11	23
LU	11	46	11	15	15
PB	22	25	57	11	13
PU	21	27	23	84	9
SU	22	16	12	7	62

All frequency bins

Reference

Prediction	LB	LU	PB	PU	SU
LB	80	4	17	0	3
LU	5	97	6	5	2
PB	13	4	95	2	0
PU	4	17	5	121	2
SU	15	6	3	0	115

Disturbance classes: LB=logged and burned, LU=logged, PB=burned, PU=undisturbed, SU=secondary.

S5.1. Recording protocols

Recorders were located halfway along the 300 m transects. All recordings forming the main acoustic dataset were made between 12th June 2018 and 16th August 2018. Recordings at each survey point were made over one or two recording periods, with each recording period varying in length between 3 and 22 days for logistical reasons. A minimum of 13 days were surveyed at each location. In addition, data was collected from three transects between 27th November and 8th

December 2017 which comprised the majority of the training data for the classifier, but was not included in the ecological analysis.

All ecoacoustic data were collected using Frontier Labs Bioacoustic Recording Units with a 16 bit 44.1 kHz sampling rate. The microphones used have 80 dB signal to noise ratio and 14dBA self-noise, a fixed gain pre-amp of 20dB, a flat frequency response (±2dB) from 80Hz to 20kHz and an 80Hz high-pass filter to filter out low-frequency wind noise(Frontier Labs, 2015). All files were recorded in wav format. Trees were selected between 10-20m from the RAS transects to reduce the chance of theft of the recorders and placed at a height of 7-10m from the ground, with the microphone in a downward facing position. The diameters of the trees were estimated to be under 1.5m whilst large enough to withstand the weight of a ladder and person. ARUs were placed away from immediately overhanging dense vegetation to avoid sound being blocked and to limit geophony from leaves and branches.

S5.2. Building the Tadarida classifier

Building classifiers using Tadarida is a three step process; firstly automatically detecting sound events and acoustic feature extraction, then manual labelling, and finally building a random forest classification algorithm in R - for full details of the detection and feature extraction process, see Bas et al., (2017). Tadarida works best over short-duration sound files, so we divided all of our recordings into files with a duration of 15 s. We initially used the default settings for detection and measurement of features, but found that it split sounds too often along the time axis (e.g. dividing single call syllables), possibly due to reflection of sound in the forest, and merging of sounds across the frequency axis. To resolve these issues, we increased frequency resolution at the expense of temporal resolution by multiplying the sampling rate by 5, so that files that had previously been read as having 15 s duration and a maximum frequency of 22.05 kHz were now interpreted by the program as being 3 s in duration with a maximum frequency of 110.25 kHz. We also reduced the default hysteresis curve start and stop settings to 24 and 19, resulting in better distinguished sound events.

We then undertook manual labelling of detected sound events to build a training dataset. As random forests can respond to data outside of the training dataset in unpredictable ways, it was important to incorporate a broad range of sound events in the training set. In order to systematically search for sound types, we used a subset of recordings comprising 96 hours of data and consisting of 3 hours of recording per night – one hour up to 30 minutes before sunrise, one hour commencing 30 minutes after sunset and 00:00-01:00, every 3rd night from each of the ARUs deployed. The majority of the manually labelled sound events came from an independent data set not used in the ecological analysis. As the independent data set only came from sites inside the protected area, we also included some recordings from the main dataset, in order to include species that were present in the survey area but not in areas of extensive forest. Whilst manually labelling, species identifications were made where possible through the author's own knowledge or by comparison to readily available sound databases (Amphibian Survival Alliance, n.d.; Emmons et al., 1997; Macaulay Library, n.d.; Marantz et al., 2006; Xeno-Canto, n.d.) or sonotyped in to similar sounding groups. Where species have more than one distinct vocalisation, these were entered as separate classes. In the case of target species, we selected one vocalisation to become the target, except for in the case of *Nyctidromus albicollis*, as the two sonotyped call types had some overlap so these were treated as separate labels, but combined at the classifier assessment stage. At the end of this process >300 sound types had been identified, which were simplified to a final 59 sound types, either by merging similar sound types or removing ones that rarely occurred.

Next, we undertook a range of data augmentation measures, including adding training data for 34 sonotypes from the Macaulay Library and Xeno-Canto. In addition, we amplified each file containing one or more manually labelled sound events at two levels, and overlaid each labelled training file over one of three files containing different intensities of rainfall, creating six new versions of each labelled file. We then used the match function in R to automatically transcribe the labelled training data from the manually assessed file to the augmented files.

Species	DSEs (n)	Collected data DSE (n)	Augmented Collected DSEs (n)	ML DSEs (n)	XC DSEs (n)	Collected 15 s files (n)	Augmented collected 15 s files (n)	ML 15 s files (n)	ML unique files (n)	XC 15 s files (n)	XC unique files (n)	Unique sites (n)
adeaff	1109	1109	NA	NA	NA	55	NA	NA	NA	NA	NA	11
adehyl	2671	2671	NA	NA	NA	88	NA	NA	NA	NA	NA	17
alltap	1523	1523	NA	NA	NA	98	NA	NA	NA	NA	NA	13
alobel	17133	17133	NA	NA	NA	254	NA	NA	NA	NA	NA	34
alobel_call	4243	4243	NA	NA	NA	68	NA	NA	NA	NA	NA	4
antser	27067	8508	1954	16605	NA	307	14	77	9	NA	NA	67
boageo	1049	1049	NA	NA	NA	29	NA	NA	NA	NA	NA	9
branch	1484	1484	NA	NA	NA	76	NA	NA	NA	NA	NA	42
cicada	23058	23058	NA	NA	NA	108	NA	NA	NA	NA	NA	8
cow	1129	125	NA	1004	NA	7	NA	6	1	NA	NA	23
crysou	11172	647	NA	6472	4053	39	NA	836	90	650	120	235
cryvar	10018	673	NA	8650	695	25	NA	105	41	62	32	95
denleu	1971	1971	NA	NA	NA	144	NA	NA	NA	NA	NA	30
denmin	12094	12094	NA	NA	NA	181	NA	NA	NA	NA	NA	16
dentri	1105	1105	NA	NA	NA	26	NA	NA	NA	NA	NA	7
dog	5907	5907	NA	NA	NA	162	NA	NA	NA	NA	NA	18

