

Assessment of acoustic indices for monitoring phylogenetic and temporal patterns of biodiversity in tropical forests

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September 2015

A thesis submitted in partial fulfilment of the requirements for the degree of Master of Science at
Imperial College London

Formatted in the journal style of Ecological Indicators

Submitted for the MSc in Computational Methods in Ecology and Evolution

Declaration

I declare that the following study is my own work, and where it contains the work of others, this has been acknowledged.

After initial guidance from my supervisor on the project topic and analyses, I believe I have worked independently on the development of the project rationale and the acoustic data analysis.

Raw acoustic data was provided via a web-based portal. I downloaded, converted, cleaned, processed and analysed the files independently. The acoustic indices were taken from published works, and were developed by many different authors as cited in the text.

Data processing and analysis was conducted with scripts written by myself in Python and R. The scripts employ several R packages developed for acoustic and phylogenetic processing, which are referenced within the text. Philip Knaute provided an outline Python script for reading and cutting .wav files in Python, which I altered considerably for use in this project. I acknowledge and am grateful to Unding Jami and David Edwards for their work in carefully identifying bird species by listening to the acoustic data.

Acknowledgements

I would like to thank my supervisor Dr. Rob Ewers, and course directors Dr. Samraat Pawar and Dr. James Rosindell for their helpful guidance on the project, as well as Philip Knaute for his assistance with earlier incarnations of this project. Particularly, I would like to thank Unding Jami and David Edwards for providing their time and expertise to carefully identify bird species in the acoustic recordings.

Abstract

In the face of environmental change, current downward trends in biodiversity are of the utmost concern to ecologists, conservationists and policy-makers. Biodiversity loss threatens ecosystem function and the services these provide. In order to detect trends in biodiversity through time, and understand the efficacy of conservation policies, the creation of long-term biodiversity datasets are of paramount importance. However, the expensive and time consuming nature of collecting monitoring data means there are very few datasets that consider time-scales of a decade or greater. Despite increasing recognition of its importance in setting conservation priorities, even fewer consider biodiversity in terms of its phylogenetic components. Continuous acoustic recordings have the potential to facilitate the development of long-term biodiversity datasets. Evidence suggests that they can reduce costs, avoid invasive sampling and undertake continuous measurements in remote locations. Recent work has developed acoustic indices which summarise biodiversity using acoustic data. However, there is only limited understanding of how these reflect the temporal dynamics and phylogenetic diversity of tropical ecosystems. This study used acoustic data from the Stability of Altered Forest Ecosystems project in Borneo, to examine the extent to which acoustic indices reflected phylogenetic diversity, and how well they can characterise daily variation in animal activity.

Phylogenetic diversity was compared to three acoustic dissimilarity indices using Mantel tests and Spearman's rank correlation. This revealed that there was no correlation between phylogenetic diversity and acoustic dissimilarity. The results suggest that in complex tropical ecosystems it is difficult to detect a phylogenetic signal in the acoustic indices. This is most likely due to factors such as habitat structure driving phylogenetic and acoustic divergence at different rates. Linear mixed-effects models were used to examine the difference between acoustic diversity and the time categories; dawn and dusk, across three different forest locations. Acoustic diversity was significantly greater at dawn than at dusk. However, there was no difference between the three locations examined. As a result, acoustic indices may be suitable to monitor temporal patterns of diversity in tropical soundscapes. However, the relationship of acoustic indices to species diversity requires further validation.

Keywords: acoustic, biodiversity, phylogeny, tropical, forest, indices

Highlights

- There was no correlation between phylogenetic diversity and acoustic dissimilarity.
- Acoustic indices are limited in the extent to which they can monitor phylogenetic diversity.
- Acoustic biodiversity was significantly greater at dawn when compared to dusk.
- Acoustic biodiversity indices were useful for monitoring temporal change.

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1 Introduction

This study was conducted against a backdrop of unprecedented anthropogenic-driven environmental change. The resulting loss of biodiversity is of utmost concern. Schipper et al. (2008) reported that 1 in 4 of the world's species of mammal are threatened with extinction, and 1 in 2 are declining. There is evidence that this biodiversity is important for ecosystem function, and while there has been heated debate on the subject, it is suggested that 95% of experimental studies support a positive relationship between species richness and ecosystem function (Kaiser 2000, Purvis & Hector 2000). Ecosystems support all life on Earth and provide vital economic and social services for human activities (Purvis & Hector 2000). As a result, ecologists, policy-makers and conservationists are being asked to make decisions which mitigate against trends in biodiversity loss that may put ecosystem function at risk (Magurran et al. 2010). However, in order to do this it is necessary to understand the patterns of biodiversity at present, and how these change over time and space.

This information is derived by monitoring biodiversity through time at locations around the world. Magurran et al. (2010) emphasised that long-term data are of particular importance in understanding biodiversity. They provide essential information on background trends and are required to elucidate anthropogenic signals from long-term natural change (Magurran et al. 2010). Furthermore, experimental studies indicate that long-term data on biodiversity change could provide early warning systems for ecosystem collapse. For example, Dai et al. (2012) reported that as populations approached catastrophic thresholds they recover more slowly from perturbations, and population fluctuations increase in size and duration as they approach a tipping point. Such trends, if identified in long-term monitoring data, could serve as early indicators of an ecosystem under stress. In addition, Strategic Goal C of the 2020 Aichi Biodiversity Targets aims to, '...improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity' (Convention on Biological Diversity 2015). In order to objectively quantify progress towards such goals, it is necessary to collect detailed and informative data on the biodiversity of target systems (Tittensor et al. 2014). However, despite their evident importance, there are still relatively few datasets that cover time-scales of decades or longer (Magurran et al. 2010).

There are even fewer datasets that consider biodiversity in terms other than species richness, abundance and evenness (Winter et al. 2013). Magurran (2004) defines biodiversity as, 'the variety and abundance of species..'. However, it is increasingly recognised that additional facets such as phylogenetic and functional diversity are important features of a wider biodiversity concept (Isaac et al. 2007, Winter et al. 2013). Phylogenetic diversity describes the different evolutionary histories of species in the tree of life and can be measured as the sum of branch lengths in a phylogenetic tree (Purvis & Hector 2000). Under this definition, species in old and sparsely populated clades represent a greater loss in biodiversity, and consequently, are a conservation priority when compared to younger species that have many close relatives (Isaac et al. 2007). The concept has been neglected by policy-makers when setting conservation priorities (Rosauer & Mooers 2013). The advantages of considering phy-

logenetic biodiversity include its independence from taxonomic identification. When the resolution of taxonomy in an area is improved, it may alter estimates of biodiversity without changes in species composition. As a result, conservation inventories are altered (Mace et al. 2003). The methodological complexities of generating a phylogeny have discouraged the use of phylogenetic diversity in many conservation arenas, and while well resolved phylogenies are increasingly available, to encourage its practical use in conservation, Rosauer & Mooers (2013) argue that much more needs to be done to make it as manageable as mapping species diversity.

However, it is possible to argue that there are also many barriers to collecting the long-term data required to map species diversity. It is a time-consuming and expensive process which often requires specially trained fieldwork assistants (Magurran et al. 2010). As a result, there is generally inadequate funding to support studies for long periods of time. Traditional methods are also invasive and use multiple observers (Pieretti et al. 2011). These observers are often subjective and may skew species estimates with their individual bias (Depraetere et al. 2012). Furthermore, the other commitments many researchers have, lack of continuous funding and the inability to access remote sites at certain times of year, often dictate inconsistent sampling efforts. This can significantly influence the amount of biodiversity detected (Magurran et al. 2010). For example, species abundance estimates will increase as sites are surveyed more thoroughly or for a longer period of time. Species abundance increases as a result of the increased effort rather than changes in the number of species (Magurran 2004). There are several other sampling factors that need careful consideration. There is a close link between the number of species and the area of the site explored. As it becomes larger, greater number of species will be detected (Magurran 2004). In addition, the underlying species abundance distribution can influence species diversity estimates; when evenness is low, rare species may be underestimated because the number of individuals is low in relation to other species (Magurran 2004). Finally, not all species are as easy for an observer to detect and sample. Therefore, obvious species tend to be overestimated (Magurran 2004).

Acoustic analysis has the potential to make a significant contribution to improving and expanding current biodiversity monitoring efforts. There are many animal species that produce characteristic sounds when they communicate. These are often distinctive species specific calls that can be used as proxy for the presence of the species in the landscape (Pijanowski et al. 2011). Primarily, the field of bioacoustics has focussed on examining the behaviour and communication of a single focal species (Sueur et al. 2014). However, the emerging field of soundscape ecology focuses on spatio-temporal patterns of sound at a landscape scale (Pijanowski et al. 2011). As a result, acoustic data is now being used to study ecological questions at a broad range of organisational levels (Sueur et al. 2014). This expansion in scale has been facilitated by sound recording technology and analysis, which has advanced greatly in recent years due to the commercial success of digital sound systems (Villanueva-Rivera et al. 2011). It is inexpensive and technologically possible to simultaneously record sound at multiple remote sites (Villanueva-Rivera et al. 2011). Consequently, acoustic data is a viable methodology for collecting biodiversity data, and with the invention of automated systems, the process need only involve limited human intervention. Modern acoustic systems can, therefore,

collect unprecedented volumes of data, considerably reduce the human costs involved and avoid invasive sampling of a habitat while maintaining an objective and consistent sampling pattern (Pieretti et al. 2011). While limitations are still apparent, in that it can only focus on species that produce vocalisations and it may be biased to more distinctive species, this negates many of the oppressive forces to long-term biodiversity monitoring discussed above (Pieretti et al. 2011). It also offers the opportunity to expand biodiversity monitoring to habitats that are difficult or expensive to access regularly, such as remote sites or sites after dark (Depraetere et al. 2012).

