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# Can Soundscape Indices Be Used To Reflect Biodiversity In An Ecuadorian Andean Tropical Montane Habitat?

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## Abstract

The measurement of biodiversity presents a challenging task for conservationists. Traditional ecological descriptors such as species richness, Shannon and Simpson diversities have long been relied on by ecologists to provide an indication of biodiversity, however, the generation of these indices requires manual assessments of local fauna through methods which can often be expensive, time consuming and invasive. Analysis of the Soundscape, the collection of sounds generated by organisms (biophony), humans (anthrophony) and non-biological sounds such as wind and water (geophony), presents new potential for biodiversity sampling. To date, a range of indices have been developed that aim to provide a value relating to acoustic characteristics of an environment, based on the spectral and temporal properties within sound recordings. Several studies have yielded promising results when using the acoustic indices for biodiversity assessments in temperate, and to some extent, tropical habitats. We here aimed to further the current understanding of soundscape indices by investigating how they behave in a tropical habitat of high avifaunal diversity. Point count data for bird species was collected from the Santa Lucia Cloud Forest Reserve, NW Ecuador (0°17'30"N, 78°40'30"W), during Summer 2014, while acoustic recordings were taken simultaneously using a handheld audio recorder. We first analysed the change in bird species composition and diversity along two environmental gradients of habitat disturbance and altitude, and investigated how the acoustic indices behaved along these same gradients. We then explored whether the acoustic indices can be used to estimate biodiversity based on their correlation with traditional ecological indices. From the point count data we found a high turnover in species composition across sample sites. Mean species richness was found to negatively correlate with increasing altitude ( $p=1.485e-05$ ) and was found to be significantly lower in sites of primary forest than in both secondary forest and silvopasture ( $p=0.0165$ ). Although each of the acoustic indices showed varying levels of change across the environmental gradients, we found that only four of the eight acoustic indices, the Normalized Difference Soundscape Index ( $NDSI$ ,  $p=0.048$ ), spectral entropy ( $H_s$ ,  $p=0.033$ ), temporal entropy ( $H_t$ ,  $p=0.031$ ), and total entropy ( $H$ ,  $p=0.031$ ), were found to significantly correlate with species composition. We found that spectral entropy ( $H_s$ ) and total entropy ( $H$ ) were the only acoustic indices to significantly correlate with ecological indices, however since the total entropy ( $H$ ) is developed as a product of the spectral entropy ( $H_s$ ) we suggest that only the  $H$  index should be utilised for biodiversity measurements. We found that while the acoustic indices have the potential to characterise certain features of a habitat or to assist in analysing bird species composition, their use for biodiversity assessment is limited. We would suggest that more work to develop and understand the indices is needed before we can reliably make use of them for measuring biodiversity.

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## LIST OF ABBREVIATIONS

AAH	Acoustic Adaption Hypothesis
ACI	Acoustic Complexity Index
ACR	Automatic Call Recognition
AD	Acoustic Diversity
AE	Acoustic Evenness
ANH	Acoustic Niche Hypothesis
ATBI	All Taxa Biodiversity Inventory
BI	Bioacoustic Index
CA	Correspondence Analysis
CCA	Canonical Correlation Analysis
DCA	Detrended Correspondence Analysis
EDIS	Ecological Disturbance Indicator Species
ESN	Effective Species Number
FFT	Fast Fourier Transform
FP	Primary Forest
FS	Secondary Forest
H	Total Entropy
H <sub>s</sub>	Spectral Entropy
H <sub>t</sub>	Temporal Entropy
MAH	Morphological Adaption Hypothesis
NDSI	Normalised Difference Soundscape Index
S	Silvopasture
SLR	Santa Lucia Reserve

# **1 Introduction**

Ever increasing pressures on natural ecosystems have driven the current extinction rate for all taxa to vastly exceed the natural background rate (Ceballos et al., 2015). So that limited conservation resources can be utilised with maximum efficiency, the identification of highly biodiverse areas has become a priority in the field of conservation biology, with a focus on the need to develop low cost, rapid and efficient methods of biodiversity assessment (Myers et al., 2000).

## **1.1 Current Methods of Biodiversity Assessment.**

Intuitively, an All Taxa Biodiversity Inventory (ATBI), in which an audit of biodiversity within 100,000 hectares of an ecosystem assembles a species inventory list for the area, would be an appropriate method of assessment (Gewin, 2002). However, with the most recent prediction of the global number of species estimated at around 8.7 million, and around 86% of existing species still awaiting description (Mora et al., 2011), calculating the actual diversity of any given ecological system is an extremely time consuming and complex task (Sueur et al., 2012).

Fortunately, use of small sets of species which are particularly sensitive to habitat disturbance known as “ecological-disturbance indicator species” (EDIS), whose presence or absence could signify the health of a particular habitat, has become an accepted approach toward biodiversity assessment (Caro, 2010). Birds have been proposed as a good candidate for an environmental health proxy; they are particularly sensitive to habitat change, occur high up in food chains and are a widespread and diverse taxon (Carignan & Villard, 2002; Gregory & Strien, 2010). The use of birds as EDIS has also been found one of the most cost effective among small vertebrates (Peck et al., 2014).

Traditional biodiversity indices, which are used as an interpretative measure of taxa biodiversity, are common in ecosystem assessment. Those that measure alpha ( $\alpha$ ) diversity are based on the observed species richness (number of species) and their relative abundances (evenness) within communities, the most common of which are the Shannon-entropy and Gini-Simpson indices (Sueur et al., 2014;



Tuomisto, 2012). While these indices are somewhat useful for describing communities, they are disproportionately affected by rare species, therefore the use of additional weighted indices (the effective number of species (ESN, exponential of the Shannon entropy) and the inverse Simpson concentration) is recommended (Jost, 2006; Hill, 1973). Between-group beta diversity ( $\beta$ ) can also be estimated by comparing similarities or differences of species lists or diversity index values at different sites (Sueur et al., 2014).

In order to obtain the ecological diversity indices, inventories that identify the species and their abundances are required, however the traditional approaches used can be inefficient for a number of reasons. Methods such as mark-recapture, mist-netting and nest-searches are highly invasive (Bibby et al., 1992; McGuire et al., 2011), and due to prevalence of rarity, particularly in tropical environments where there is high species richness and high levels of endemism (Haselmayer & Quin, 2000), sample numbers can often be restricted to one or a few individuals, providing a poor representation of the true population density (Riede, 1993). While point counts, where visual and auditory cues are used to identify the presence of individuals along a transect are more widely used, a set of highly trained observers able to recognise hundreds of species is often required, making this method time consuming and expensive (Celis-Murillo et al., 2009; Hobson et al., 2002).

## **1.2 Acoustic Approaches**

The cross disciplinary field of bioacoustics, integrating animal behaviour, physiology and anatomy, evolution, and communication theory among others, has long been recognised as a useful tool for conservation (Baptista & Gaunt 1997; Pijanowski et al., 2011b), however its use has gained popularity in recent years. Improvements in sound recording technology and cost reductions have allowed scientists to make use of the acoustic signals produced by animals to support species identification and abundance estimation, inferring information about populations and community dynamics (Farina & Pieretti, 2013; Blumstein et al., 2011; McGuire et al., 2011; Obrist et al., 2010). Considerable research been conducted in ocean systems, especially in the fields of marine mammal

communication, and tracking (Charif et al., 2001; McConnell et al., 2013), and somewhat in terrestrial environments for identifying and estimating populations of elephants, anurans and birds (Acevedo & Villanueva-Rivera, 2006; Courch & Paton, 2002; Frommolt & Tauchart, 2014; Thompson et al., 2009).

The utilisation of audio recordings to build faunal inventories, specifically avifauna, has long been practiced (Haselmayer & Quinn, 2000; Parker, 1991), and is a desirable method of data collection in both qualitative and quantitative respects. There is no requirement for ornithological experts to collect the data, who can be particularly expensive during avian breeding seasons when they are in greatest demand, this allows further time to replicate the methods or to extend the study area, obtaining a more comprehensive dataset (Hobson et al., 2002). Additionally, sound recordings can be stored digitally, creating a permanent record of the acoustic conditions. The recordings can be re-listened to and output volumes can be adjusted, reducing the possibility of confusion during choruses (Haselmayer & Quinn, 2000). Regardless of experience, significant inter-observer variability can still occur, specifically when identifying rare species. The use of a spectrogram to accompany a sound recording can provide a cross reference to reduce variability, as well as improving accuracy and long term quality control of data collection (Farina & Pieretti, 2013; Hobson et al., 2002; Rempel, 2005).