engfrei	1040	1040	NA	NA	NA	18	NA	NA	NA	NA	NA	2
gecko	3067	3067	NA	NA	NA	144	NA	NA	NA	NA	NA	77
glahar_social	18858	5794	NA	13064	NA	279	NA	43	9	NA	NA	74
hercac	2864	2864	NA	NA	NA	26	NA	NA	NA	NA	NA	7
hercac_call	1208	1208	NA	NA	NA	13	NA	NA	NA	NA	NA	2
i5	1716	1716	NA	NA	NA	58	NA	NA	NA	NA	NA	10
lf7	869	869	NA	NA	NA	13	NA	NA	NA	NA	NA	4
lopcri_social	4910	2853	NA	2057	NA	297	NA	15	2	NA	NA	40
lursem_call	899	NA	NA	899	NA	NA	NA	27	10	NA	NA	10
lursem_social	12174	204	NA	11970	NA	10	NA	29	10	NA	NA	18
megcho_call	1858	1858	NA	NA	NA	126	NA	NA	NA	NA	NA	30
megwat_social	31240	12397	NA	18843	NA	394	NA	41	11	NA	NA	76
nycaet_song	1022	166	NA	647	209	16	NA	66	13	45	7	22
nycalb	2139	2139	NA	NA	NA	117	NA	NA	NA	NA	NA	22
nycalb2	3010	168	NA	2842	NA	6	NA	5	2	NA	NA	19
nycgra_call	868	347	NA	521	NA	37	NA	10	5	NA	NA	20
nycgra_social	3811	319	NA	3413	79	58	NA	134	26	23	10	54
nycgri	9156	187	NA	6819	2150	21	NA	542	68	193	82	171
nycleu	3262	2485	NA	515	262	78	NA	62	11	20	11	34

nycoce	2948	2786	NA	162	NA	298	NA	1	1	NA	NA	15
odoguj	1813	1813	NA	NA	NA	22	NA	NA	NA	NA	NA	2
ortho1	8926	8926	NA	NA	NA	297	NA	NA	NA	NA	NA	60
ortho3	839	839	NA	NA	NA	55	NA	NA	NA	NA	NA	26
ortmot	3440	3440	NA	NA	NA	88	NA	NA	NA	NA	NA	12
pristi2	1036	1036	NA	NA	NA	139	NA	NA	NA	NA	NA	35
pulper_social	14362	3555	NA	10807	NA	154	NA	20	3	NA	NA	20
rhimag	3279	3279	NA	NA	NA	56	NA	NA	NA	NA	NA	17
rhysim_alarm	3595	40	NA	3555	NA	2	NA	16	3	NA	NA	8
rhysim_call	1404	916	NA	488	NA	58	NA	7	5	NA	NA	11
rhysim_call2	2038	NA	NA	2038	NA	NA	NA	17	4	NA	NA	5
rhysim_social	13101	2352	NA	10749	NA	67	NA	33	6	NA	NA	13
rooster	2500	2500	NA	NA	NA	80	NA	NA	NA	NA	NA	12
scicru	1465	1465	NA	NA	NA	23	NA	NA	NA	NA	NA	5
strhuh_call	2324	353	NA	1971	NA	64	NA	32	6	NA	NA	20
strhuh_call2	1798	437	NA	1361	NA	21	NA	50	7	NA	NA	25
strhuh_social	5270	5270	NA	NA	NA	564	NA	NA	NA	NA	NA	25
tingut_social	2245	1216	NA	1029	NA	77	NA	18	6	NA	NA	21
tintao_social	1453	34	NA	1213	206	4	NA	209	23	58	11	39

tintao_song	970	237	NA	733	NA	35	NA	11	4	NA	NA	19
tralf	824	824	NA	NA	NA	39	NA	NA	NA	NA	NA	12
tranr	7566	7566	NA	NA	NA	351	NA	NA	NA	NA	NA	51
trasq	2633	2633	NA	NA	NA	106	NA	NA	NA	NA	NA	15
wd	1811	1811	NA	NA	NA	80	NA	NA	NA	NA	NA	20

S5.3. Optimising classification thresholds

First, we obtained a set of candidate thresholds using the ROCR package. We built receiver operating characteristic (ROC) curves, and calculated the optimal thresholds with false positives weighted from zero to ten compared to false negatives. We then used classifier accuracy metrics to assess which candidate threshold best matched our classification priorities of high precision and low variance of error. To assess if the variance of error had decreased, we calculated the variance of recall and the variance of precision across survey locations at each threshold. We then calculated the harmonic mean of the variance values, to give the variance F score. Next, we calculated four bespoke classifier accuracy statistics for the impact of each of these thresholds, heavily weighting in favour of precision. These consisted of; precision plus F1 score, precision plus the area under the curve, precision plus the variance of precision and precision plus the variance F score. We ranked each threshold by metric from lowest to highest score, multiplied the ranks of precision plus area under the curve and precision plus the variance of precision by 1.5, and took the sum of the ranks. The threshold with the highest summed rank was selected as the optimal threshold.