However, the analysis of large collections of acoustic recordings in order to garner valid and biologically relevant information still represents a significant hurdle. Manual analysis and aural identification by human observers has proven very successful. Studies have been able to identify single species or conduct surveys of species richness by identifying all taxa in a recording (Celis-Murillo et al. 2009, Wimmer et al. 2013). This method of manual analysis can be very accurate when they are undertaken by knowledgeable and experienced experts (Wimmer et al. 2013). However, their subjective nature makes them difficult to quantify and compare (Deecke & Janik 2006). Furthermore, the method quickly becomes prohibitive as the size of the dataset becomes larger. There are currently three complementary approaches to address this issue under active research. Firstly, machine learning and pattern recognition techniques attempt to automate species classification. There have been successful implementations of such automated systems that have classified species of amphibian, bird (Acevedo et al. 2009), insect (Chesmore 2004) and bat (Walters et al. 2012). These have the potential to analyse large amounts of data quickly but sacrifice the accuracy of human judgements (Deecke & Janik 2006, Wimmer et al. 2013). Their potential has been further demonstrated by the successful development of large scale acoustic monitoring systems such as the European bat classification tool *iBatsID* (Walters et al. 2012), *Arbimon*, an automated remote suite of microphones in Puerto Rico and Costa Rica (Aide et al. 2013), and *Amibio*, a network of 17 monitoring stations in Greece (Jahn et al. 2013). Secondly, web technologies permit the exploitation of a team of online citizen scientists. Shamir et al. (2014) asked users to classify whale calls. They were successfully able to identify whales from different locations. However, they demonstrated computer analysis could outperform citizen scientists on some occasions. This highlights the need for careful analysis and consideration of the disparity in the skill level of people taking part (Dickinson et al. 2012, Shamir et al. 2014). Lastly signal processing techniques can be used to derive biodiversity indices. The development of acoustic indices is of particular interest for long-term biodiversity monitoring because they can facilitate the rapid assessment of biodiversity without identifying individual species. This approach is of particular use in environments where the diversity of overlapping sounds makes it difficult for listeners to discern individual species (Gasc et al. 2013).

Sound has two properties that can be used to develop indices, amplitude and frequency. An acoustic index is a statistic that summarises one or both of these aspects in the signal. They are based on the Acoustic Niche Hypothesis (ANH) proposed by Krause (1987), which suggests that species are in competition for acoustic space. Therefore, they will seek to minimize interference by vocalising at different frequencies or times. Acoustic indices exploit this to assess diversity by calculating the oc-

cupancy of different frequency bands, which can be used to represent different species (Villanueva-Rivera et al. 2011). The complexity of the soundscape can, therefore, be linked to the number of species present in the landscape. Although it is argued that biodiversity indices neglect the multi-dimensional nature of biodiversity (Purvis & Hector 2000), the development of an index is attractive because they can distil biodiversity into one or more values that can be easily tracked through time and presented to policy-makers. Sueur et al. (2008) wrote the seminal work on acoustic indices for biodiversity assessment from acoustic data. They presented two indices, the H index which measures species richness, and the D index which calculates acoustic dissimilarity between communities. In the time since this benchmark paper, there has been a proliferation of indices that have considered specific environmental traits (Depraetere et al. 2012, Rodriguez et al. 2014) and species (Pieretti et al. 2011). A recent review of the development of these indices suggests there are 21 different alpha acoustic indices and seven beta diversity measures (Sueur et al. 2014). As described above, the majority of these use measures of amplitude or frequency to determine diversity (Depraetere et al. 2012, Gasc et al. 2013, Pieretti et al. 2011, Sueur et al. 2008, Villanueva-Rivera et al. 2011). However, relatively fewer try to decompose the sounds into those relating to anthrophony, biophony and geophony. Kasten et al. (2012) achieved this by classifying sounds in the frequency range 0 - 2 kHz as mechanical signals, and those between 2 and 8 kHz as biological sounds. These components were determined in a temperate environment, and it is unlikely it would have meaningful application the the tropical location due to the much greater diversity of sounds (Sueur et al. 2014)

The relationship between acoustic indices and biodiversity has been demonstrated on simulated communities by Sueur et al. (2008). The index H which measures the spectral and temporal entropy of the frequency spectrum and signal amplitude envelope respectively, increased with species richness following a logarithmic scale, and the acoustic dissimilarity index D, which compared the difference in the frequency spectra and signal amplitude envelopes of two files increased linearly with the number of unshared species (Sueur et al. 2008). However, Depraetere et al. (2012) questioned the applicability of these findings to temperate settings where the background anthropogenic and geophonic noise dominates over biophonic components. In this setting they suggest, the H index generates inaccurate values. They proposed a new index; Acoustic Richness (AR), which considered the overall amplitude of the signal, an area neglected by the H index. The index was corroborated against observed richness values in a temperate woodland.

The indices above focus on abundance and evenness. However, Depraetere et al. (2012) indicated that the extent to which acoustic indices reflect different types of biodiversity was of critical importance. In addition, given the focus of conservation strategies on maintaining, not only species diversity but phylogenetic diversity, it is important to understand how acoustic indices may be able to contribute to the monitoring and detection of these facets and their trends (Depraetere et al. 2012, Isaac et al. 2007). Gasc et al. (2013) examined if phylogenetic and functional diversity was reflected in acoustic diversity indices, and concluded that acoustic diversity, as measured by dissimilarity indices, reflect phylogenetic diversity calculated as tree branch length. This study was conducted with a community of temperate birds that were counted during manual surveys. Bird songs were then

selected from a variety of sources, such as the online bird song database Xeno-Canto (www.xeno-canto.org). This result suggests that acoustic indices may have application in monitoring phylogenetic diversity.

Acoustic indices have also been used to examine spatial and temporal patterns of diversity in temperate and tropical locations. Due to continued environmental change, it is a particular challenge to understand soundscape dynamics in reference to natural and anthropogenic variation (Rodriguez et al. 2014). Studies have shown that anthropogenic noise can have an impact on the timing and level of biological sounds by masking. Masking occurs where noise inhibits the perception of sound and as a result, the producer may alter their signal (Joo et al. 2011). Birds, primates and cetaceans have been observed to alter their vocalisations in response to noise (Barber et al. 2010). Furthermore, Francis et al. (2011) demonstrated that noise altered bird behaviour. They reported reduced nest occupancy near gas well compressors in some species of flycatcher. This is of particular relevance to tropical forest locations that are undergoing human modification. Acoustic data may not only reveal changes in the number of species, but important ecological changes reflected in the soundscape (Pijanowski et al. 2011).

Few studies have examined tropical soundscapes but it is recognised that they are dramatically different to temperate locations due to the high levels of diversity (Rodriguez et al. 2014). The limitations of traditional biodiversity monitoring methodologies are felt acutely in tropical systems, and as a result, traditional data is also particularly sparse in these locations. The drivers of ecological change can differ significantly between locations (Magurran 2004) and tropical ecosystems host approximately two thirds of terrestrial biodiversity (Gardner et al. 2009). In Borneo remote sensing evidence suggests that forest area has declined by 30.2% since 1973 (Gaveau et al. 2014) and there is little understanding about the response of species and communities to such stress (Gardner et al. 2009). Therefore, specific long-term datasets are required to assess the dynamics of biodiversity in the region, which at present remain largely unknown. (Molleman et al. 2006).

In summary, it has been demonstrated that acoustic data has the potential to be employed in biodiversity monitoring, and as a result, address the shortcomings in current collections of data. These data are required to help mitigate against the loss of species and ecosystem function in the face of environmental change. Acoustic indices, in particular, have demonstrated their potential to measure biodiversity but there remains only a limited understanding of how they reflect the temporal patterns and phylogenetic diversity in tropical ecosystems, especially those that are undergoing human modification. This study aims to address these shortcomings by examining the temporal and phylogenetic components of acoustic indices with data recorded at the Stability of Altered Forest Ecosystems project (SAFE) in Borneo. Specifically, it will address the following research questions:

Question 1: Do acoustic indices reflect the phylogenetic diversity of avian communities in tropical ecosystems?

Gasc et al. (2013) demonstrated the existence of a correlation between acoustic dissimilarity indices

and phylogenetic diversity in temperate ecosystems. This study aims to extend this to the tropical forest setting. Unlike Gasc et al. (2013) who devised a set of species calls from third party recordings, this study will examine an assemblage of birds recorded in the field at fixed monitoring stations. This will help test the indices for phylogenetic diversity in relation to more realistic monitoring data that contains greater heterogeneity in recording quality. The relationship between song divergence and genetic divergence in birds is complex (Wilkins et al. 2013). There are several factors that may drive their concurrent divergence at different rates. For example, habitat structure, sexual selection and cultural learning (Irwin et al. 2008, McCracken & Sheldon 1997, Wilkins et al. 2013). However, in light of the conclusions by Gasc et al. (2013) it is possible to hypothesise that:

Hypothesis 1.1: Species separated by greater phylogenetic distance will be more acoustically divergent.

The aim of Question 1 is to address if acoustic indices could be used by conservationists and policy-makers to measure phylogenetic diversity. As a result, the measures of acoustic dissimilarity and phylogenetic diversity have been extracted from literature on this area. It is predicted that the acoustic dissimilarity indices, spectral dissimilarity (D_f), Symmetric Kullback-Leibler divergence and the Kolmogorov-Smirnov distance will be positively correlated with phylogenetic distance (the pairwise difference in total branch length between two species in a phylogenetic tree) and evolutionary distinctiveness. This second measure has not previously been examined in relation to acoustic indices. It is included here because of its usefulness in assessing conservation priorities. It has been shown to incorporate species value and extinction risk, and was robust to uncertainty (Isaac et al. 2007).

Question 2: Are acoustic indices able to detect variation in daily animal diversity within a tropical rainforest location?

The level of animal acoustic activity in a day is known to vary. The dawn chorus is a time of particular activity for diurnal birds and other times of day are dominated by cicadas and amphibians (Rodriguez et al. 2014). Rodriguez et al. (2014) revealed that acoustic diversity indices are able to detect these patterns in activity. They reported distinct differences in acoustic structure at different times of the day and higher levels of activity at dawn in a neotropical forest in French Guiana. As a result it is possible to hypothesise that:

Hypothesis 2.1: Acoustic diversity will be greater at dawn than at dusk.

It is important to further validate the ability of acoustic indices to detect variation in species activity in order to determine their usefulness for ongoing monitoring. This study will utilise a common acoustic diversity index, H , to detect variation at three locations in Malaysian Borneo. It is possible to predict that the index, H , will be greater at dawn.

2 Methodology

2.1 Study Area and Data Collection

Acoustic data was recorded at the Stability of Altered Forest Ecosystems (SAFE) project in Malaysian Borneo. The project is located in an area of lowland dipterocarp forest currently undergoing conversion to oil palm plantation (Ewers et al. 2011). SAFE is taking advantage of this planned work to examine the impact of forest fragmentation on the ecosystem.