While the extraction of individual birdcalls by Automated Call Recognition (ACR) software, which uses oscillation detectors and pattern recognition to detect individual birdcalls has had some success (Bardeli et al., 2009; Blumstein et al., 2011; Towsey et al., 2012; Wimmer et al., 2010), the high diversity and complexity of bird songs can leave this system vulnerable to error and can still be costly and time consuming, requiring a level of manual input i.e. Human-in-the-loop semi automation (Bardeli et al., 2009; Blumstein et al., 2011; Rempel et al., 2005; Towsey et al., 2012).

While much of the previous use of bioacoustics has focussed on a single species approach, species do not exist in a closed system, and are instead integrated as part of a larger interactive system, it is therefore becoming increasingly necessary to conduct biodiversity assessments on a higher level such as that of the community, landscape or ecosystem. Soundscape ecology aims to incorporate bioacoustics with ecology by identifying unique acoustic patterns on a macro or

community level (Pijanowski et al., 2011a; Pijanowski et al., 2011b; Sueur, 2014; Sueur et al., 2012).

The soundscape, defined as “the collection of biological, geophysical and anthropogenic sounds that emanate from a landscape and which vary over space and time, reflecting important ecosystem processes and human activities” (Pijanowski et al., 2011a), consists of three main components: “biophony” (the sounds created by organisms), “geophony” (the non-biological sounds of wind, rain, rivers etc.), and “anthrophony” (those sounds caused by humans) (Krause, 1987; Pijanowski et al., 2011a).

All sounds are made up of fluctuations in high and low air pressure, caused when an object is vibrated. The pressure wave emanating from the source of the vibration consists of two basic measurable properties, frequency and amplitude. The frequency, which is usually expressed as Hertz (Hz), is measured as the number of waveform repetitions per unit time; a high frequency of repetition creates a high pitch noise, whereas a low frequency results in a low pitch noise. Amplitude (or intensity) is measured as the magnitude of the change in pressure of the sound wave, which is interpreted as volume (or loudness), expressed as decibels (dB) (Everest and Pholmann, 2009; Villanueva-Rivera et al., 2011).

Many animals make use of acoustics for intraspecific interactions such as territorial defence, mate attraction or orientation and for interspecific interactions such as predator deterrence, and prey location (Blumstein et al., 2011; Obrist et al., 2010). However, acoustic signals are costly to produce, and it is therefore in each organism’s best interests to ensure that their particular signal is transmitted and received efficiently (Bradbury & Vehrencamp, 2000). The physical constraints that shape the way in which animals transmit these signals is the focus of several theories: the Morphological Adaption Hypothesis (MAH) focuses on the sender of the signal and suggests that the physical attributes such as body size and trachea length influence the amplitude of the sound that the organism is able to produce (Pijanowski et al., 2011a; Wiley, 1991). The Acoustic Adaption Hypothesis (AAH) focuses on the ability of the sender to adjust the attributes of its sound depending on the medium or habitat through which the sound must travel (Pijanowski et al., 2011a). This hypothesis has received mixed support; where some studies found

evidence that the environment influenced the evolution of vocalisations (Brown et al., 1995; Slabbekoorn et al., 2002), others found no correlation (Daniel & Blumstein, 1998; Sueur & Aubin, 2003).

The varied ability of organisms to communicate through the use of sound led the American musician, author and bio-acoustician, Bernie Krause, to develop the Acoustic Niche Hypothesis (ANH), which posits that organisms can adjust their signals in both time and frequency to avoid overlapping with other sounds, thereby maximising transmission to mates or conspecifics and minimising interference with other vocalising individuals. The hypothesis has received much support, and acoustic partitioning has been observed many times among birds, crickets, anurans and insects (Ficken et al., 1974; Grafe, 1996; Henry & Wells, 2010; Marten et al., 1977; Otte, 1992; Pijanowski et al., 2011b; Sueur, 2002).

The ANH can be considered a highly useful concept from a conservation perspective. Much like an ecosystem, the acoustic spectrum within a soundscape is considered a finite niche, in which each organism will adapt to fill a space by a process of long-term competitive exclusion and partitioning of resources (Krause, 1993; Krause, 1987). Therefore, an undisturbed community consisting of natives should exhibit a more complete series of spectral and temporal vocalisations as each organism occupies its realized niche, while the presence of invasive species could disrupt the biophony and alter the natural acoustic partitioning (Pijanowski et al., 2011b). The acoustic environment would display increased heterogeneity in an area of high biodiversity such as the tropics, where a wider range of frequencies should be occupied (Gage et al., 2001; Krause & Gage, 2003; Pijanowski et al., 2011a; Pijanowski et al., 2011b). On the contrary, a disturbed habitat should display reduction in both species richness and birdcall syllable diversity (Laiolo, 2010), so according to the ANH, the heterogeneity of the soundscape will be lower.

Scientists are now using the epistemological framework of soundscape studies to ascertain knowledge about species composition and environmental health, through the use of a new set of acoustic indices that give numerical values based on different aspects of the acoustic properties within a recording.

### 1.3 Acoustic Indices

Many acoustic indices have been developed in the last 6 years (Towsey et al., 2013), which are widely based on statistical analysis of the Fourier Transform (FFT) or the time wave representations of the amplitude and frequencies within acoustic recordings. One of the simplest applications of soundscape indicators measures changes in sound pressure levels within an environment, for example Rodriguez et al. (2013) used peaks in amplitude levels to map spatial and temporal differences in a neo-tropical forest, highlighting a complex structure of soundscapes within a single ecological system.

A more recent approach is to analyse spectral properties of a recording through differences in time variations or magnitude of frequency and amplitude modulations. This study considers the effectiveness of a selection of these indices as tools for biodiversity assessment, which are described below.

#### ***Normalized Difference Soundscape Index (NDSI)***

Under the assumption that anthrophony occurs most prevalently between 1-2kHz and biophony between 1-8kHz, the *NDSI* aims to estimate the level of biological sound relative to anthropogenic sound (Kasten et al., 2012; but see Qi et al., 2007). As a simple calculation, this cannot necessarily predict biodiversity, however it does seek to describe the “health” of a habitat, under the assumption that a habitat of less human disturbance is in better condition. The *NDSI* has been shown to reflect seasonal and diurnal variation in landscapes thus may be useful for long-term investigative studies into human-animal interactions. Where  $\beta$  is the power spectral density (the intensity of the sound) of biophony and  $\alpha$  is the power spectral density of anthrophony, it is calculated as follows:

$$NDSI = (\beta - \alpha) / (\beta + \alpha)$$

The *NDSI* is given as a ratio in the range of [+1 to -1] where +1 indicates a soundscape with no anthrophony (Kasten et al., 2012).

A range of entropy indices has also been developed. Based on traditional ecological indices such as Shannon-Entropy and Gini-Simpson, which measure diversity of

species within a community, the entropy indices measure the complexity or heterogeneity of spectral properties of the soundscape recordings.

### ***Temporal Entropy ( $H_t$ )***

This computes the Shannon or Renyi Entropy of a temporal envelope, whereas Shannon is measured on a set of categories (species) differing in frequencies, this measure uses specified time units as categories and the probability mass function of the amplitude envelope as their frequencies. Where  $A(t)$  is the probability mass function of the amplitude envelope, this is computed as:

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

(Sueur et al., 2008b)

A noisy signal with many continuous loud calls will give a temporal entropy value close to 1, whereas the temporal entropy of a quiet signal is close to 0; however, a sustained signal with a flat envelope such as the sound from continuous running water would also result in high temporal entropy (Sueur et al., 2008b).

### ***Spectral Entropy ( $H_s$ )***

Similarly to temporal entropy, the spectral entropy is computed as the Shannon entropy of a frequency spectrum, however a mean spectrum is first computed using a Short Time Fourier Transform (STFT), so that the mean spectrum is transformed into a probability mass function,  $S(f)$  of length  $N$ . This is therefore computed as:

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

(Sueur et al., 2008b)

A value of high spectral entropy would be given from a recording with high variation in spectral flatness, such as white noise, which has equal energy at all frequencies (Marler & Slabbekoorn, 2004). Alternatively a pure tone would give a low spectral entropy value.