S5.4: GLMM AIC table

Basic model: Detections/Survey~Forest_Class+Lunar_Illumination+(1|Survey_Point)

Zero-inflation:0=~Gradient, 1= ~1, 2=~. No zi in model name=no zero-inflation parameter

Family: bb=betabinomial, bin=binomial, pm=poisson, nbm=negative binomial, hurdle= truncated poisson

Model	**dAIC**	**df**
Species:	**M. usta**	
zibb1	0	11
zibb0	6.1	17
zibb2	10	19
bb	15.4	10

zibin0	730.6	16
zibin2	730.8	18
bin	1042.8	9
zibin1	1593.8	10
zinbm2	136187.3	19
zinbm0	137729.5	17
zinbm1	139010.6	11
nbm	139959.2	10
zihurdle2	158843.8	18
zipm2	158848.5	18
zipm0	161004.8	16
zihurdle0	162593	16
zipm1	163476.6	10
zihurdle1	165326.1	10
pm	176468.3	9
Species:	**L. cristata**	
bb	0	10
zibb1	0.5	11
zibb0	8.5	17
zibin2	1317.6	18
zibin0	1338.2	16
zibin1	1358.8	10
bin	1695.7	9
zinbm2	150074.9	19
zinbm0	153645.2	17
zinbm1	155199.2	11
nbm	157605.2	10
zihurdle2	178440.9	18
zipm2	178442.2	18

zipm0	182522.3	16
zipm1	184419	10
zihurdle0	186336.7	16
zihurdle1	189313.5	10
pm	200901.3	9
zibb2	NA	19
Species:	**P. perspicillata**	
zibb1	0	11
bb	5.1	10
zibb0	9.8	17
zibin2	85.8	18
zibin1	89.4	10
zibin0	90.5	16
bin	344.4	9
zinbm2	46052.2	19
zinbm0	46837.7	17
zinbm1	47118.2	11
nbm	47314.9	10
zipm2	48999.2	18
zihurdle2	49010.1	18
zipm0	49849.8	16
zipm1	50348.5	10
zihurdle0	52649.7	16
zihurdle1	55538.1	10
pm	63601.6	9
zibb2	NA	19
Species:	**G. hardyi**	
zibb1	0	11
zibb0	2.2	17

bb	9	10
zibin0	649.4	16
zibin1	657.4	10
bin	1007.6	9
zinbm2	96303.5	19
zinbm0	99837.1	17
zinbm1	101049.3	11
nbm	101954	10
zihurdle2	114014.1	18
zipm2	114050.9	18
zipm0	119115.7	16
zipm1	120024	10
zihurdle0	125429.5	16
zihurdle1	128628.9	10
pm	136752.7	9
zibin2	NA	18
zibb2	NA	19
Species:	**N. grandis**	
bb	0	10
zibb1	2	11
zibb0	12.8	17
zibin2	60.2	18
zibin1	86.2	10
zibin0	88.4	16
bin	210.3	9
zinbm2	47856.2	19
zinbm0	49592.1	17
zipm2	49752.5	18
zihurdle2	49777.8	18

zinbm1	49863.8	11
nbm	49864.3	10
zipm0	52140	16
zipm1	52636.9	10
zihurdle0	56826.5	16
pm	58832.9	9
zihurdle1	60367	10
zibb2	NA	19
Species:	**N. griseus**	
bb	0	10
zibb1	0.4	11
zibin1	39.6	10
bin	113.3	9
zinbm1	18985.3	11
nbm	19002.4	10
zipm1	20588.6	10
pm	24498.9	9
zihurdle1	25429.3	10
zinbm2	48430	19
zipm0	NA	16
zipm2	NA	18
zinbm0	NA	17
zihurdle0	NA	16
zihurdle2	NA	18
zibin0	NA	16
zibin2	NA	18
zibb0	NA	17
zibb2	NA	19
Species:	**N. leucopterus**	

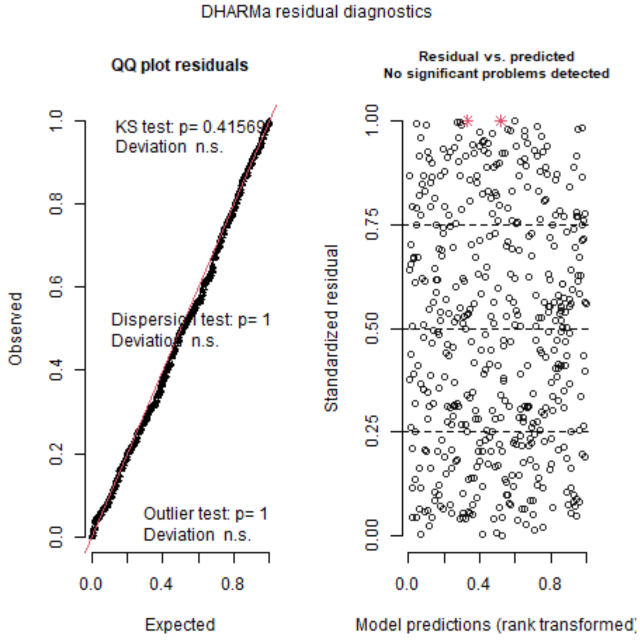
zibin1	0	10
bb	5	10
bin	11.1	9
zipm1	1649.6	10
nbm	1960.6	10
pm	2233.5	9
zipm0	NA	16
zipm2	NA	18
zinbm0	NA	17
zinbm1	NA	11
zinbm2	NA	19
zihurdle0	NA	16
zihurdle1	NA	10
zihurdle2	NA	18
zibin0	NA	16
zibin2	NA	18
zibb0	NA	17
zibb1	NA	11
zibb2	NA	19
Species:	**N. ocellatus**	
zibin1	0	10
zibb1	534.7	11
bb	537.6	10
bin	974.8	9
zinbm1	31549.2	11
nbm	32011.6	10
zipm1	36378.7	10
pm	48152.8	9
zipm0	NA	16

zipm2	NA	18
zinbm0	NA	17
zinbm2	NA	19
zihurdle0	NA	16
zihurdle1	NA	10
zihurdle2	NA	18
zibin0	NA	16
zibin2	NA	18
zibb0	NA	17
zibb2	NA	19
Species:	**A. sericocaudatus**	
zibb1	0	11
bb	7.9	10
zibb0	8.4	17
zibin2	953.2	18
zibin0	993.5	16
bin	1404.2	9
zinbm2	92571.5	19
zinbm0	96506.9	17
zinbm1	97230.1	11
nbm	97655.5	10
zipm2	117866.6	18
zihurdle2	118066	18
zipm0	123062.2	16
zipm1	124732.8	10
zihurdle0	132888.1	16
zihurdle1	139146.1	10
pm	144170	9
zibb2	NA	19