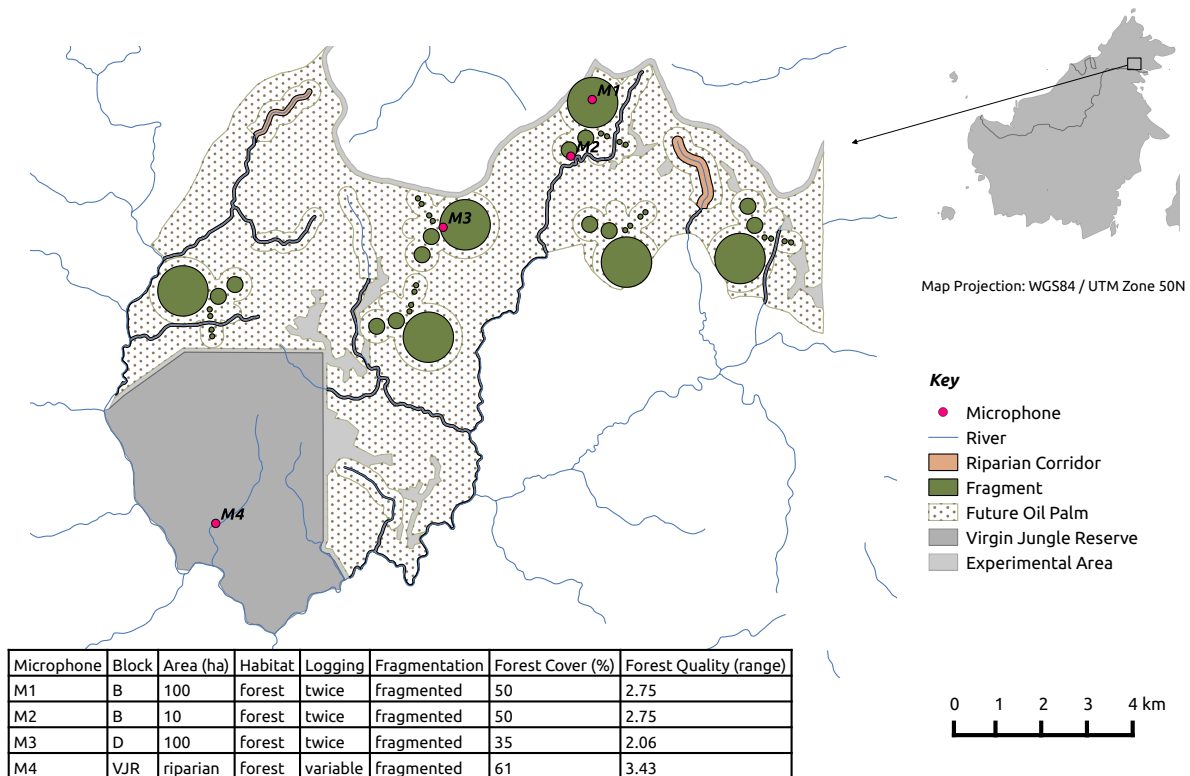


Figure 1: Study area for the Stability of Forest Ecosystems project in Malaysian Borneo. Full description of the study area and description of the experimental design can be found at Ewers et al. (2011). Microphones M1 to M4 are located along a gradient of forest fragmentation as demonstrated in the attribute table on the bottom left. Block B and D are made up of forest fragments of sizes (a) one 100 ha plot, (b) two 10 ha plots, (c) 4 1 ha plots and (d) the adjacent deforested land. Virgin Jungle Reserve is an area of 2200 hectares that has been selectively logged and will become isolated during conversion. Forest Quality represents the average value for the area on a qualitative scale from 1 to 5; 1 being poor and 5 very good (Ewers et al. 2011). GIS base layers provided by SAFE Project.

The area is the location for the deployment of a long-term real time acoustic monitoring project. The acoustic data will be used to track biodiversity through time using acoustic indices, automated species detection and the crowd-sourced identification of species calls. The system will be unique in its scale, level of automation and the continuous nature of its sampling. As part of this ongoing project,

four solar-powered Wildlife Song Meter SM3 bioacoustic recorders (Wildlife Acoustics Inc., Concord, MA, USA) were deployed with omni-directional microphones (sensitivity: 20Hz - 20kHz). These are located across a transect of forest fragmentation as shown in Figure 1. This study utilised three of these microphones (M1 to M3, Figure 1), which are located between 1 and 3 kilometres apart. The distance between microphones ensures there is no overlap in the sound recordings between locations. Microphone M1 is located at the centre of a 100 ha forest fragment with 50% forest cover. M2 is located at the edge of a 10 ha fragment with 50% forest cover and M3 at the edge of a 100 ha fragment with 35% forest cover.

The microphones are mounted securely in a rain-proof casing 2m above ground height to an embedded metal pole as shown in Figure 2. Sound was recorded for 55 minutes out of every hour, 24 hours a day, and transmitted via the mobile data network as lossless .wac format files (sample rate: 16kHz, quantisation: 16 bit), labelled with location and recording start-time. These files were downloaded via a secure web-based portal hosted by Biomachines (www.biomachines.com). This study downloaded, cleaned and analysed the data from this portal but did not contribute to the design or collection of the original acoustic data described above.



Figure 2: Image of microphone at SAFE project. From the top components are: solar panels and two microphones at 2m, controller, SM3 sound recorder and battery boxes. They are mounted to secured pole via U-mounts.

2.2 Phylogenetic Diversity and Acoustic Dissimilarity Indices

In order to compare acoustic dissimilarity and phylogenetic diversity, it was necessary to identify the species present in the recordings, extract their calls and determine the phylogenetic relationship of the species. In order to identify the species present, two experts were asked to listen to the recordings. A systematic sampling regime was used to extract a total of 120, 45 second clips from the acoustic data shown in Table 1. The days selected are an artefact of those that were available due to mechanical issues and file distortion. The aim of this sampling was to maximise the variation

in the species that were detected and produce a set of data that was of feasible length for manual aural identification. The first 45 seconds of every hour was extracted for the dates shown in Table 1. Additional clips were taken every half hour for the periods from 5:00 to 07:00 and 17:30 to 19:30 to offer further resolution for these particularly diverse periods of the day. Wimmer et al. (2013) demonstrated that sampling of the data is effective for generating an accurate representation of the species in a community from acoustic data.

2.2.1 Pre-Processing of Audio Files

The sound files (Table 1) were downloaded from Biomachines' servers and converted to .wav format using the WAC2WAV conversion software (Wildlife Acoustics Inc., Concord, MA, USA). Each set of files began with a different start time as designated in the file name. Therefore, a custom Python script was used to align the files in time and extract each 45 second clip. A high pass filter was applied at 2 kHz to remove background noise from mechanical and geophonic sources using the batch processing feature 'chains' from the open source audio editor program Audacity ®2.1.0 (Audacity Team 1999-2015). The clips were then listened to using headphones to detect any remaining anthropogenic and geophonic noise. Those that were found to contain rain or chain saw noise were removed from the analysis.

Date	Location	Hours
22/04/2015	3	3
23/04/2015	3	24
24/04/2015	3	1
25/04/2015	2	5
26/04/2015	2	16
27/04/2015	2	1
28/04/2015	2	4
29/04/2015	2	1
08/06/2015	1	7
09/06/2015	1	24
10/06/2015	1	11
12/06/2015	3	14
13/06/2015	3	2

Table 1: Date, location and the number of hours of data available from which 120, 45 second clips were extracted for analysis. The files were aligned in time and clips extracted using Python.

2.2.2 Manual Aural Identification

Two experts with extensive experience of species identification in the study area listened to each file. The species were identified from the calls present in each clip. The objective was to achieve the most accurate record of the species present in each clip possible. Therefore, the listener was required to listen to every clip in its entirety at least once but was permitted to listen to the clips in full

or in part as many times as required, in order to generate an accurate identification. Listeners were also required to use head-phones to minimise interference from extraneous sounds while listening to the recordings, and maximise the volume of the recordings to improve their ability to discriminate between sounds. They were asked to record the name of the species, the time the species began to call and whether the call was in the foreground or the background of the clip. The skilled listeners were able to identify a total of 47 species.

2.2.3 Acoustic Dissimilarity Indices

From the list of species that were identified by listeners, a subset of 20 birds as shown in Table 2 were used in this study. These species were used because a suitable call for analysis could be extracted from the acoustic community. A clip was used only when it met the following two requirements:

1. The species could be heard calling repeatedly or continuously for 25 seconds.
2. The expert listeners classified the call as in the foreground.

The 25 second segment was extracted from the original clip and was subject to further filtering to reduce background noise from concurrent calling species. A low pass filter was applied at 5 kHz again using the batch processing feature of the program Audacity. This removed high frequency sounds, particularly cicadas, dominant above this frequency.

Common name	Scientific name
Bushy-crested hornbill	<i>Anorrhinus galeritus</i>
Little spiderhunter	<i>Arachnothera longirostra</i>
Great argus	<i>Argusianus argus</i>
Rhinoceros hornbill	<i>Buceros rhinoceros</i>
Plaintive cuckoo	<i>Cacomantis merulinus</i>
Banded bay cuckoo	<i>Cacomantis sonneratii</i>
Lesser green leafbird	<i>Chloropsis cyanopogon</i>
Greater green leafbird	<i>Chloropsis sonnerati</i>
Slender-billed crow	<i>Corvus enca</i>
Short-tailed babbler	<i>Malacocincla malaccensis</i>
Dark-necked tailorbird	<i>Orthotomus atrogularis</i>
Ashy tailorbird	<i>Orthotomus ruficeps</i>
Black-capped babbler	<i>Pellorneum capistratum</i>
Bornean black magpie	<i>Platysmurus leucopterus</i>
Yellow-bellied prinia	<i>Prinia flaviventris</i>
Black-headed bulbul	<i>Pycnonotus atriceps</i>
Spectacled bulbul	<i>Pycnonotus erythrophthalmos</i>
Helmeted hornbill	<i>Rhinoplax vigil</i>
Malaysian pied fantail	<i>Rhipidura javanica</i>
Rufous-tailed shama	<i>Trichixos pyrropygus</i>

Table 2: The 20 species identified by expert listeners through manually listening to each of the 120 files. These species were used for phylogenetic and acoustic comparison.

Acoustic dissimilarity is difficult to calculate because small differences in the alignment of a frequency spectrum can result in inflated values of difference (Sueur et al. 2014). As a result, the dissimilarity between the species calls was calculated using three measures that characterise the mean frequency spectrum of the acoustic signal using distinct methods. Towsey et al. (2014) demonstrated that using a combination of indices can result in more confidence in the conclusions than a single measure. The processed .wav files were loaded into R using the package tuneR (R Core Team 2014, Ligges et al. 2014). The following calculations were conducted using functions from the R package Seewave (Sueur, Aubin & Simonis 2008).