### ***Total entropy (H)***

The total entropy is computed as the product of the temporal and spectral entropies, ultimately measuring the heterogeneity across the frequency spectrum and the amplitude envelope:

$$H = H_t \times H_f \text{ with } H \in [0,1]$$

(Sueur et al., 2008b)

Sueur et al. (2008b) were able to successfully correlate the Acoustic Entropy index ( $H$ ) with species richness in a simulated environment and demonstrated some success in a Tanzanian tropical forest; modifications of this index have also been tested in a temperate habitat (Depraetere et al., 2012). However there is still a need for assessment in a variety of different locations to test the capabilities of each index for a range of ecological conditions and spatial scales

### ***Acoustic Diversity (AD)***

The  $AD$  index is calculated by dividing the spectrogram into frequency bins and then, in a similar way to  $H_s$  and  $H_t$ , applying the Shannon index to the proportion of the signals in each bin above a 50dB threshold (Villanueva-Rivera et al., 2011).

### ***Acoustic Evenness (AE)***

Similarly to  $AD$ ,  $AE$  is calculated by dividing the spectrogram into frequency bins and taking the proportion of the signals in each bin above a 50 dB threshold, however the Gini-Simpson index is applied to these bins (Villanueva-Rivera et al., 2011). The  $AE$  and  $AE$  indices have been shown to reflect observed distinctions in gross acoustic activity e.g. between diverse habitats or dawn and dusk choruses (Villanueva-Rivera et al., 2011).

Further indices have been developed which analyse absolute differences in spectral properties of a recording.

### ***Acoustic Complexity Index (ACI)***

The *ACI*, proposed by Pieretti et al. (2011) is based on the “observation that many biotic sounds, such as bird songs, are characterized by an intrinsic variability of intensities, while some types of human generated noise (such as car passing or airplane transit) present very constant intensity values” (Pieretti et al., 2011). It is calculated from a number of steps, measuring the dissimilarities between intensities registered in adjacent frequency bins, and then summing the dissimilarity values of all frequency bins in a recording; recordings with highly variable intensities will give a higher *ACI* value. The *ACI* has been found difficult to use as a diversity measure due to its sensitivity to the signal amplitude and window length, however it correlates well with the number of bird vocalisations (Farina et al., 2011; Sueur et al., 2008b; Pieretti et al., 2011).

### ***Bioacoustic Index (BI)***

The *BI* is calculated as the total area under the mean frequency spectrum (minus the minimum value of the lowest bin). The area values are thus a function of both the sound level and the number of frequency bands used by the avifauna, and was shown to be strongly correlated with counts from a direct ornithological survey (Boelman et al., 2007).

It is the aim of this study to explore how each of these indices behave in a tropical habitat of high avifaunal diversity, and whether they can match the ability of traditional ecological indices to detect patterns of species diversity, by addressing several questions: i) How does species diversity and composition change with habitat disturbance and altitude, according to traditional ecological indices? ii) Can a change been seen in acoustic index values with changing habitat disturbance and altitude? iii) Which of the acoustic indices, if any, correlates best with the ecological indices. Ultimately allowing a recommendation for the use of acoustic indices as a measure of biodiversity.



## 2 Materials and Methods

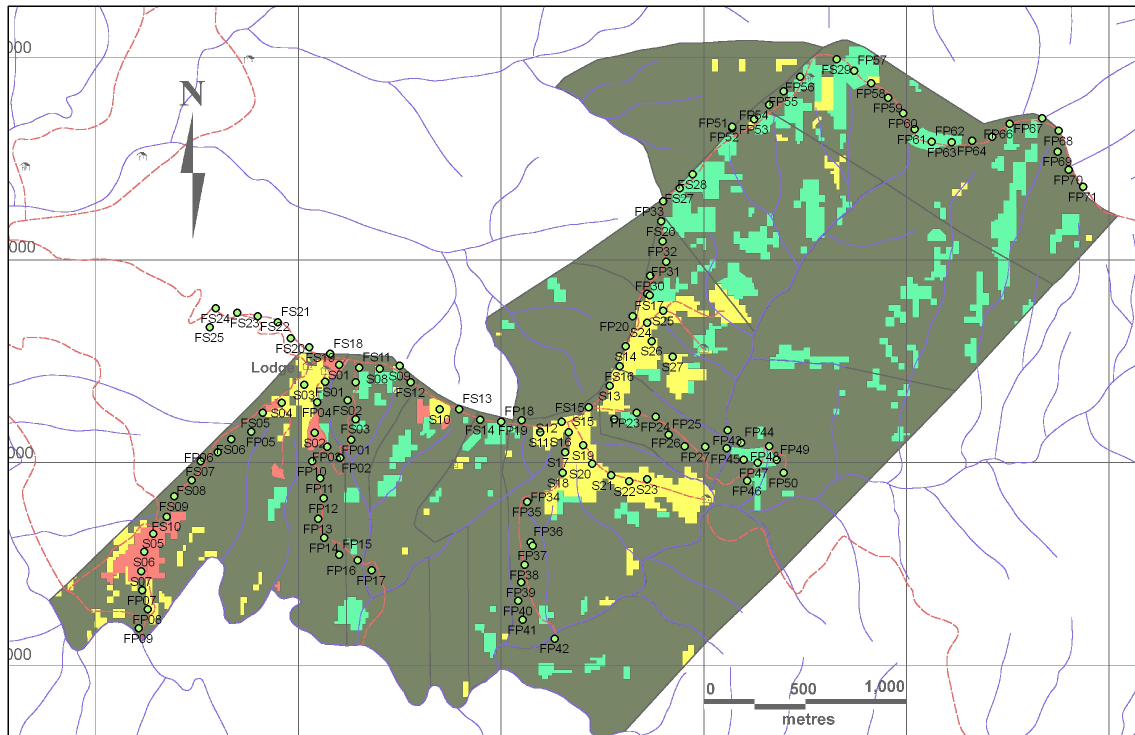
### 2.1 Study Area

Field surveys were conducted over a 5-week period from September 18<sup>th</sup> to October 21<sup>st</sup> 2014, in the Santa Lucía Cloud Forest Reserve (SLR, 0°17'30"N, 78°40'30"W) on the Western slopes of the Andes in the province of Pichincha, North West Ecuador. The reserve was selected due to its tropical location and high level of species diversity and endemism. This is a lower montane cloud forest, with a humid subtropical climate covering over 1800 acres and spanning an elevational range of 1400-2560m; topography is defined by steep sloping valley systems of varying aspect. The annual rainfall ranges from 1500-2800mm and average annual temperature is 16°C.

The SLR was awarded reserve status 20 years ago, where small areas had previously been cleared for pasture and fruit farming; the reserve therefore comprises of a mosaic of habitat types: ancient primary forest (FP), with small areas of secondary regrowth (FS), and silvopasture (S) (Myers et al., 2000, Peck et al, 2014). The silvopasture sites typically consist of pasture planted with nitrogen-fixing Andean alder (*Alnus acuminata*), and Elephant Grass (*Pennisetum purpureum*) and are used as grazing paddocks for mules, which provide local transport.

### 2.2 Acoustic Survey Methods & Species Identification

Avifauna was surveyed in a total of 125 sites, located at least 100m apart using a GPS navigator (accurate to the nearest 7 metres) along the accessible footpaths, to avoid spatial pseudo-replication and acoustic overlap (Fig. 1). Of the 125 sites, 71 were in primary forest (FP), 28 in secondary forest (FS) and 26 were silvopasture (S, pasture planted with nitrogen-fixing Andean alder, *Alnus acuminata*). Up to eight sites per day were surveyed using *in situ* point count sampling by local experienced ornithologist Jorge Noë Morales (hereafter, 'Noë') during the dawn chorus from 0600 to 0830.



**Figure 1.** Map of the Santa Lucía Cloud Forest Reserve with sample sites detailed. Colours are indicative of land use: Primary Forest (Dark Green), Secondary Forest (Light Green), Silvopasture (Yellow), Soil/Bare Earth (Red).

Birds were identified to species level through both visual and auditory cues for 10 minutes, following a 2-minute acclimatization period (Ralph et al, 1995).

Noë made note of each individual bird that was seen or heard, the time of observation and where possible, an estimated distance from him and estimated canopy height. Recordings were obtained at chest height synchronously to point counts using a handheld Olympus DM-650 (Olympus, Pennsylvania, USA) digital recorder with a 4GB internal memory. After each session, recordings were transferred to an external hard drive.

## 2.3 Data Pre-processing

Observations that were classified as ‘seen’ in the point count data were removed, leaving only observations which were ‘heard’ so that ecological data could be fairly compared to the acoustic index values produced. Using the multi-track audio editor, Audacity (Version: 2.0.6, <http://audacity.sourceforge.net>), each audio recording was visually inspected and clipped to remove Noë’s voice from the beginning and end of the recordings (in which he stated the name of the site and time of observation) and each recording was cut down to 8 minutes in length, based on the shortest recording. During this manual inspection of the audio

spectrum, obvious anthropogenic sounds (e.g. coughs & coat zipper sounds) were removed from the recordings using the selective trim function of the program; this process was viable for a relatively small data set, however on a larger scale, such intricate manipulation of the recordings would be unfeasible.