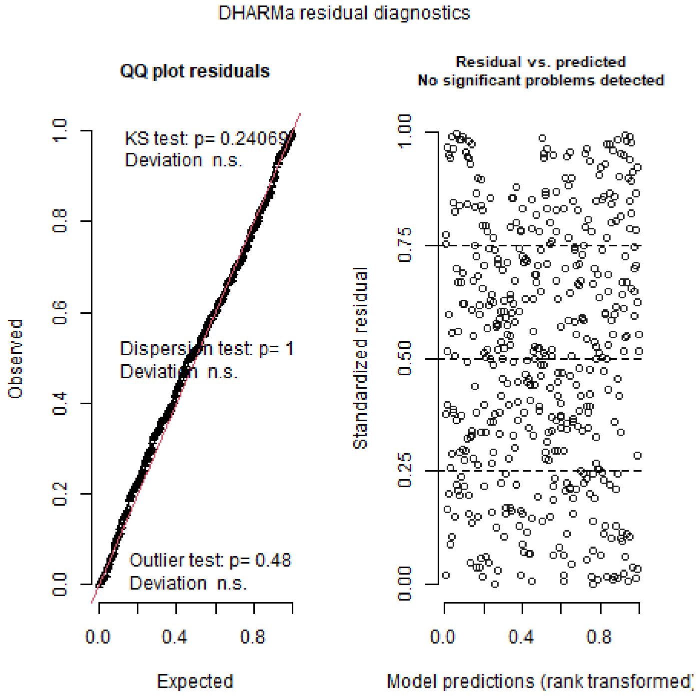
Species:	***N. albicollis***	
zibb1	0	11
zibb0	9.1	17
bb	20.2	10
zibin0	356.5	16
zibin1	370	10
bin	706.3	9
zibb2	1562.1	19
zinbm2	53010.5	19
zinbm0	55582.3	17
zinbm1	56409.3	11
nbm	57079.3	10
zipm2	59310.5	18
zihurdle2	59330.9	18
zipm0	62564.4	16
zipm1	64027.3	10
zihurdle0	69924.9	16
zihurdle1	75296.6	10
pm	80784.9	9
zibin2	NA	18

S5.5. GLMM diagnostic plots

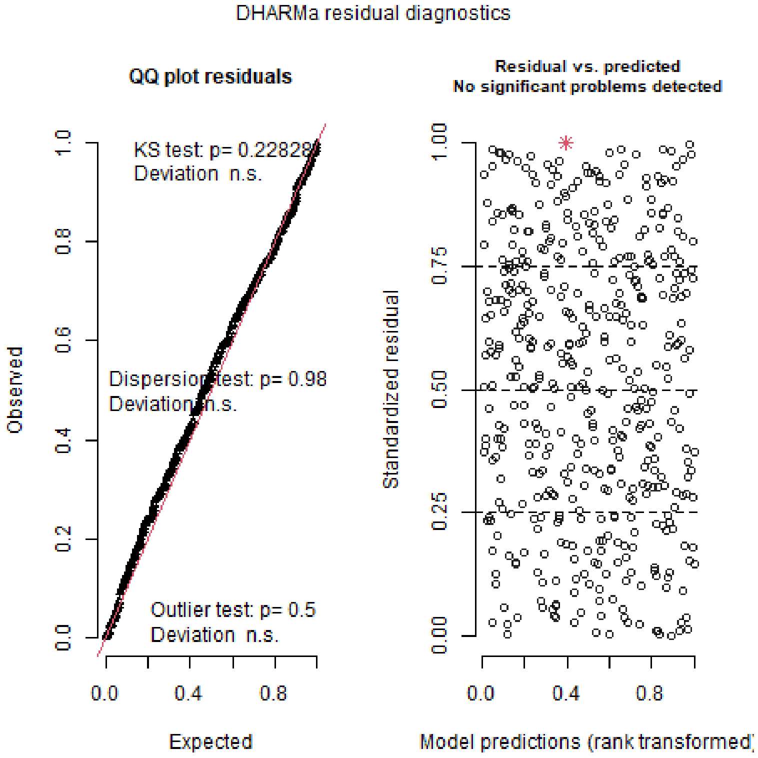
Megascops usta:



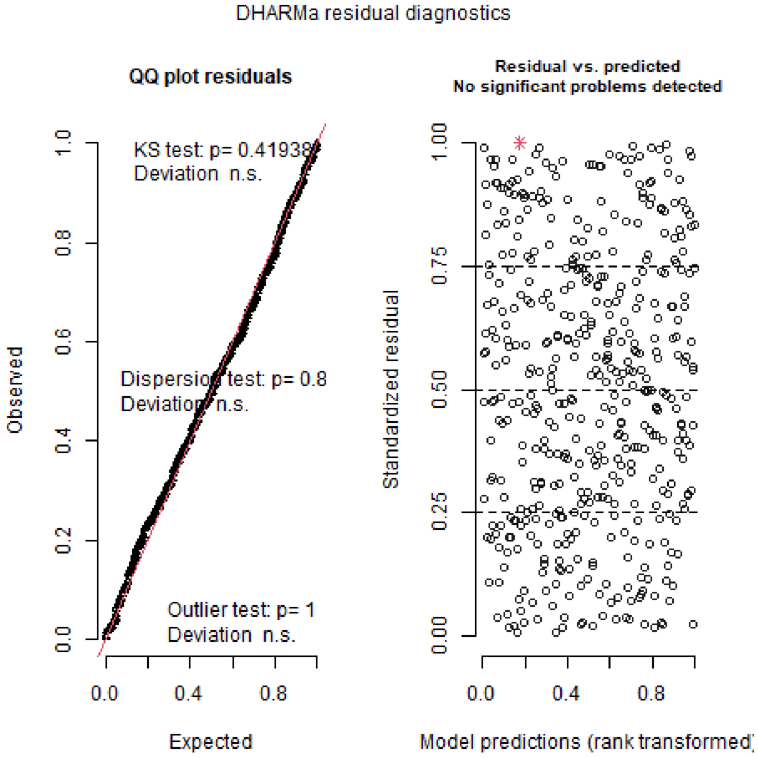
Lophostrix cristata:



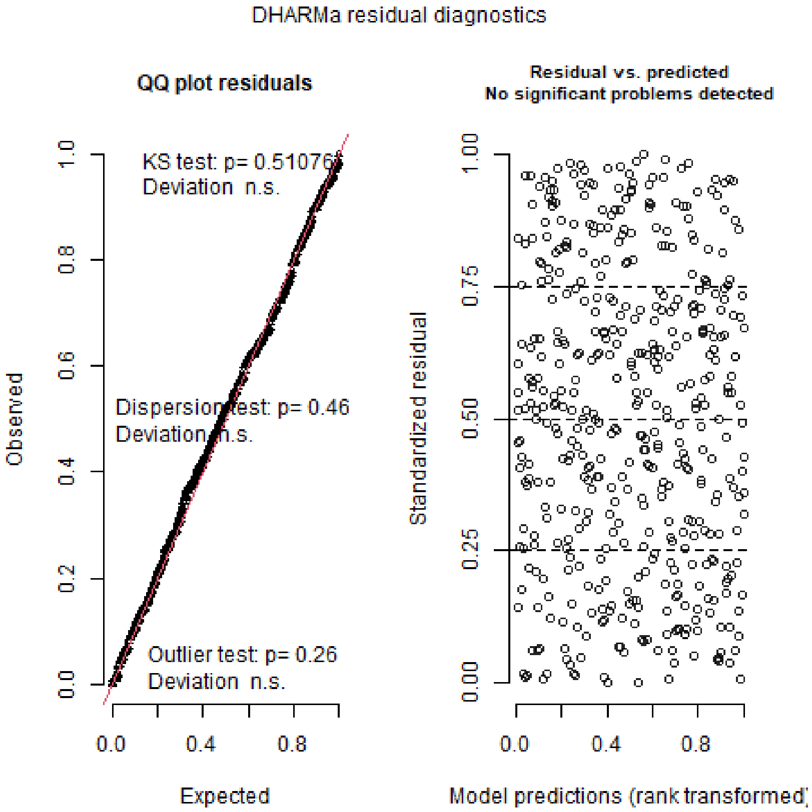
Pulsatrix perspicillata:



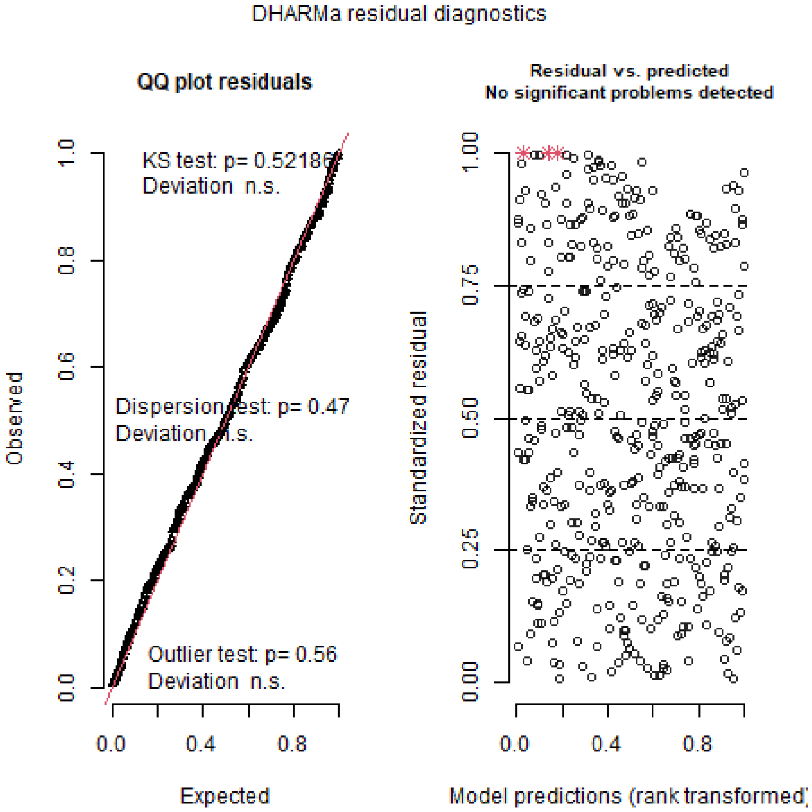
Glaucidium hardyi:



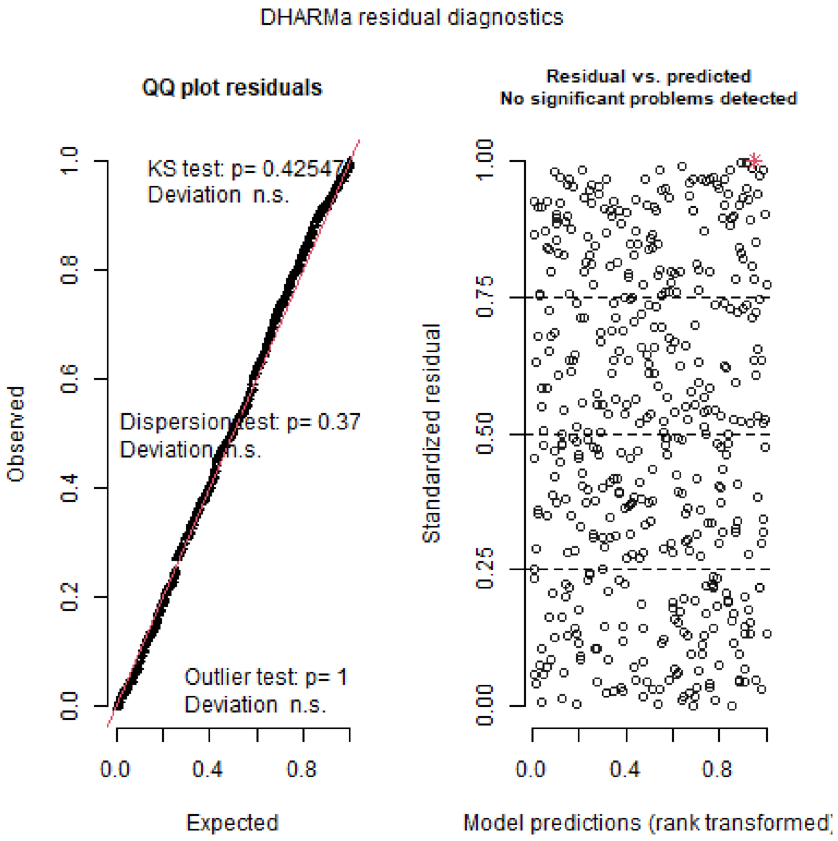
Nyctibius grandis:



Antrostomus sericocaudatus:



Nyctidromus albicollis:



S5.6. Out-of-bag accuracy metrics for target species

Stratified out-of-bag accuracy metrics by DSE for ten target species from the Tadarida classifier.

Species	AUC	F1	Precision	Recall	Specificity
Megascops usta	0.958	0.904	0.880	0.930	0.986
Lophostrix cristata	0.937	0.809	0.750	0.879	0.995
Pulsatrix perspicillata	0.981	0.922	0.879	0.969	0.994

Glaucidium hardyi	0.929	0.854	0.840	0.868	0.989
Nyctibius grandis	0.846	0.683	0.671	0.695	0.996
Nyctibius griseus	0.894	0.791	0.788	0.795	0.994
Nyctibius leucopterus	0.735	0.483	0.490	0.476	0.995
Nyctiphrynus ocellatus	0.935	0.839	0.808	0.873	0.998
Antrostomus sericocaudatus	0.874	0.779	0.793	0.766	0.981
Nyctidromus albicollis	0.827	0.646	0.634	0.660	0.994

S5.7. Out-of-bag accuracy metrics for non-target sonotypes

Sonotype	Sensitivity	Specificity	Pos.Pred.Value	Neg.Pred.Value	Precision	Recall	F1	Prevalence	Detection.Rate	Detection.Prevalence	Balanced.Accuracy
adeaff	0.942	1.000	0.953	1.000	0.953	0.942	0.947	0.004	0.003	0.003	0.971
adehyl	0.863	0.999	0.920	0.999	0.920	0.863	0.891	0.008	0.007	0.008	0.931
alltap	0.876	0.999	0.806	0.999	0.806	0.876	0.840	0.005	0.004	0.005	0.938
alobel	0.812	0.986	0.764	0.989	0.764	0.812	0.787	0.055	0.044	0.058	0.899
alobel_call	0.853	0.997	0.823	0.998	0.823	0.853	0.837	0.013	0.012	0.014	0.925
boageo	0.655	1.000	0.895	0.999	0.895	0.655	0.757	0.003	0.002	0.002	0.827

branch	0.651	0.998	0.668	0.998	0.668	0.651	0.659	0.005	0.003	0.005	0.825
cicada	0.998	1.000	0.999	1.000	0.999	0.998	0.998	0.073	0.073	0.073	0.999
cow	0.701	1.000	0.966	0.999	0.966	0.701	0.812	0.004	0.003	0.003	0.850
crysou	0.944	0.998	0.957	0.998	0.957	0.944	0.951	0.036	0.034	0.035	0.971
cryvar	0.881	0.991	0.762	0.996	0.762	0.881	0.817	0.032	0.028	0.037	0.936
denleu	0.620	1.000	0.965	0.998	0.965	0.620	0.755	0.006	0.004	0.004	0.810
denmin	0.956	0.993	0.837	0.998	0.837	0.956	0.893	0.038	0.037	0.044	0.974
dentri	0.924	1.000	0.888	1.000	0.888	0.924	0.906	0.004	0.003	0.004	0.962
dog	0.639	0.991	0.572	0.993	0.572	0.639	0.604	0.019	0.012	0.021	0.815
engfrei	0.965	1.000	0.988	1.000	0.988	0.965	0.977	0.003	0.003	0.003	0.983
gecko	0.748	0.995	0.589	0.998	0.589	0.748	0.659	0.010	0.007	0.012	0.871
hercac	0.615	1.000	0.971	0.996	0.971	0.615	0.753	0.009	0.006	0.006	0.808
hercac_call	0.538	1.000	0.964	0.998	0.964	0.538	0.691	0.004	0.002	0.002	0.769
i5	0.900	1.000	0.990	0.999	0.990	0.900	0.942	0.005	0.005	0.005	0.950
lf7	0.861	1.000	0.949	1.000	0.949	0.861	0.903	0.003	0.002	0.002	0.930
lursem_call	0.862	1.000	0.902	1.000	0.902	0.862	0.881	0.003	0.002	0.003	0.931
lursem_social	0.890	0.996	0.911	0.996	0.911	0.890	0.900	0.039	0.034	0.038	0.943
megcho_call	0.691	0.998	0.717	0.998	0.717	0.691	0.704	0.006	0.004	0.006	0.845
nycaet_song	0.631	1.000	0.931	0.999	0.931	0.631	0.752	0.003	0.002	0.002	0.816