The mean frequency spectrum was calculated using a short-time Fourier Transform, which computes the discrete-time Fourier Transform on successive sections of the sound wave using a sliding window (Sueur 2014). The Fourier Transform was calculated using a non-overlapping hanning window and 512 point window length. The Fourier Transform decomposes the sound wave into a sum of sine and cosine functions, each with a specified frequency and amplitude (Sueur 2014). The mean spectrum can be calculated by averaging the Fourier Transform matrix resulting in a set of amplitude levels per frequency. Figure 3 demonstrates a plot of two mean frequency spectra.

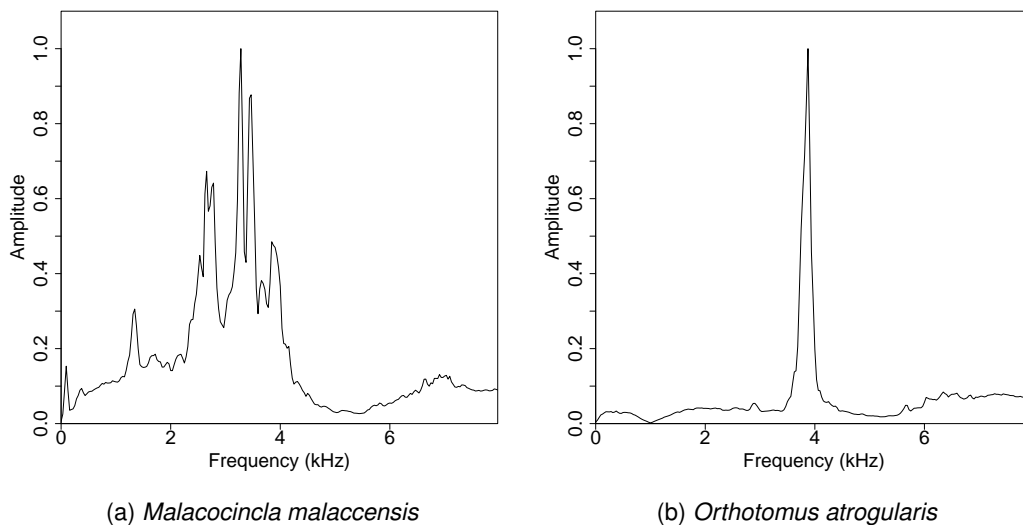


Figure 3: Example mean frequency spectrum plots from two bird calls. The spectrum is calculated using short-time Fourier Transform with a non-overlapping hanning window and 512 point window length.

The Symmetric Kullback-Leibler divergence (KL) or relative entropy calculates the distance between two distributions. In this application it is used to compare the distributions of two frequency spectra (Fig. 3) (Sueur, Aubin & Simonis 2008). It has been used by Gasc et al. (2013) and Lellouch et al. (2014) to calculate the dissimilarity between temperate bird calls successfully, and was used here to examine the calls of tropical birds. The pointwise difference was calculated using the function `kl.dist()` as follows:

$$KL = \frac{1}{2} \left[\sum_i x_i \log_2(x_i/y_i) + \sum_i y_i \log(y_i/x_i) \right] \quad (1)$$

where x_i is the amplitude at successive frequency bins of the mean spectrum of bird 1 and y_i is amplitude at successive frequency bins of the mean spectrum of bird 2 (Kullback & Leibler 1951, Lellouch et al. 2014).

The KL is a non-symmetric measure of distance. This means the distance of spectrum 1 to spectrum 2 is not equal to the distance of spectrum 2 to spectrum 1 (Sueur, Aubin & Simonis 2008). As a result, the divergence was calculated in both directions. The symmetric divergence was generated by calculating half the sum of the individual divergence as shown in Equation 1 (Lellouch et al. 2014, Sueur, Aubin & Simonis 2008).

The second measure of dissimilarity was the Kolomogorov-Smirnov (KS) distance (Eq. 2). The KS compares the difference between two empirical cumulative distribution functions (ECDF) and was again used by Gasc et al. (2013) and Lellouch et al. (2014) in the comparison of acoustic data. Their results indicate that it is a practical measure that can detect differences in acoustic bird call data. KS was calculated using the function `ks.dist()` as follows:

$$KS = \max_i |X_i - Y_i| \quad (2)$$

where X is the ECDF for bird call 1 and Y is the ECDF for bird call 2 (Lellouch et al. 2014).

The measure spectral dissimilarity D_f was developed by Sueur et al. (2008). The original index calculated both the spectral and the temporal dissimilarity. However, the temporal component of the index has been discredited due to the necessity for temporal alignment of the amplitude envelopes, which it is suggested, is very difficult to achieve (Sueur et al. 2014).

The spectral dissimilarity is determined by first calculating the mean spectrum using a short time Fourier Transform (Fig. 3). This is then transformed into the probability mass function $S(f)$ and used to calculate the spectral dissimilarity using the function `diffspec()` as follows:

$$D_f = \frac{1}{2} \sum_{f=1}^N |S_1(f) - S_2(f)|, \quad \text{with } D_f \in [0, 1] \quad (3)$$

where $S_1(f)$ is the probability mass function of bird call 1 and $S_2(f)$ is the probability mass function of bird call 2.

2.2.4 Phylogenetic Diversity

Phylogenetic information for the 20 bird species listed in Table 2 was extracted from the global bird phylogeny developed by Jetz et al. (2012). The phylogeny was constructed using a Bayesian approach with molecular and taxonomic data. The detailed methodology for the construction of the tree is described by Jetz et al. (2012). A distribution of 100 trees were extracted from the website www.birdtree.org. Using a distribution of trees accounts for phylogenetic uncertainty (Rubolini et al. 2015). The resulting phylogenetic relationships for a single tree is shown in Appendix A.

Phylogenetic distance between each species was calculated as, the pairwise difference in total branch length between two species in the phylogenetic tree using the function `cophenetic()` from the R package *ape* (Paradis et al. 2004). A matrix of pairwise distances was calculated for each of the 100 trees individually.

Evolutionary distinctiveness (ED) measures the relative contribution of each species to phylogenetic diversity and was first proposed by Isaac et al. (2007). This was calculated for each tree by first computing the clade matrix. The clade matrix is a binary matrix where columns represent the phylogeny tips and the rows represent the phylogeny nodes (Orme et al. 2013). The matrix shows to which nodes a tip subtends (Orme et al. 2013). ED was calculated using the function `ed.calc()` in the R package *caper* (Orme et al. 2013). The length of each branch is divided by the number of species at its tips. The ED for each species is the sum of values for each branch from which a species is descended (Isaac et al. 2007). A distance matrix was calculated between the resulting values using the function `dist()`.

2.2.5 Statistical Analysis of Dissimilarity Matrices

The correlation between the acoustic and phylogenetic distance matrices was calculated using Spearman's rank correlation. Spearman's correlation is considered appropriate because the data are not clearly linear. A Mantel test with 999 permutations was used to assess the significance of the correlation. A Mantel test is commonly used to assess correlation between distance matrices and has been used successfully by Lellouch et al. (2014) and Gasc et al. (2013) to test for correlation between acoustic and phylogenetic measures. The permutation approach takes account of possible autocorrelation between species and acoustic recordings measured at the same location or close together in time. Correlation was computed separately for each of the 100 possible trees.

2.3 Temporal Patterns of Acoustic Diversity

2.3.1 Acoustic Diversity Indices

At the SAFE project between April and June sunrise and sunset took place from approximately 06:00 to 06:15 and 18:20 to 18:35 respectively. The available clips were classified as *dawn* when they fell within the time range 05:00 to 07:00 and *dusk* when they fell within the time range 17:30 to 19:30.

To assess how acoustic diversity varies in time, the index H was calculated as described by Sueur et al. (2008). The index is based on the popular Shannon index of diversity, which has been widely implemented to assess biodiversity and is given by the equation $H' = -\sum_{i=1}^N p_i \ln p_i$ where N is the total number of species and p_i is the abundance of the i th species (Magurran 2004). As an acoustic index, time units are a set of categories and the abundances are given by the probability mass function of the amplitude envelope. The amplitude envelope of the sound signal, which shows the pattern of amplitude through time, was calculated using the function H and the argument for the Hilbert Transform. The temporal component of the index is given by:

$$H_t = -\sum_{t=1}^n A(t) \times \log_2 A(t) \times \log_2(n)^{-1}, \quad \text{with } H_t \in [0, 1] \quad (4)$$

where $A(t)$ is the probability mass function of the amplitude envelope and n is the length of the signal as digitised points (Sueur et al. 2008).

The spectral entropy is calculated as follows:

$$H_f = -\sum_{f=1}^N S(f) \times \log_2 S(f) \times \log_2(N)^{-1}, \quad \text{with } H_f \in [0, 1] \quad (5)$$

where $S(f)$ is the mean frequency spectrum, the calculation of which is described in Section 2.4.1 (Sueur et al. 2008).

The acoustic entropy (H) is then calculated as the product of each separate component as shown below:

$$H = H_t \times H_f \quad (6)$$

where H_t is the temporal entropy (Eq. 4) and H_f is the spectral entropy (Eq. 5) This creates an index between 0 and 1 where 0 is a pure tone and 1 produces random noise (Sueur et al. 2008). The H index (Eq. 6) was calculated as part of this study for 60 of the 120 clips that were classified with the time category *dawn* or *dusk*.

2.3.2 Statistical Analysis of Temporal Data

The H index was averaged by location, time category and date. The influence of location and time category (dawn or dusk) on acoustic diversity was assessed using a linear mixed-effects model. This type of model will deal with the spatial and temporal pseudo-replication of the samples by including random effects (Crawley 2012). The non-independence of the data was accounted for by assigning the random effect, date. Sampling was not consistent, therefore, there was not a measurement for each time category across all locations and on each date. In all models the random effect date was given the structure of a random intercept model to take account of the individual variation that may occur on each day (Winter 2013). The models were fit using maximum likelihood estimation and compared using the Likelihood Ratio Test with the R package *lme4* (Bates et al. 2015). This test is applicable here because the comparison is between nested models with the same fixed effect structure (Zuur et al. 2009). The model was validated to ensure it met the assumptions of the linear mixed-effects model, the output of which is available in Appendix B.