After further filtering of unusable recordings, a total of 109 sites were included for analysis (58 FP, 26 FS and 25 S). Sites were categorised into four 'altitude bands' (Band 1 – 1400m – 1699m, band 2- 1700m – 1999m, band 3 – 2000m – 2299m, band 4 – 2300m – 2599m), based on an expected turnover in floral species composition every 300 metres (Personal communication, Dr Mika Peck, March 26<sup>th</sup>, 2015); species accumulation curves were created (Fig.2) and Chao1 estimations (Table.1) were calculated for each of the environmental conditions (habitat type and altitude bands) using the 'fossil' package of R (Vavrek, 2011).

## **2.4 Generation of Indices**

### **2.4.1 Ecological Indices**

Calculations of ecological diversity indices were computed using the R Software (R Core Team, 2014) and R Studio (RStudio, 2014) packages 'vegan' (Oksanen et al., 2015) and 'BiodiversityR' (Kindt & Coe, 2005). Species richness (number of species) for each site was calculated using the '*specnumber*' function. Shannon diversity, Gini-Simpson and Inverse-Simpson were calculated using the '*diversity*' function with arguments 'shannon' 'simpson' and 'inv', respectively, Effective Species Number (ESN) was calculated by taking the exponential of the Shannon index.

### **2.4.2 Soundscape Indices**

Soundscape analyses were undertaken using statistical programming Software R (R Core Team, 2014) with the packages 'seewave', 'tuneR' and 'soundecology'. The left stereo channel of each recording was loaded into R with the function '*readWave*', and a high-pass filter at 1000Hz was applied to attenuate the noise from occasional aeroplanes. The cut-off frequency of the filter was selected based on the most common occurrence of aeroplane noises, following a visual inspection of the spectrogram. Entropy indices,  $H_s$ ,  $H_t$  and  $H$  were calculated using the package 'seewave' with the '*sh*', '*th*' and '*H*' functions accordingly (Sueur et al., 2008a). The 'soundecology' package was used to compute each of the other indices with

'acoustic\_complexity' (*ACI*), 'ndsi' (*NDSI*), 'acoustic\_diversity' (*AD*), 'acoustic\_evenness' (*AE*) and 'bioacoustic\_index' (*BI*) functions (Villanueva-Rivera & Pijanowski, 2015).

## **2.5 Indirect Gradient Analysis**

The extent of species turnover was visualised using a Detrended Correspondence Analysis (DCA) with the '*decorana*' function in the R package (R Core Team, 2014) 'vegan' (Oksanen et al., 2015). The gradient lengths of the first two axes were above 4 standard deviation units of species turnover, signifying the data as too heterogeneous for linear methods, so unimodal methods of analysis were deemed appropriate for use.

## **2.6 Species Accumulation Curves**

An uneven amount of sites were sampled for each of the habitat types and altitude bands. To estimate the number of species that would have been discovered with equal sampling effort, species accumulation curves based on the point count data were created for each of the environmental conditions (habitat type and altitude) and Chao1 estimations were calculated using the '*chao1*' function of the R package 'fossil' (Vavrek, 2011).

## **2.7 Ordination Procedures**

### **2.7.1 Unconstrained ordination**

In order to gain an overview of the main trends of species composition in the data, a unimodal unconstrained ordination procedure, Correspondence Analysis (CA), was performed. Scaling 1 was chosen to represent the ordination of sites in multidimensional space. Two separate CA biplots were created with points indicating either habitat type or altitude band. As the intention was to perform further analysis on the data using constrained techniques, in which rare species can have an unduly large influence on the analysis (Bocard et al., 2011), an experimental CA was performed on the species data in which species occurring only once were removed.

### **2.7.2 Constrained ordination**

To identify the main cause of the change in community composition a Canonical Correspondence Analysis (CCA) was performed with the two environmental variables (habitat type and altitude band) as covariates. Eigenvalues were

obtained to determine which variable had a more significant effect on the species turnover.

A CCA between acoustic index values and abundance data of species at each observational point was performed. To test the model for significance, the data was permuted 999 times using a Monte-Carlo permutation test. Variables that were useful for explaining variance in species data were determined by manual forward selection, where the full model was compared against a further set of models, in which each one had a variable removed.

## **2.8 Statistical Analysis**

Since the probability distribution of the raw indices data failed the Shapiro-Wilk test of normality, an additional logarithmic transformation  $\log(1+X)$  was attempted, however the data could still not be interpreted as normal for all variables therefore non-parametric multivariate ordination was deemed appropriate.

Mean values for each index were calculated and Kruskal-Wallis tests were performed to test the significance of each acoustic index when controlling for each environmental condition, significant results were further tested post-hoc using Nemenyi tests with a Tukey distance approximation.

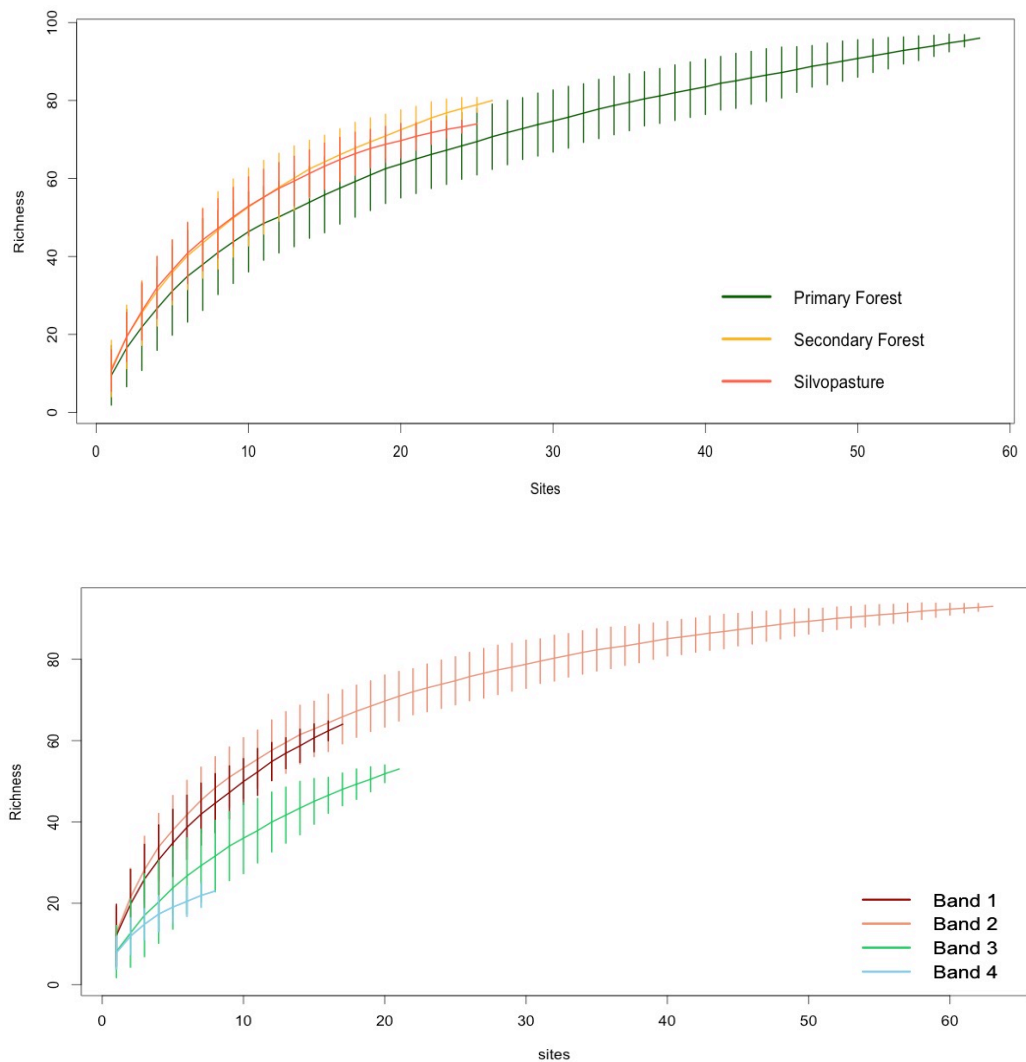
Spearman's rank correlation analyses were performed between acoustic indices and ecological indices in order to test how well the acoustic indices could predict the diversity measures.