nycgra_call	0.620	1.000	0.905	0.999	0.905	0.620	0.736	0.003	0.002	0.002	0.810
odoguj	0.686	0.999	0.842	0.998	0.842	0.686	0.756	0.006	0.004	0.005	0.843
ortho1	0.978	0.998	0.922	0.999	0.922	0.978	0.949	0.028	0.028	0.030	0.988
ortho3	0.670	1.000	0.966	0.999	0.966	0.670	0.791	0.003	0.002	0.002	0.835
ortmot	0.562	0.992	0.444	0.995	0.444	0.562	0.496	0.011	0.006	0.014	0.777
pristi2	0.895	1.000	0.917	1.000	0.917	0.895	0.906	0.003	0.003	0.003	0.948
rhimag	0.848	0.999	0.905	0.998	0.905	0.848	0.876	0.010	0.009	0.010	0.924
rhysim_alarm	0.793	0.996	0.699	0.998	0.699	0.793	0.743	0.011	0.009	0.013	0.894
rhysim_call	0.729	0.999	0.782	0.999	0.782	0.729	0.754	0.004	0.003	0.004	0.864
rhysim_call2	0.283	0.998	0.466	0.995	0.466	0.283	0.352	0.006	0.002	0.004	0.640
rhysim_social	0.914	0.995	0.890	0.996	0.890	0.914	0.902	0.042	0.038	0.043	0.955
rooster	0.155	0.999	0.591	0.993	0.591	0.155	0.246	0.008	0.001	0.002	0.577
scicru	0.978	1.000	0.992	1.000	0.992	0.978	0.985	0.005	0.005	0.005	0.989
strhuh_call	0.647	0.999	0.876	0.997	0.876	0.647	0.745	0.007	0.005	0.005	0.823
strhuh_call2	0.530	0.999	0.796	0.997	0.796	0.530	0.636	0.006	0.003	0.004	0.765
strhuh_social	0.640	0.995	0.677	0.994	0.677	0.640	0.658	0.017	0.011	0.016	0.817
tingut_social	0.841	0.996	0.615	0.999	0.615	0.841	0.710	0.007	0.006	0.010	0.919
tintao_social	0.766	1.000	0.927	0.999	0.927	0.766	0.839	0.005	0.004	0.004	0.883
tintao_song	0.763	0.999	0.657	0.999	0.657	0.763	0.706	0.003	0.002	0.004	0.881

tralf	0.466	0.999	0.470	0.999	0.470	0.466	0.468	0.003	0.001	0.003	0.732
tranr	0.574	0.994	0.704	0.990	0.704	0.574	0.632	0.024	0.014	0.020	0.784
trasq	0.508	0.998	0.661	0.996	0.661	0.508	0.574	0.008	0.004	0.006	0.753
wd	0.626	0.998	0.684	0.998	0.684	0.626	0.654	0.006	0.004	0.005	0.812

S5.8. Species detections by forest class

Forest class	Species	Mean (SD)	Median	Max
Undisturbed	Megascops usta	48.4+/-30.179	39	96
Logged	Megascops usta	131.25+/-119.349	121	269
Burnt in 2015	Megascops usta	265.4+/-111.749	296	415
Burnt in 2015 + Logged	Megascops usta	125+/-93.195	121	243
Burnt < 2015 + Logged	Megascops usta	121.5+/-151.854	51	349
Burnt < 2015 + in 2015 + Logged	Megascops usta	56.667+/-45.654	36	109
Secondary forest	Megascops usta	165.333+/-153.266	108	339

Undisturbed	Lophostrix cristata	124+/-61.388	142	181
Logged	Lophostrix cristata	424.75+/-356.421	402	882
Burnt in 2015	Lophostrix cristata	356.2+/-256.883	223	767
Burnt in 2015 + Logged	Lophostrix cristata	329.75+/-220.893	325.5	556
Burnt < 2015 + Logged	Lophostrix cristata	107.75+/-172.442	34	363
Burnt < 2015 + in 2015 + Logged	Lophostrix cristata	76+/-24.759	67	104
Secondary forest	Lophostrix cristata	96+/-72.09	60	179
Undisturbed	Pulsatrix perspicillata	5.4+/-4.98	6	12
Logged	Pulsatrix perspicillata	3.25+/-2.062	3	6
Burnt in 2015	Pulsatrix perspicillata	6+/-11.247	1	26
Burnt in 2015 + Logged	Pulsatrix perspicillata	12+/-8.042	15.5	17
Burnt < 2015 + Logged	Pulsatrix perspicillata	22.5+/-12.477	23	35

Burnt < 2015 + in 2015 + Logged	Pulsatrix perspicillata	43.667+/-22.898	51	62
Secondary forest	Pulsatrix perspicillata	15.667+/-5.132	17	20
Undisturbed	Glaucidium hardyi	22.4+/-16.965	20	51
Logged	Glaucidium hardyi	163+/-147.289	154.5	312
Burnt in 2015	Glaucidium hardyi	116.8+/-75.748	92	222
Burnt in 2015 + Logged	Glaucidium hardyi	103.25+/-95.395	92.5	227
Burnt < 2015 + Logged	Glaucidium hardyi	24.25+/-34.413	12	73
Burnt < 2015 + in 2015 + Logged	Glaucidium hardyi	149+/-219.11	24	402
Secondary forest	Glaucidium hardyi	32.667+/-40.513	20	78
Undisturbed	Nyctibius grandis	3+/-5.612	1	13
Logged	Nyctibius grandis	24.5+/-21.142	21.5	53
Burnt in 2015	Nyctibius grandis	29.6+/-14.96	27	48