3 Results

3.1 Question 1: Phylogenetic and Acoustic Dissimilarity

Table 3 demonstrates that there was significant positive correlation between the three acoustic dissimilarity indices. The strongest correlation was found between the Kullback-Leibler and Kolmogorov-Smirnov measures.

Acoustic Distance	D_f	KL
D_f	-	-
KL	$\rho = 0.868, p = 0.001$	-
KS	$\rho = 0.802, p = 0.001$	$\rho = 0.774, p = 0.001$

Table 3: Spearman's rank correlation coefficient and significance values for Mantel tests with 999 permutations between each of the acoustic measures. The three measures were significantly correlated. They each compare the spectral component of sound and the close correlation suggests that the measures reliably capture this component of acoustic signals. D_f = spectral dissimilarity, KL = Symmetric Kullback-Leibler divergence and KS = Kolmogorov-Smirnov distance.

There was no significant correlation between phylogenetic distance and the acoustic dissimilarity measures. In addition, on average, there was no significant correlation between evolutionary distinctiveness and any of the acoustic measures. The average Spearman's correlation coefficient and p-values for all 100 phylogenetic trees are reported in Table 4. As a result, it is possible to reject the hypothesis that species separated by greater phylogenetic distance will be more acoustically divergent.

However, there is a weak significant correlation between evolutionary distinctiveness and the symmetric Kullback-Leibler divergence (Spearman's correlation: $0.262 > \rho > 0.200$, $0.05 > p > 0.02$) for 31% of the possible phylogenetic trees generated to represent the relationship between the selected species (Fig. 4). This suggests that additional data is required to resolve the level of correlation between these measures with any certainty.

The absence of correlation between the phylogenetic and acoustic measures is evident in Figures 4 and 5. *Argusianus argus* is clearly the most phylogenetically distinct species when considering phylogenetic distance or evolutionary distinctiveness (Fig 4(a) and 5(a)), but is not distinct acoustically from species such as *Cacomantis merulinus* and *Pellorneum capistratum* (Fig. 5(b) and Fig. 4(b)). *Prinia flaviventris* tends to be the most distinct acoustically when considering any of the acoustic measures (Fig. 5(b) and Fig. 4(b)). All the measures agree on the divergence of the calls of the species *Buceros rhinoceros* and *Prinia flaviventris* as well as *Anorrhinus galeritus* and *Prinia flaviventris*. *Buceros rhinoceros* and *Anorrhinus galeritus* are closely related in terms of phylogenetic distance and evolutionary distinctiveness (Fig 4(a) and 5(a)).

Acoustic Distance	Phylogenetic Distance	Evolutionary Distinctiveness
D_f	$\rho = 0.118, p = 0.904$	$\rho = 0.154, p = 0.102$
KL	$\rho = 0.127, p = 0.181$	$\rho = 0.173, p = 0.085$
KS	$\rho = -0.006, p = 0.488$	$\rho = -0.004, p = 0.478$

Table 4: Spearman's rank correlation coefficient and significance values for Mantel tests with 999 permutations between each of the acoustic and phylogenetic measures. There were no significant correlations between either phylogenetic distance or evolutionary distinctiveness. D_f = spectral dissimilarity, KL = Symmetric Kullback-Leibler divergence and KS = Kolmogorov-Smirnov distance.

3.2 Question 2: Temporal patterns of Acoustic Diversity

Acoustic diversity was compared, using a linear mixed effects model, at three different locations (Fig. 1) for two time categories; dawn and dusk. Figure 6 shows the variation in acoustic diversity between the location and time categories. The acoustic index, H, varied from 0.738 to 0.955. The likelihood ratio test was used to compare four models and determine the significance of the factors location and time category on acoustic diversity.

Model A was the maximal model, and included three fixed effects; time category, location, and interaction between these two variables. Model B removed the fixed effect location. There was no significant difference between the explanatory power of this and the maximal model (Table 5). As a result, it is possible to conclude that location did not significantly effect acoustic diversity. Model C further removed the effect of interaction between location and time category. This model was significantly different to Model B ($\chi^2 = 11.62$, $df = 4$, $p = 0.02$) and as a result it is possible to suggest that in combination location and time category had a significant effect on acoustic diversity. Particularly,

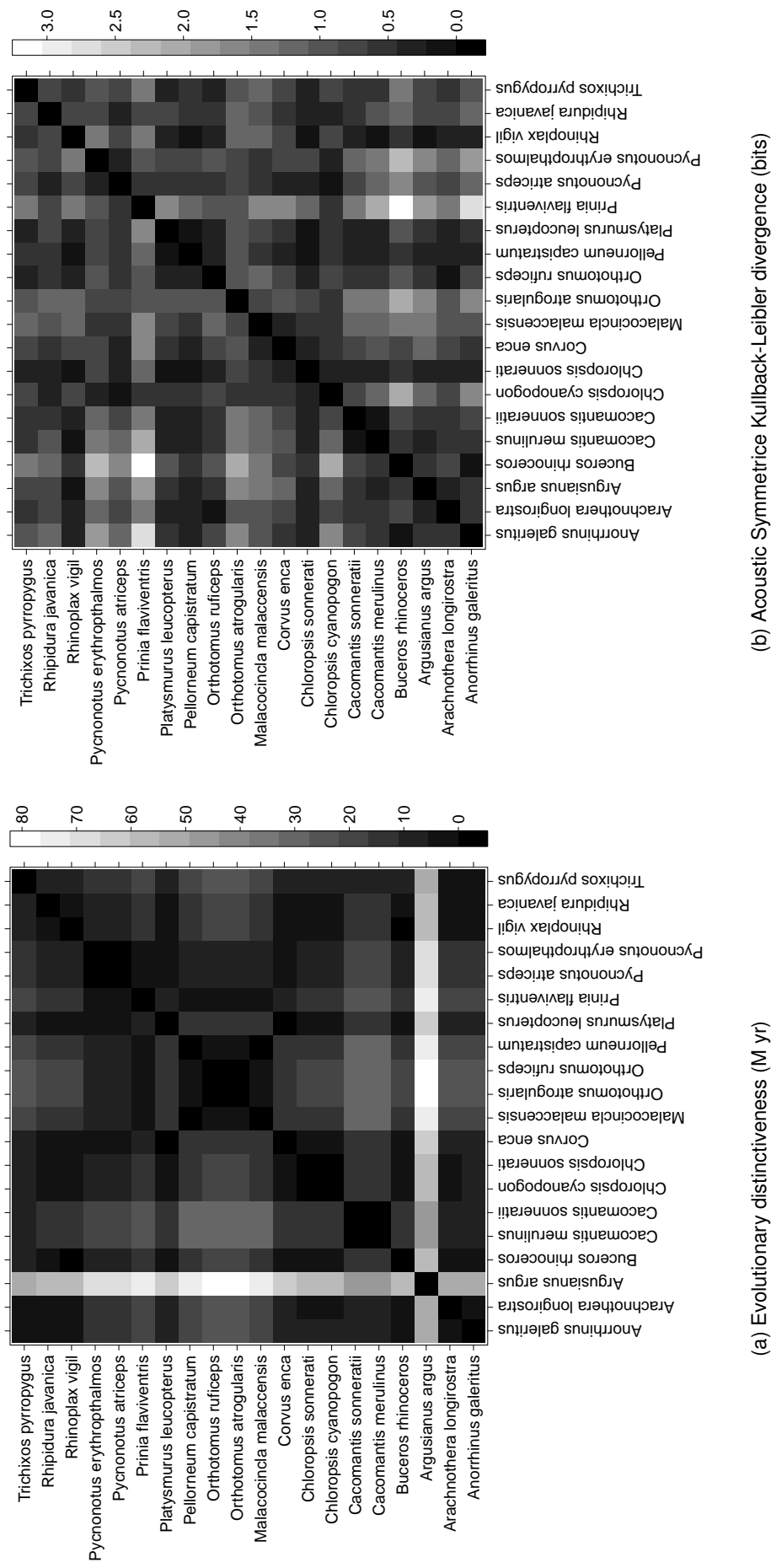


Figure 4: (a) Evolutionary distinctiveness between each species. (b) The acoustic dissimilarity of the species calls measured using the Symmetric Kullback-Leibler divergence. On several occasions there was a significant weak correlation between these measures. *Prinia flaviventris* and *Buceros rhinoceros* are the most acoustically distinct but this is not reflected as strongly in the evolutionary distinctiveness of the species.