## 3 Results

### 3.1 Indirect Gradient Analysis

The gradient lengths of the first two axes determined from the Detrended Correspondence Analysis (DCA) were 4.99 (axis 1) and 5.73 (axis 2), expressed in standard deviation units of species turnover. Indicating a unimodal response from species along the environmental gradients (habitat type or altitude).

### 3.2 Species Accumulation Curves



**Figure 2.** Species Accumulation curve for each separate habitat type (top) and altitude band (bottom). Vertical lines represent 95% confidence intervals.

The point count data found that species in silvopasture and secondary forest sites are initially accumulated at a fairly equal pace (Figure 2, top), although the Chao1 estimation (Table 1) predicts that species accumulation in silvopasture sites is expected to plateau at 84 species whereas secondary forest is predicted to total 101 species. The species accumulation curve for primary forest initially rises at a lower rate than the other habitat types, although Chao1 estimates a much higher total species richness of 153 species.

Chao1 estimates of species in altitude bands 1 and 2 are highest at 84 and 97 respectively (Table 1). Band 3 does not accumulate species as quickly, however it plateaus close (albeit slightly lower) to the first two bands at 71 species (Figure 2, bottom). Point counts in band 4 (the highest altitude range) accumulated the smallest species count (n=22), and produced a Chao1 estimation of only 30 species; considerably lower than all other altitude ranges.

<i>Habitat Type</i>	<i>Number of Individuals</i>	<i>Recorded Species</i>	<i>Chao1 estimate</i>	<i>95% CI (LL, UL)</i>
<i>FP</i>	796	96	153	(140, 166)
<i>FS</i>	396	80	101	(96, 107)
<i>S</i>	358	74	84	(81, 88)
<i>Altitude Band</i>				
1	245	63	84	(78, 89)
2	996	92	97	(95, 99)
3	235	52	71	(65, 76)
4	74	22	30	(26, 34)

**Table 1.** Number of individuals sampled, species richness, Chao1 estimates and lower (LL) and upper (UL) confidence intervals across each habitat type (top) and altitude band (bottom)

### 3.3 Unconstrained Ordination

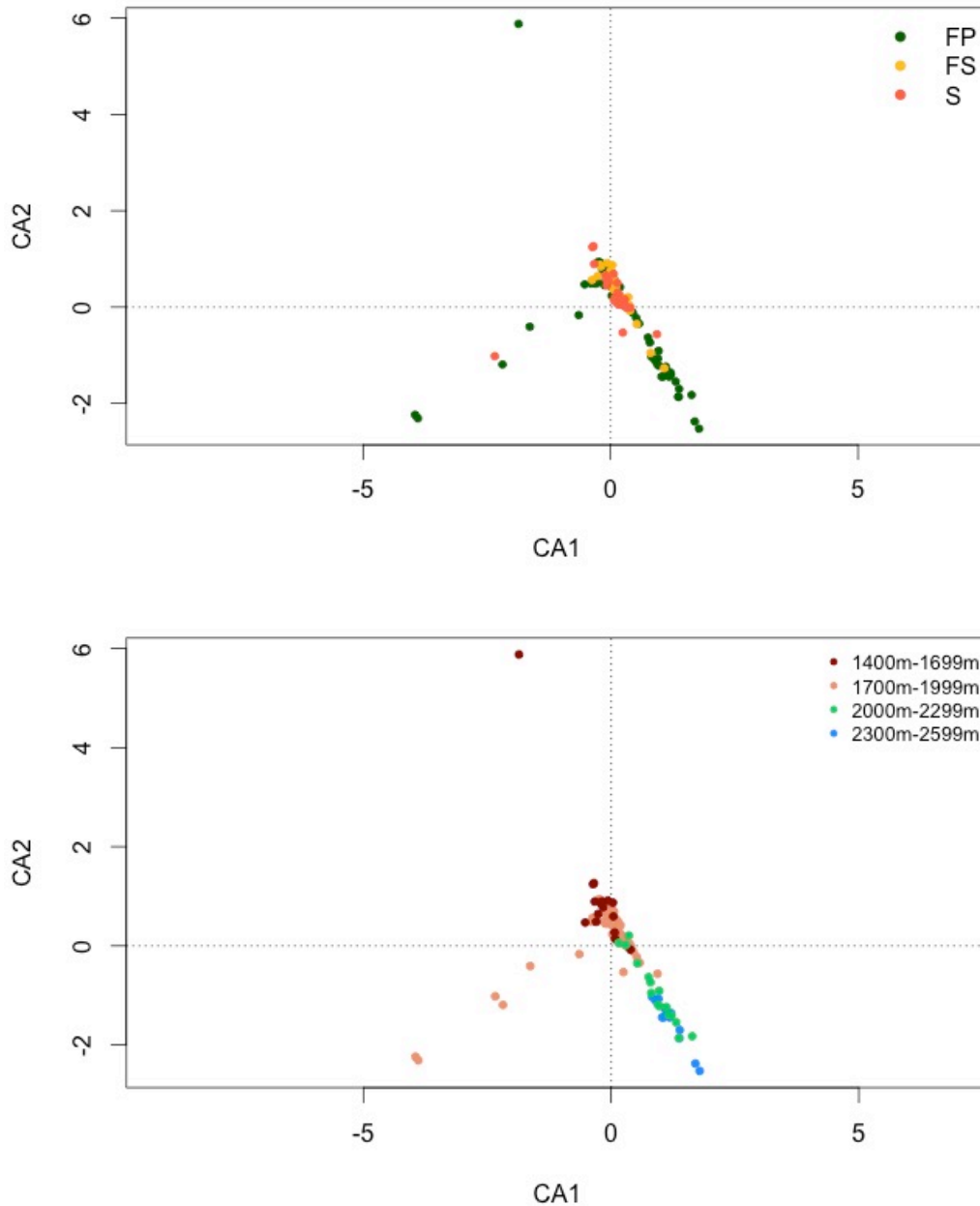
The total inertia of unconstrained ordination in Figure 3 (in correspondence analysis this is the Chi-squared statistic of a data matrix, standardised to unit total) is  $X^2 = 10.99$ . The first canonical axis, CA1 has an eigenvalue of 0.61, explaining over 5.5% of the total species variability. CA2 has an eigenvalue of 0.53, explaining

around 4.8% of the remaining variability and therefore around 2.4% of the total variability

Due to the high number of sites and species recorded, it would have been unreasonable to plot each individual data point, so the interactive '*ordtkplot*' function of the 'vegan' package, was used to identify the site names and the associated species from the ordination plot. The right hand axis of CA1 shows a distinct group of primary forest sites identified as the sample points ranging from FP 51 to FP 71. This is an area in the far North East of the reserve, which is exclusively made up of primary forest sample points, however the general area surrounding these sites (approximately 2km<sup>2</sup>) is a mosaic of primary and secondary forest habitat type. A further cluster consisting of primary forest and one silvopasture site can be seen in the left hand axes between CA1 and CA2 (FP 47 to FP 50 & S 23), which were all strongly associated with the Andean Cock of the Rock (*Rupicola peruvianus*); inspection of the point count data showed this species to be highly abundant in these sites (n=5, 10, 20 21 & 5 respectively).

A cluster of sites can be seen relatively close to the centre of the ordination plot; this primarily consists of silvopasture and secondary forest sample points indicating that these habitat types share many common species, however within this cluster, a slight distinction can be seen between secondary forest and silvopasture sites along axis 2. A few primary forest sites are also visible around the centre of the ordination plot, although due to the high number of observation points and species, it is difficult to determine which of the species are shared amongst these points.





**Figure 3.** Correspondence Analysis (CA) biplots of the bird species data.  
 (Top) Each point on the plot represents an individual site colour coded by habitat type (FP=green, FS=yellow, S=red).  
 (Bottom) Each point on the plot represents an individual site coded by altitude band (Band 1= dark red, band 2= orange, band 3 = green, band 4 =blue)  
 The first two axes explain 5.5% and 2.4% of the variability respectively.