Burnt in 2015 + Logged	Nyctibius grandis	25+/-18.991	27	45
Burnt < 2015 + Logged	Nyctibius grandis	5.75+/-10.21	1	21
Burnt < 2015 + in 2015 + Logged	Nyctibius grandis	9.667+/-8.737	12	17
Secondary forest	Nyctibius grandis	1.333+/-0.577	1	2
Undisturbed	Nyctibius griseus	0+/-0	0	0
Logged	Nyctibius griseus	5+/-8.124	1.5	17
Burnt in 2015	Nyctibius griseus	1.4+/-2.608	0	6
Burnt in 2015 + Logged	Nyctibius griseus	2.25+/-2.062	2	5
Burnt < 2015 + Logged	Nyctibius griseus	1+/-1.414	0.5	3
Burnt < 2015 + in 2015 + Logged	Nyctibius griseus	5.333+/-3.512	5	9
Secondary forest	Nyctibius griseus	31+/-34.395	25	68

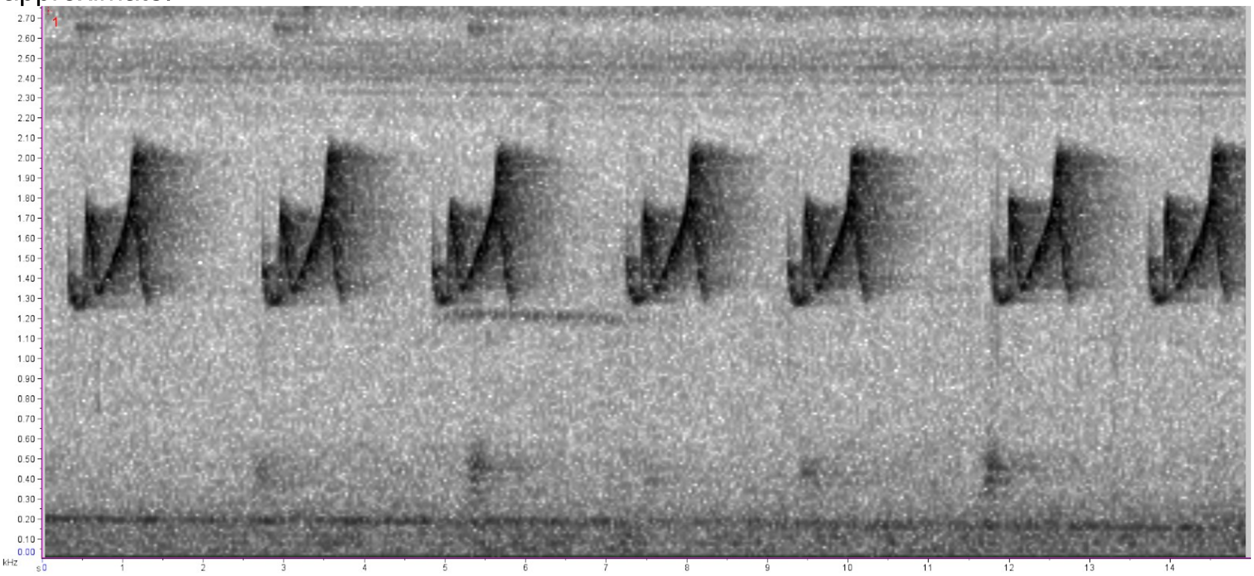
Undisturbed	Nyctibius leucopterus	0+/-0	0	0
Logged	Nyctibius leucopterus	0+/-0	0	0
Burnt in 2015	Nyctibius leucopterus	0.4+/-0.894	0	2
Burnt in 2015 + Logged	Nyctibius leucopterus	0+/-0	0	0
Burnt < 2015 + Logged	Nyctibius leucopterus	0+/-0	0	0
Burnt < 2015 + in 2015 + Logged	Nyctibius leucopterus	7+/-12.124	0	21
Secondary forest	Nyctibius leucopterus	0+/-0	0	0
Undisturbed	Nyctiphrynus ocellatus	0.4+/-0.894	0	2
Logged	Nyctiphrynus ocellatus	57.75+/-115.5	0	231
Burnt in 2015	Nyctiphrynus ocellatus	19.2+/-14.007	27	33
Burnt in 2015 + Logged	Nyctiphrynus ocellatus	42+/-84	0	168
Burnt < 2015 + Logged	Nyctiphrynus ocellatus	3+/-6	0	12

Burnt < 2015 + in 2015 + Logged	Nyctiphrynus ocellatus	0+/-0	0	0
Secondary forest	Nyctiphrynus ocellatus	96+/-163.686	3	285
Undisturbed	Antrostomus sericocaudatus	11.2+/-19.537	3	46
Logged	Antrostomus sericocaudatus	47.5+/-88.425	5	180
Burnt in 2015	Antrostomus sericocaudatus	227.4+/-195.745	138	473
Burnt in 2015 + Logged	Antrostomus sericocaudatus	211+/-170.759	239	364
Burnt < 2015 + Logged	Antrostomus sericocaudatus	92.75+/-185.5	0	371
Burnt < 2015 + in 2015 + Logged	Antrostomus sericocaudatus	149+/-51.971	129	208
Secondary forest	Antrostomus sericocaudatus	57.333+/-91.621	9	163
Undisturbed	Nyctidromus albicollis	1.4+/-2.074	1	5
Logged	Nyctidromus albicollis	22.25+/-27.597	15.5	58
Burnt in 2015	Nyctidromus albicollis	3+/-3.464	2	8

Burnt in 2015 + Logged	Nyctidromus albicollis	144+/-170.749	82.5	388
Burnt < 2015 + Logged	Nyctidromus albicollis	206.5+/-252.842	155	516
Burnt < 2015 + in 2015 + Logged	Nyctidromus albicollis	88.333+/-71.347	127	132
Secondary forest	Nyctidromus albicollis	3.333+/-2.887	5	5

S5.9: Spectrogram of 21st July 2018 at 21:05 showing a typical series of *A. sericocaudatus* calls.

The recording is 15 s in duration containing 7 *A.sericocaudatus* calls (1.2-2.2 kHz, throughout), 5 *L.cristatus* calls (0.2-0.7 kHz, 2.5 - 12 s) and a single *G. hardyi* call (1.2 kHz, 4.5-7.5 s) taken from logged forest burnt after 2015 on. Frequencies and times are approximate.



No method is perfect.