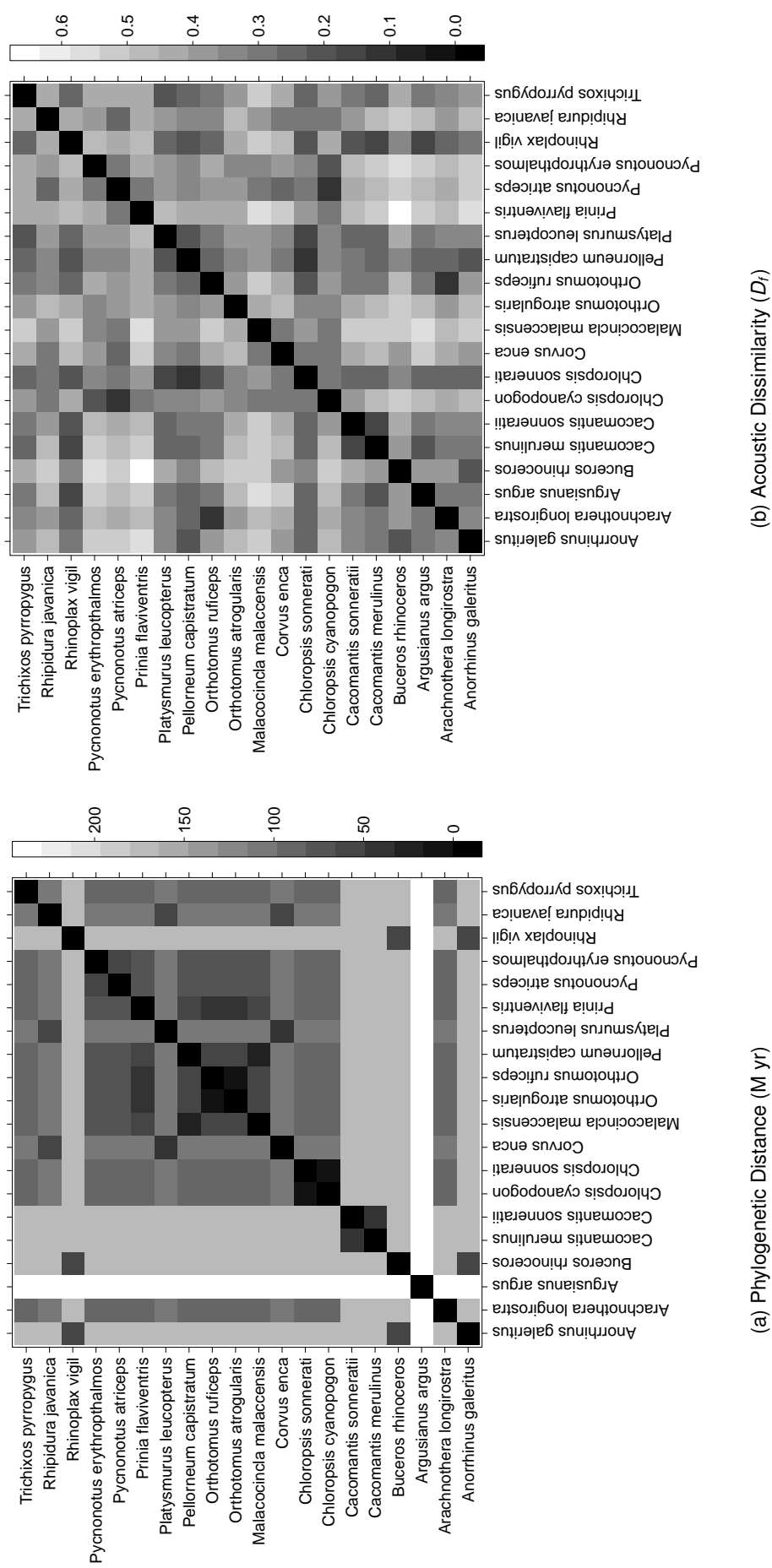


Figure 5: (a) Phylogenetic distance measured as the pairwise difference in total branch lengths of species on the phylogenetic tree. (b) Acoustic dissimilarity measured using spectral dissimilarity (D_f). There was no correlation between the two measures. *Argusianus argus* is the most phylogenetically distinct species but *Prinia flaviventris* is the most acoustically distinct.

the index H is lower during dusk at Location 3. It is evident in Figure 6 that the difference between dawn and dusk is much greater there than at Location 1 or 2. This suggests that the extent to which acoustic diversity varies between dawn and dusk can differ between each location.

Model D was the null model and was compared to Model C which contained only the fixed effect of category. These two models were significantly different in their explanatory power ($\chi^2 = 14.27$, $df = 1$, $p = 0.0002$). A significant level of variation in the acoustic diversity index was explained by the time category. Acoustic diversity was on average greater at dawn ($H = 0.878$ to 0.913) than dusk ($H = 0.782$ to 0.855). This provides evidence in support of the hypothesis that, acoustic diversity will be greater at dawn than at dusk.

The individual model output and validation plots are available in Appendix B. Model B was considered the minimum adequate model in that it was significantly better than the null model but not worse than the maximal model. For the random effect, date, variance is estimated to be zero for all models. This represents a degenerate model (Bates 2010). There may still be variation associated with date but it is not of sufficient magnitude to result in its incorporation into the model (Bates 2010). This may also occur due to lack of data with which to fit the model, and as a result, the output is similar to an linear model (Bates 2010).

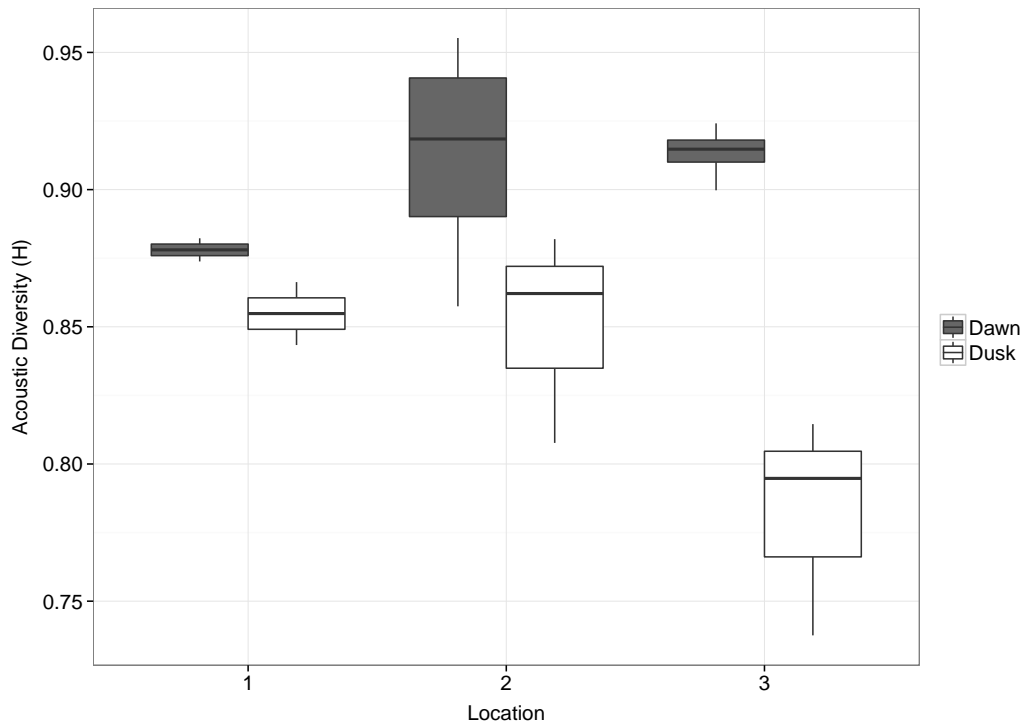


Figure 6: Boxplots of acoustic diversity index H for dawn and dusk values at three locations. Location 1 is at the centre of a 100 ha fragment with 50% forest cover, Location 2 is at the edge of a 10 ha fragment with 50% forest cover, Location 3 is at the edge of a 100 ha fragment with 35 % forest cover. There were significant differences between the acoustic diversity at dawn and dusk but no significant variation between locations.

	Df	logLik	deviance	Chisq	Chi Df	Pr(>Chisq)
Model A	8	40.06	-80.12			
Model B	8	40.06	-80.12	0.00	0	1.0000
Model C	4	34.25	-68.50			
Model B	8	40.06	-80.12	11.62	4	0.0204
Model D	3	27.11	-54.23			
Model C	4	34.25	-68.50	14.27	1	0.0002

Table 5: Results from likelihood ratio tests to test for significance of the factors location and time category. All models include the random effect, date. Model A includes location, time category and their interaction; Model B includes time category and interaction between time category and location; Model C includes time category; Model D is the null model. There was significant explanatory power provided by the factors *time category* and the interaction between *time category* and *location*.

4 Discussion

Comprehensive and accurate data on the dynamics of biodiversity are a priority for ecologists and conservationists (Mace et al. 2003, Magurran et al. 2010). Such data can help elucidate the impacts of anthropogenic-driven environmental change on ecosystem function, and determine the success of policies to mitigate recent downwards trends in biodiversity (Magurran et al. 2010). It has been highlighted that acoustic data may facilitate the development of long-term and consistent biodiversity datasets (Sueur et al. 2014). Studies have demonstrated its benefits over traditional monitoring methods and the field of soundscape ecology has been rapidly expanding (Depraetere et al. 2012, Pijanowski et al. 2011, Sueur et al. 2014). There are now several acoustic biodiversity indices that analyse the amplitude and frequency of sound signals to produce a single measure of acoustic diversity or dissimilarity. Phylogenetic diversity is increasingly recognised as an important facet of biodiversity that may be used for setting conservation priorities (Isaac et al. 2007, Winter et al. 2013). Gasc et al. (2013) examined if acoustic indices could reflect phylogenetic and functional diversity using a set of bird calls from a temperate region in France. They concluded that acoustic dissimilarity carries a phylogenetic signal containing information regarding evolutionary time. As a result, it is suggested that acoustic indices have the potential to be employed to monitor, not only species abundance, but phylogenetic diversity. This study examined the relationship between acoustic dissimilarity and phylogenetic diversity for 20 bird species from a lowland dipterocarp forest in Malaysian Borneo. The acoustic soundscape in Borneo is considerably more diverse than its temperate counterpart and studies have demonstrated that tropical soundscapes are unique (Rodriguez et al. 2014). As a result, this study aimed to understand if acoustic dissimilarity indices could be used to monitor phylogenetic diversity in these unique tropical soundscapes. This study found no correlation between the pairwise difference in total branch length between species, evolutionary distinctiveness and any of the three acoustic dissimilarity measures. As a result, in contrast to previous findings by Gasc et al. (2013), the hypothesis that species separated by greater phylogenetic distance are more acoustically divergent was rejected.

The relationship between genetic and acoustic divergence in birds is complex and variable (Tobias

et al. 2010, Wilkins et al. 2013). There are several competing hypotheses that may be governing divergence and driving the development of genetic and acoustic divergence at different rates (Wilkins et al. 2013). Broadly, these include ecological selection, sexual selection, a combination of both or stochastic processes (Wilkins et al. 2013). It is likely that acoustic divergence in this location is not being driven by any single force but by a combination of competing forces in each different species (Wilkins et al. 2013). A strong linear relationship would predict a dominant role for neutral processes (Irwin et al. 2008). However, the correlation between acoustic divergence and ecological factors such as body size and habitat were not identified in this study. This limits the understanding of acoustic divergence in this community. However, it is possible to suggest important factors that may degrade the correlation between phylogenetic diversity and acoustic divergence. It is reported that habitat structure can place significant constraints on the development of acoustic signals. For example, species from areas of dense vegetation tend to exhibit lower frequency sounds and have narrower frequency ranges (McCracken & Sheldon 1997) because these are subject to less attenuation by vegetation than high frequency sounds (Boncoraglio & Saino 2007). The species examined in this study live in very similar habitats. Tropical forests have a particularly dense vegetation structure and as a result, it is possible to suggest that this could have an impact on acoustic divergence. In particular, it may explain why species such as *Argusianus argus* and *Pellorneum capistratum*, that are phylogenetically distinct have closely related acoustic signals. Furthermore, it may explain to some extent the different conclusions reached by this study compared to Gasc et al. (2013). In a temperate location where habitat structure is less dense, it may play a lesser role in mediating acoustic divergence. As a result, while it may be possible to use acoustic data to determine phylogenetic diversity in these environments, it would have limited application in tropical soundscapes.