The three sites exhibiting the most the distinct species composition of the silvopasture sites on the bottom of axis CA2 were identified as sites S: 5,6 & 7. Although these were classified into the silvopasture habitat type, cross-referencing with the map revealed that these sites occur within a relatively large area of

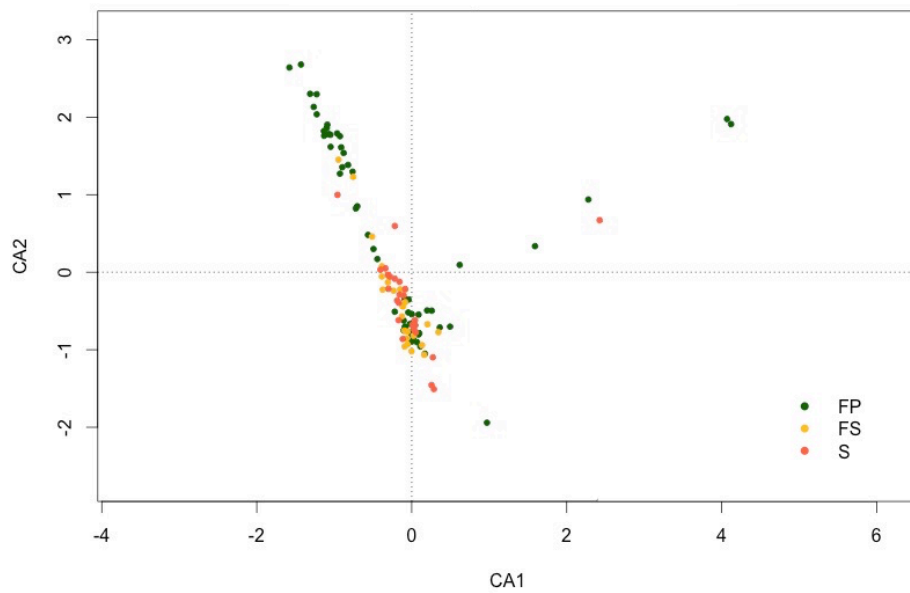
soil/bare earth at a fairly low altitude of around 1600m. Four species were common between these sites, the Booted racket-tail (*Ocreatus underwoodii*), the Brown Violetear (*Colibri delphinae*), the Golden Tanager (*Tangara arthus*) and the Immaculate Antbird (*Myrmeciza immaculata*), all of which are typically found along borders and in adjacent clearings on montane forests at a range of altitudes from 900- 2200m, although are mostly found below 1500m (Ridgley & Greenfield, 2001).

The extreme outlier at the highest point of axis CA2 was identified as FP 09 (the most Westerly site on the map), which is an isolated area of primary forest, surrounded by a mosaic of secondary forest and silvopasture sites; it is the lowest altitudinal point at 1420m. Six species were recorded within this point, which is not particularly abnormal among the dataset, however three of these species were recorded exclusively in this site, resulting in a relatively unique community structure.

The biplot of the CA with sites colour coded by altitude band (Figure 3, bottom) shows a clear gradient of change in species composition across sites, with an intuitively more obvious distinction between sites in different altitude ranges than was observed for different habitat types.

This initial exploration of the data shows a turnover of species composition between sites and appears to coincide with a gradient, which is linked to either habitat type or altitude or a combination of both. In the SLR, many of the primary forest sites occur within higher altitude ranges, so from the CA alone it is not entirely clear which of the environmental gradients has more of an effect on the species composition observed.

The difference in eigenvalues for axes 1 and 2 when rare species were removed from the analysis (Figure 4) was negligible at a reduction of less than 1%, the removal of rare species was therefore deemed unnecessary, a decision that was further justified by the potential for rare species to represent EDIS and consequently may be useful in the final analyses (Poos & Jackson, 2012).



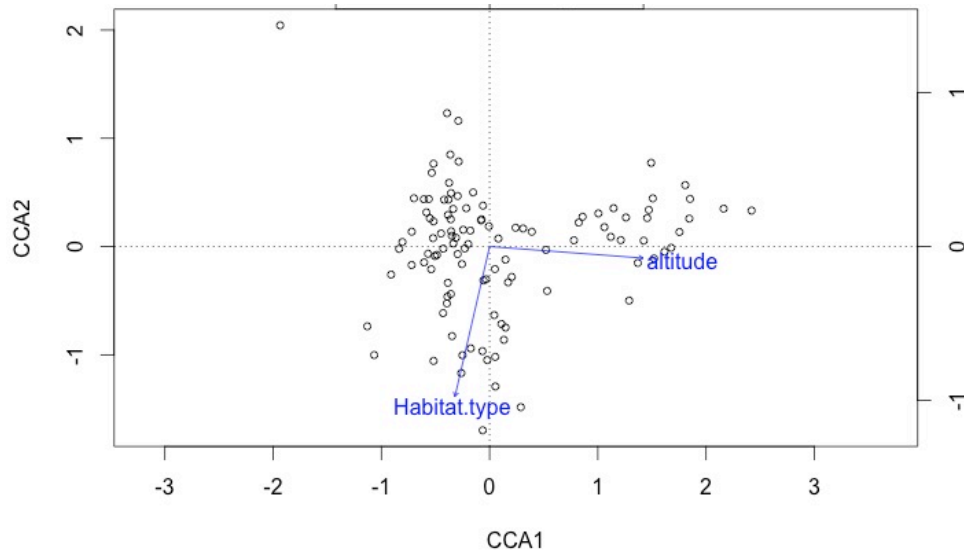
**Figure 4.** Correspondence Analysis (CA) biplots of the bird species data with rare (occurring only once) species removed. Each point on the plot represents an individual site colour coded by habitat type (FP=green, FS=yellow, S=red). The first two axes explain 6.3 % and 2.7% of the variability respectively.

### 3.4 Constrained Ordination

#### 3.4.1 Environmental Variables

The model containing the two environmental variables as predictors of the species dataset (Figure 5) was found statistically significant at  $p > 0.001$  yielding two canonical functions (Given in terms of ‘inertia’; in constrained ordination this is equivalent to the phi coefficient, which is similar to the Pearson correlation coefficient) of  $r_\phi = 0.46$  and  $0.20$ , from a total inertia of  $r_\phi = 10.98$ , the two variables together therefore explain 6% of the variation in the species data; according to Leps & Smilauer, (2003) this explanation is a relatively good predictor considering the high number of species and sample points.

Altitude had a stronger effect on species data, accounting for 0.69% of the explained inertia, whereas habitat accounted for only 0.31%.

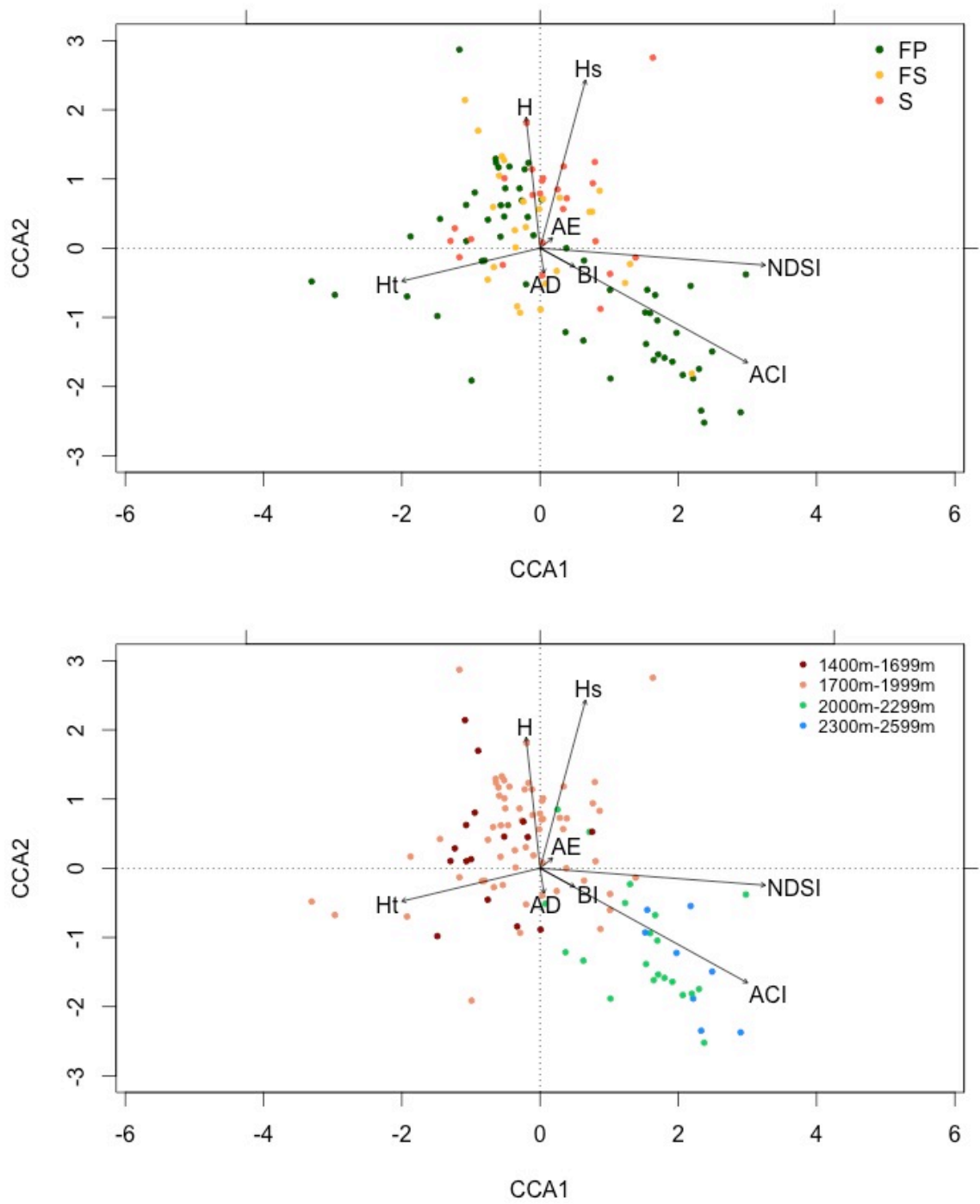


**Figure 5.** CCA of the predictor variables constrained by environmental data, altitude and habitat type. Points represent the position of sites in multidimensional space.

### 3.4.2 Acoustic Variables

The positions of sites on the biplots (Figure 6, bottom) show two defined clusters of high and low altitude. While the definition between sites of different habitat type (Figure 6, top) is less clear there are two clusters that consist of mostly primary forest sites. Using the '*orditkplot*' function, these were identified as the sites in which Andean Cock of the Rock are associated (in the left axis), and the high altitude sites (far right in the positive axis of CCA 1).

The position of arrows on the biplots (Fig. 6) suggest that higher values of Temporal Entropy ( $H_t$ ) are associated with low altitude and degraded habitat, whereas Spectral Entropy ( $H_s$ ) and Total Entropy ( $H$ ) appear to correlate with Silvopasture and to a lesser extent, low altitude.



**Figure 6.** CCA of the predictor variables constrained by acoustic indices: temporal entropy ( $H_t$ ), spectral entropy ( $H_s$ ), total entropy ( $H$ ), acoustic complexity index ( $ACI$ ), normalized soundscape diversity index ( $NDSI$ ), acoustic evenness ( $AE$ ) & acoustic diversity ( $AD$ ). (Top) Colours indicate the habitat type assigned to each site (FP=green, FS=yellow, S=red). (Bottom) Colours represent altitude bands (Band 1= dark red, band 2= orange, band 3= green, band 4= blue).

Sites of high altitude and some primary forest sites are associated with the Acoustic Complexity Index (*ACI*), and the Normalised Difference Soundscape Index (*NDSI*), although permutation tests found only *NDSI* to be a significant predictor. The Acoustic Diversity Index (*AD*), Acoustic Evenness (*AE*) and Bioacoustic Index (*BI*) do not appear to show any correlation with species composition.

The model containing the eight acoustic variables as predictors of the species dataset was found statistically significant at  $p < 0.001$ . Yielding eight constrained canonical functions of  $r_\phi = 0.28, 0.18, 0.16, 0.12, 0.10, 0.09, 0.08, 0.06$  (combined  $r_\phi = 1.083$ ), this model explains just over 10% of the variation in the species data. Monte-Carlo permutation tests with 999 permutations identified the entropy indices  $H_s$ ,  $H_t$  and  $H$  as significant predictors of the species data at  $p = 0.033$ ,  $p = 0.031$  and  $p = 0.031$  respectively, and *NDSI* at  $p = 0.048$ . Manual forward selection of the variables confirmed this outcome.

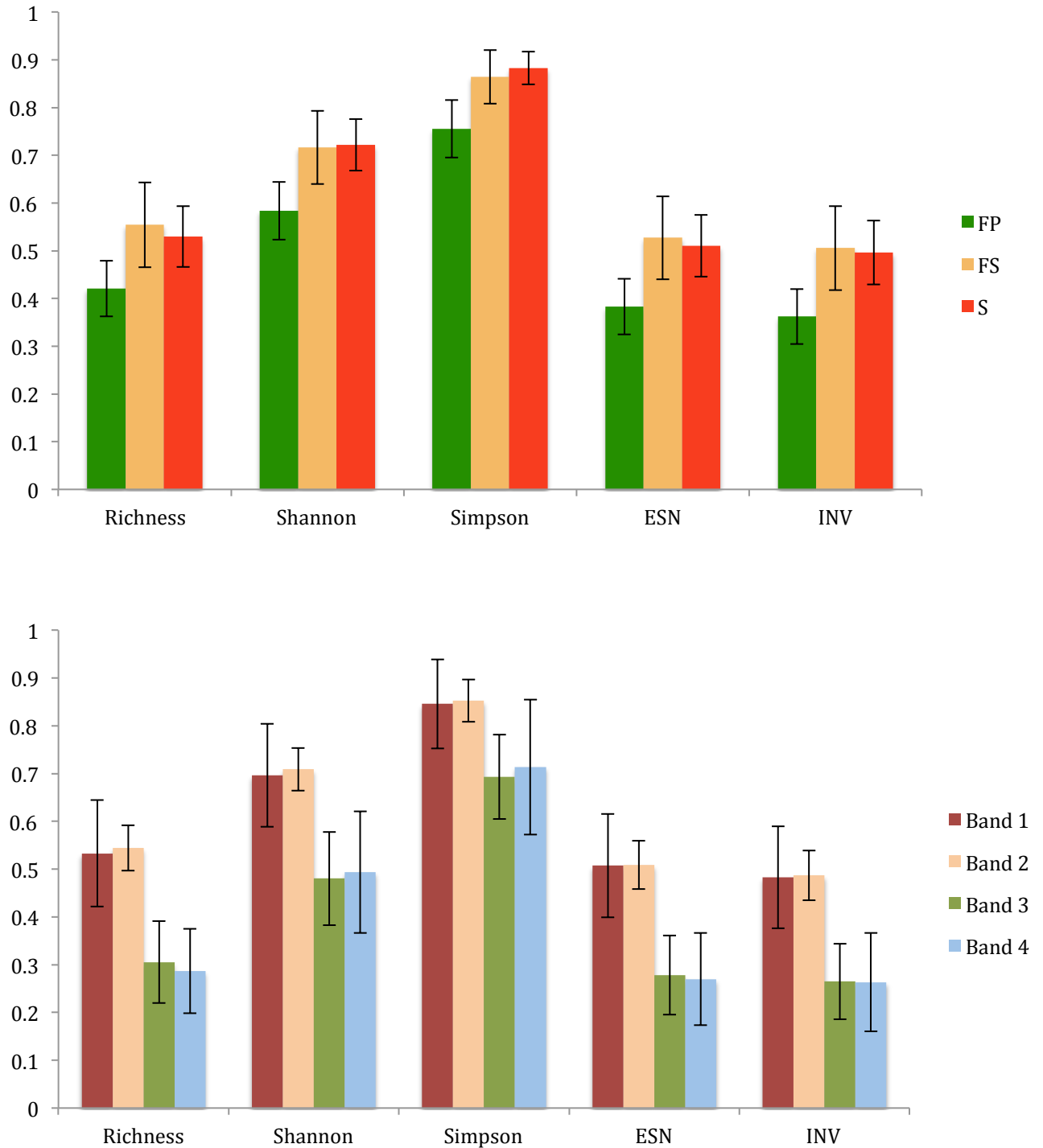
### **3.5 Mean index values**

#### **3.5.1 Ecological Indices**

Values for each of the ecological indices calculated from the point counts are given in Appendix 2.1, and mean values for each index (Appendix 1.1) at each habitat type and altitude are plotted in Figure 7. Kruskal-Wallis tests found a significant difference across the habitats for each ecological index (Table 2).

The bar plots in Figure 7 show a consistent trend of lower species richness and species diversity and evenness in FP sites than in both FS and S sites.

Post hoc investigations using a Tukey approximation, found FP significantly different from FS and S for all indices, except Richness, in which FP was not significantly different from S between habitat types. All indices were found significant between altitude bands 1 & 2 and 3 & 4 except for Gini-Simpson, in which altitude band 1 and 3 were not significantly different.