It is important to note that this study focussed on the use of acoustic dissimilarity indices that have been developed to examine biodiversity. These focus on the spectral analysis of the acoustic signal. However, habitat structure is known to strongly influence the spectral components of sound (Boncoraglio & Saino 2007). In contrast, it is highlighted by McCracken & Sheldon (1997) that the number of syllables, syllable structure and fundamental frequency are more closely linked to phylogenetic distance in birds because they reflect the structure of the vocal apparatus and the behaviour of the species. Consequently, as part of future work it may be possible to develop specific phylogenetic acoustic indices. These may be able to resolve the relationship with more clarity than was possible in this study by characterising the phylogenetically salient components in the soundscape.

The acoustic community in this study was composed of a number of oscine passerines such as *Prinia flaviventris*; the most acoustically distinct species in this study. This group are known to be highly flexible in their vocalisations and can learn songs from their conspecifics (Beecher & Brenowitz 2005). In this study several species were acoustically divergent but not phylogenetically diverse. Cultural acquisition of song in some species could provide a mechanism by which genetically similar species could acquire divergent acoustic patterns (Wilkins et al. 2013). Furthermore, as part of this study *Buceros rhinoceros* and *Prinia flaviventris* are the most acoustically divergent species and while they are phylogenetically distinct, they are not as divergent as their song may suggest. They

do, however, upon visual inspection, have a very different body mass and beak morphology. There is evidence to suggest that larger animals have lower pitched signals (Wilkins et al. 2013). Beak and body size may have evolved in relation to ecological selection driving acoustic divergence.

These competing drivers of acoustic and genetic change suggest that it may be difficult to use acoustic data to elucidate phylogenetic diversity. As a result, acoustic data could be limited to an examination of species richness and evenness, or the relationship between phylogenetic diversity and acoustic divergence needs to be more fully understood. This study focussed on assessing phylogenetic difference using measures developed in the context of setting conservation priorities (Isaac et al. 2007). However, these all represent pairwise comparisons between individual species. It is difficult to isolate a single species in acoustic monitoring recordings, and as a result, examining the acoustic community as a whole may be more pertinent. This would require the phylogenetic diversity of the whole community to be assessed. However, such community wide comparisons may be a challenge because, while a relationship between acoustic and genetic divergence has been reported in many taxa (Wilkins et al. 2013), the complexities of the relationship are equal to that in birds. For example, there is evidence to suggest that for some South American species of frog, genetic distance and call divergence are not related (Heyer & Reid 2003).

This study concludes that, in tropical locations, it may not be possible to monitor phylogenetic diversity with acoustic data. However, this study had several limitations which suggest this conclusion should be treated with caution. There were a limited number of species and a limited number of calls used in the study. In comparison to the 196 species used by Gasc et al. (2013), this study only examined a single example of a call for 20 species. This study could be improved by including a greater number of species and by assessing more than one call per species. This could assist in conclusively resolving the correlations between evolutionary distinctiveness and the acoustic index, KL. In addition, the species calls were extracted from clips of acoustic data from biodiversity monitoring stations that record all ambient noise. Gasc et al. (2013) used clips from a database of calls and, therefore, could place a higher criteria on signal quality. As a result, the dissimilarity measures are less likely to be influenced by extraneous factors in the background of the recordings. While efforts were taken to minimise this, it is likely that the acoustic dissimilarity measures in this study were impacted by background noise. This may highlight that in a practical biodiversity monitoring setting, where the environment is diverse and contains many overlapping calls, it is not possible to extract a meaningful phylogenetic signal.

This study also examined variation in the acoustic diversity index, H, between dawn and dusk across three different locations. These locations varied in their level of forest degradation and fragmentation. Temporal soundscape dynamics have the potential to reveal patterns of biodiversity and changes in animal behaviour linked to forest degradation (Pijanowski et al. 2011, Rodriguez et al. 2014). However, it is important to understand if acoustic diversity indices reflect known patterns of animal diversity (Rodriguez et al. 2014). Long-term data will offer the opportunity to examine patterns through time in unprecedented detail (Magurran et al. 2010). In support of hypothesis 2.1, the level of acoustic

diversity was shown to be greater at dawn than at dusk. The limited number of data points somewhat undermines the level of confidence that can be placed in this conclusion. Nevertheless, this supports identical conclusions by Rodriguez et al. (2014) and Depraetere et al. (2012) in tropical and temperate settings respectively. The dawn chorus is generally recognised as a time of peak acoustic diversity, and has been extensively reported in observational studies (Berg et al. 2006, Henwood & Fabrick 1979). The acoustic diversity index correctly reflected this pattern, which demonstrates its usefulness as a method for monitoring biodiversity in tropical locations.

However, the extent to which H reflects species diversity is unclear. The morning dawn chorus is characterised by bird species, whereas, Gogala & Riede (1995) reported that in Borneo the acoustic space at dusk is dominated by cicada species followed by crickets, grasshoppers and frogs. These are often lower in amplitude and more uniform in their vocalisations. As a result, it is possible to question if this reflects species diversity or the dominance and variation in the vocal repertoire of birds. Gasc et al. (2015) recently examined the limitations and bias in acoustic biodiversity indices. They revealed none of the indices tested were able to represent species richness accurately under field conditions. Consequently, it is possible to suggest that further work is required to validate the meaning of biodiversity indices.

The SAFE project is studying the impact of forest fragmentation on ecosystem processes (Ewers et al. 2011). The three locations in this study represent different levels of forest fragmentation. Location 1 is at the centre of a large 100 ha fragment, Location 2 is at the edge of a 10 ha fragment and Location 3 at the edge of a 100 ha fragment. This study revealed no significant differences between the sites. However, data that spans a greater number of days may reveal patterns that were not detected here. The linear mixed-effects model suffered from the small number of data points available to fit it and in order to improve it, future work should use measurements for a greater number of days. The results suggest that at Location 3 during the hours of dusk there was significantly lower acoustic diversity. This may reflect a difference in the species composition or the abundance of species present (Gasc et al. 2015). There is, however, not sufficient information to suggest whether this has arisen because of changes in the acoustic community as a result of the habitat quality and structure. As data accumulates over time this pattern should be explored further.

The primary application of acoustic indices is to reveal patterns and trends in biodiversity. They are of particular use in this role because they are objective, relatively cheap compared to field studies and require little human intervention (Pieretti et al. 2011). This study has revealed that they are able to examine the temporal patterns of biodiversity but are limited in their ability to describe biodiversity beyond species richness and abundance. The acoustic dissimilarity indices, D_f , KL and KS were all closely correlated. They each examine the spectral component of the acoustic recordings. This supports finding by Gasc et al. (2013) and suggests that the indices could be used interchangeably to examine acoustic dissimilarity. It increases the confidence which can be placed in the analysis of the sound recordings that these measures are closely correlated (Towsey et al. 2014). The acoustic data recorded as part of this study was complex, with many overlapping biological sounds as well as

anthropogenic noise, heavy thunder storms and areas of distortion. Cleaning and filtering the data with respect to minimising the impacts of extraneous noise while maintaining all the biological information was a significant challenge. As part of this study particularly erroneous files were removed by manual aural identification but this is prohibitive in the context of long-term data and should be addressed further (Gasc et al. 2015).

Acoustic indices only represent one possible mechanism by which information about biodiversity can be extracted from acoustic data. Given the shortcomings revealed here, further validation could be provided by individual species identification using pattern recognition and the power of crowd-sourced expert listeners. Acoustic indices could also benefit from validation with traditional biodiversity data collected with traditional methodologies (Gasc et al. 2015). The limited number of studies that have validated acoustic indices have done so with simulated communities or in temperate locations (Depraetere et al. 2012, Sueur et al. 2008). Therefore, validation in tropical locations is essential.

In conclusion, this study addressed two questions concerning the use of acoustic biodiversity indices for biodiversity monitoring. Firstly, it asked if acoustic dissimilarity indices reflected the phylogenetic diversity of avian communities in tropical ecosystems. The results demonstrate that acoustic dissimilarity was not correlated with phylogenetic diversity. It is possible to suggest that competing factors may drive acoustic divergence between species in isolation from genetic divergence. Particularly in tropical ecosystems, where the habitat structure and acoustic communities are highly complex, it is difficult to discern phylogenetic diversity from acoustic data. As a result, the ability of acoustic indices to monitor biodiversity and set conservation priorities using phylogenetic diversity is limited. However, in order for these results to be conclusive a greater number of species and calls should be examined. Secondly, this study examined if acoustic diversity indices were able to detect variation in daily animal activity. This study suggests that daily activity is greater at dawn than at dusk but showed no variation between three locations with different levels of forest fragmentation. This advocates the use of acoustic indices to monitor temporal patterns of biodiversity. However, this pattern should be further examined over longer time-scales and the extent to which this reflect species diversity needs further validation.

Appendices

A Phylogenetic Tree of Bird Species

Phylogenetic relationships were calculated using a distribution of 100 trees extracted from www.birdtree.org. Figure A.1 is an example of the phylogenetic relationship between the bird species used in this study.

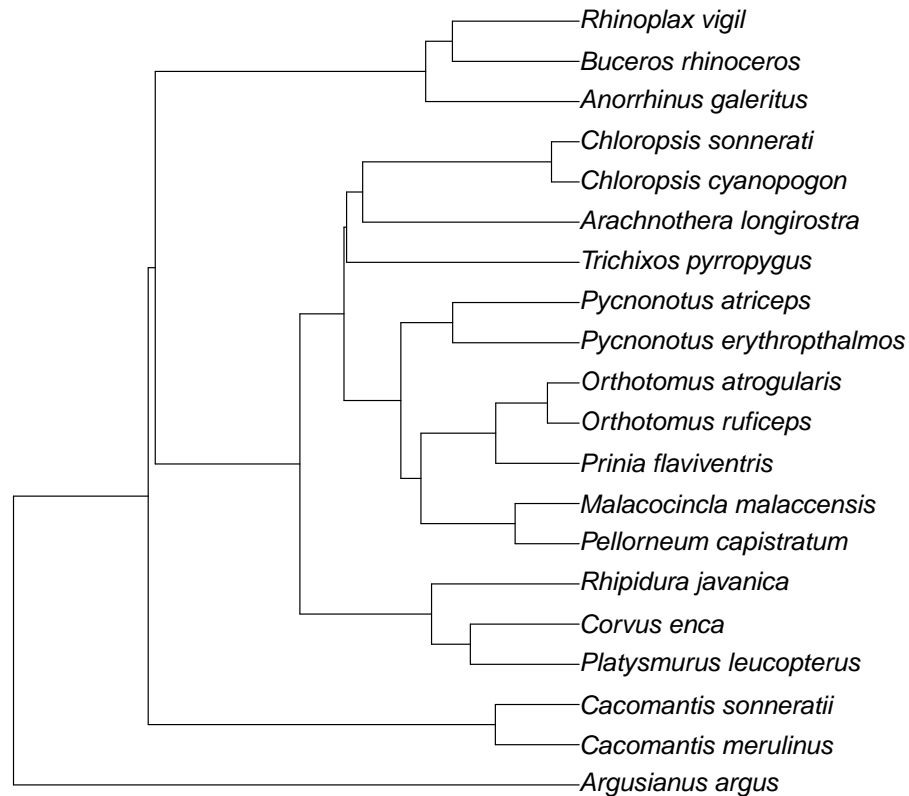


Figure A.1: An example of the phylogenetic relationship for the 20 bird species included in the study. The phylogenetic tree is one of 100 trees extracted from www.birdtree.org and developed by Jetz et al. (2012).

B Linear Mixed-Effects Model Output and Validation

Four mixed effects models were compared as listed below. The output from the models can be found in Table B.1. Model validation assessed if each model met the assumptions of the linear mixed effects model. Figure B.1 shows quantile-quantile plots for all four models. These validate the assumption that the errors of the model are normally distributed. Figure B.2 shows the residual and fitted values for all four models. This plot examines the homogeneity of variance (Zuur et al. 2009). Figure B.1 and Figure B.2 show some deviation from ideal output. However, given the small number of samples and variation in the system, they can be considered within an acceptable range (Zuur et al. 2009).

Model A was the maximal model and was given by the equation:

$$H_{ij} = (\alpha + d_{0j}) + \beta_1 L_{ij} + \beta_2 C_{ij} + \beta_3 L_{ij} C_{ij} + \epsilon_{ij} \quad (B.1)$$

In Model B the fixed effect, location, is removed and is given by the equation:

$$H_{ij} = (\alpha + d_{0j}) + \beta_1 C_{ij} + \beta_2 L_{ij} C_{ij} + \epsilon_{ij} \quad (B.2)$$

Model C incorporates the fixed effect time category and is given by the equation:

$$H_{ij} = (\alpha + d_{0j}) + \beta_1 C_{ij} + \epsilon_{ij} \quad (B.3)$$

Model D is the null model and is given by the equation:

$$H_{ij} = (\alpha + d_{0j}) + \epsilon_{ij} \quad (B.4)$$

where:

H = Acoustic diversity

α = Intercept parameter

D = Random intercept for date

C = Time category

L = Location

β_{1-3} = Slope parameters

ϵ = Error term

j = Number of days

	Model A	Model B	Model C	Model D
(Intercept)	0.870*** (0.013)	0.906*** (0.011)	0.878*** (0.018)	0.878*** (0.018)
Random Effect: Date	0.000	0.000	0.000	0.000
CategoryDusk		-0.080*** (0.017)	-0.023 (0.026)	-0.023 (0.026)
CategoryDawn \times Location2			0.034 (0.023)	
CategoryDusk \times Location2			-0.004 (0.024)	
CategoryDawn \times Location3			0.035 (0.023)	
CategoryDusk \times Location3			-0.073** (0.024)	
Location2				0.034 (0.023)
Location3				0.035 (0.023)
Location2 \times CategoryDusk				-0.039 (0.033)
Location3 \times CategoryDusk				-0.108** (0.033)
Log-likelihood	23.677	34.249	40.061	40.061
N	18	18	18	18

Table B.1: Linear mixed-effects model analysis for four models comparing the variation in acoustic diversity for two time categories (dawn and dusk) and three locations. The table contains values for parameters, intercept and slope and the log-likelihood value.

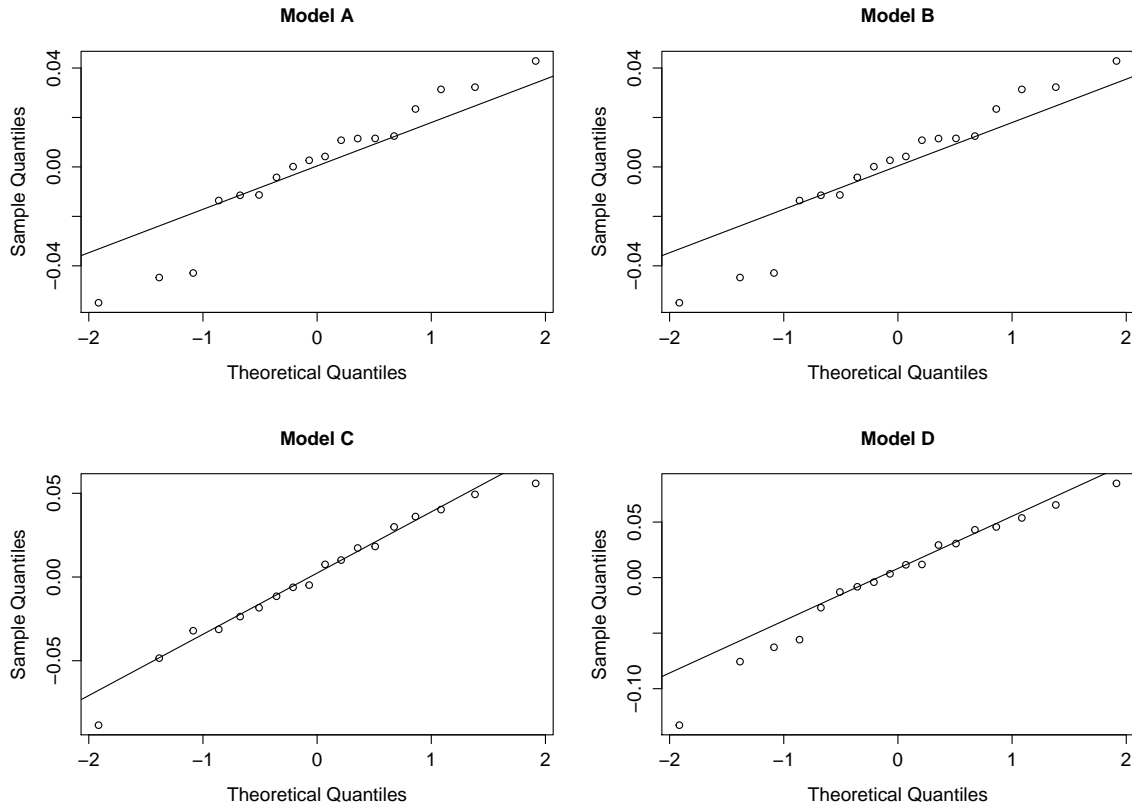


Figure B.1: Diagnostic quantile-quantile plots for all four linear mixed-effects models. Although, there is some deviation from normality in the errors, this is considered acceptable.

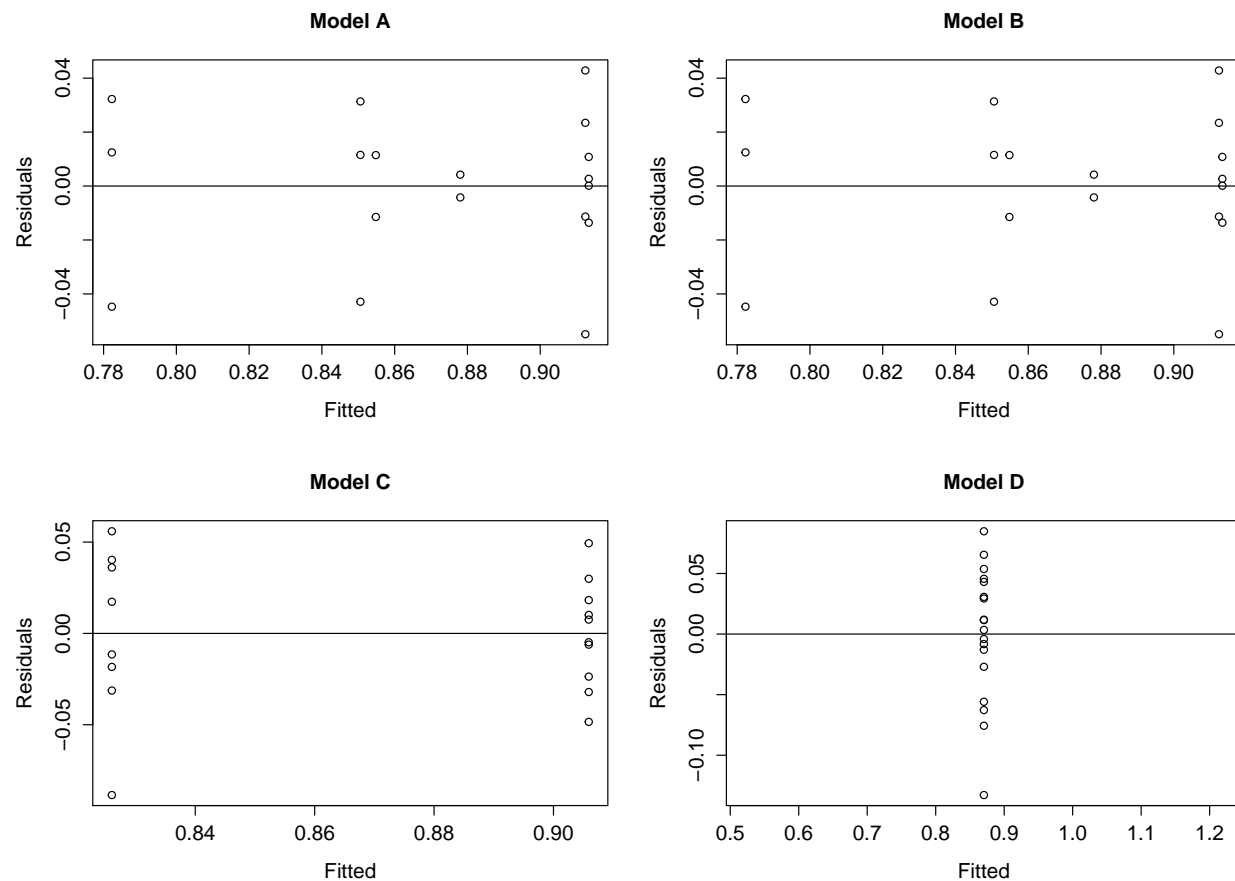


Figure B.2: Diagnostic residuals vs fitted plots for linear mixed-effects models. These examine homogeneity of variance. The variance is generally well spread throughout the model.

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