**Figure 7.** Bar plots of average values of ecological indices results for each habitat type (top) and altitude band (bottom). Error bars indicate 95% confidence intervals. Species richness (Richness), Shannon diversity (Shannon), Gini-Simpson (Simpson), Effective Species Number (ESN) and Inverse-Simpson (INV). Each index is scaled between 0 and 1 for comparison.

	<i>P-Value</i>	Chi-Square	Post Hoc (by habitat type)			
Richness	0.0165 *	8.2128		<i>FP</i>	<i>FS</i>	
			<i>FS</i>	0.036*	-	
			<i>S</i>	0.088	0.957	
Shannon & ESN	0.0055 *	10.4108		<i>FP</i>	<i>FS</i>	
			<i>FS</i>	0.020*	-	
			<i>S</i>	0.031*	0.994	
Gini-Simpson & Inverse Simpson	0.0053 *	10.4823		<i>FP</i>	<i>FS</i>	
			<i>FS</i>	0.021*	-	
			<i>S</i>	0.028*	0.998	
	<i>P-Value</i>	Chi-Square	Post Hoc (by altitude band)			
Richness	1.485e-05*	20.0791		<i>1</i>	<i>2</i>	<i>3</i>
			<i>2</i>	0.998	-	-
			<i>3</i>	0.009*	0.002*	-
			<i>4</i>	0.035*	0.009*	0.987
Shannon & ESN	3.27e-05*	23.4396		<i>1</i>	<i>2</i>	<i>3</i>
			<i>2</i>	1.000	-	-
			<i>3</i>	0.009*	0.003*	-
			<i>4</i>	0.042*	0.145*	0.994
Gini-Simpson & Inverse Simpson	9.455e-05*	21.2247		<i>1</i>	<i>2</i>	<i>3</i>
			<i>2</i>	1.000	-	-
			<i>3</i>	0.156	0.006*	-
			<i>4</i>	0.063*	0.023*	0.996

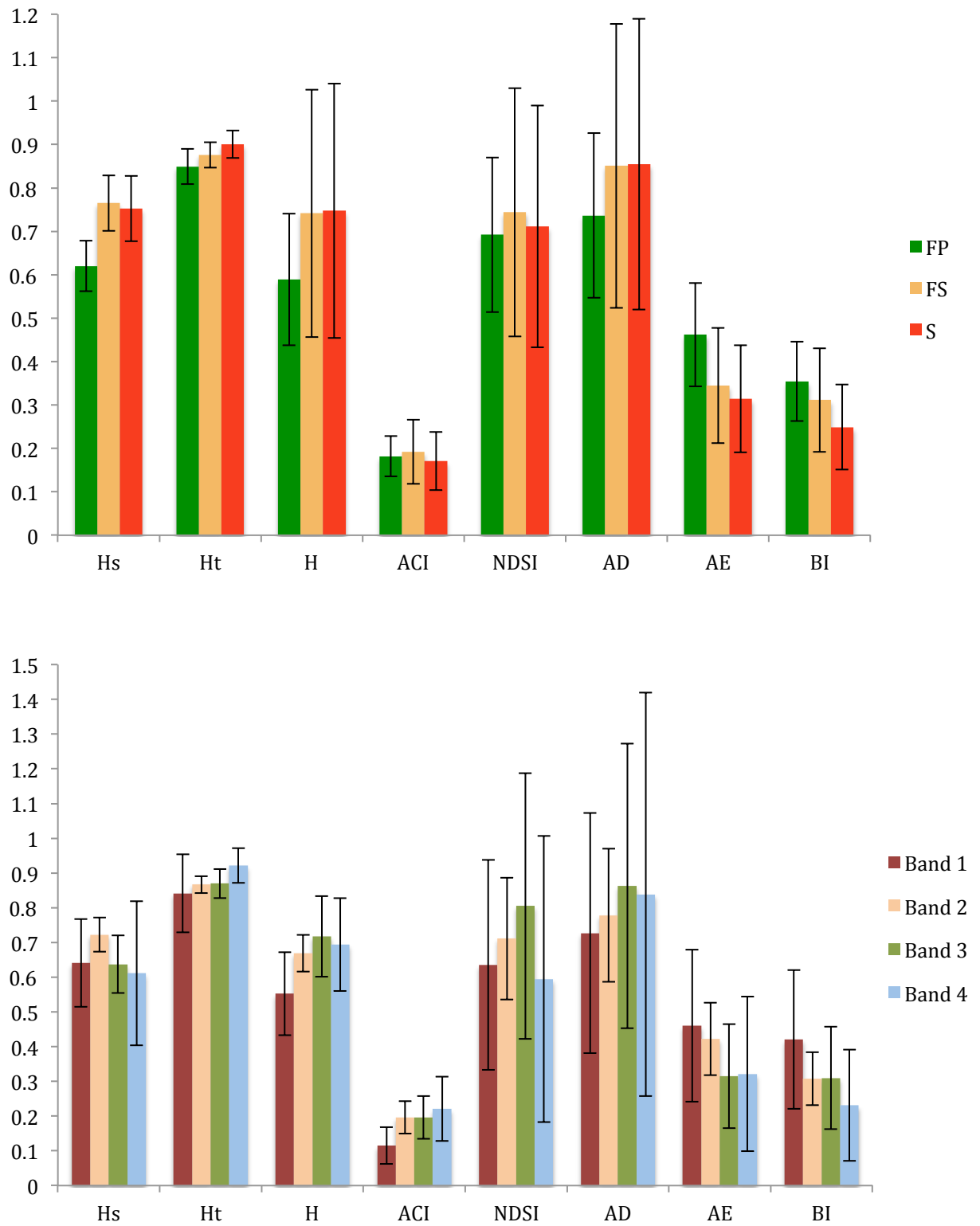
**Table 2.** Results from the Kruskal-Wallis rank sum significance tests between each habitat type (top) and each altitude band (bottom) for each ecological index. Results are significant at  $p < 0.05$  (indicated by \*). Results from post-hoc tests comparing each condition using the Tukey approximation are given in the right hand column. Significant results are indicated with an asterisk.

### 3.5.2 Acoustic Indices

Values for each of the acoustic indices calculated are given in Appendix 2.2, and mean values for each index (Appendix 1.2) at each habitat type and altitude are plotted in Figure 8.

The bar plots in Figure 8 show a pattern of decreasing value with increasing habitat disturbance for *AE* and *BI* whereas *AD* shows the opposite trend, these differences were found significant across habitat types (*AD*,  $p=0.019$ ; *AE*,  $p=0.015$ ; *BI*,  $p=0.049$ ) by the Kruskal-Wallis tests (Table 3.).





**Figure 8.** Bar plots of average values of acoustic indices results for each habitat type (top) and altitude band (bottom). Error bars indicate 95% confidence intervals. Spectral Entropy ( $H_s$ ), Temporal Entropy ( $H_t$ ), Total Entropy ( $H$ ), Acoustic Complexity Index (ACI), Normalized Soundscape Diversity Index (NDSI), Acoustic Diversity (AD), Acoustic Evenness (AE) and Bioacoustic Index (BI). Each index is scaled between 0 and 1 for comparison.

For each of these indices (*AE*, *AD* and *BI*) post hoc investigation attributed the significance to a difference between FP and S habitat types.

*ACI* and *NDSI* values were not significant across habitat types, although showed a highest mean value in FS sites.  $H_s$  and  $H$  were significantly different across habitat types ( $p=0.001$  and  $p=0.0007$  respectively); this was attributable to a much lower value in FP sites than both FS and S. For both of these indices, FS and S were not different from each other. Despite a trend of increasing mean value with habitat disturbance in  $H_t$ , this was non-significant.

Each of the indices that displayed no significant differences across habitat types showed a significant difference across the altitude bands. The bar plots showed an increase in *ACI* values with increasing altitude which was significant at  $p=0.001$ , post hoc tests revealed a difference between band 3 and bands 1 and 2; band 4 had the highest mean value but was not significantly different from any other altitude band. Mean *NDSI* values peaked in altitude band 3 and dropped in altitude band 4, post hoc tests found that the two lowest bands were not significantly different from each other nor were the two highest bands, however each of the two lowest bands was different from the two highest bands. Mean  $H_t$  values increased with increasing altitude, similar to *NDSI*, bands 1 and 2 were not different and bands 3 and 4 were not different; although the mean of band 4 was higher than band 2, post hoc did not present a difference for these bands, due to the overlapping confidence intervals.

	<i>P-Value</i>	Chi-Square (df = 2)	Post Hoc (by habitat type)		
<i>H<sub>s</sub></i>	0.001*	13.325		<i>FP</i>	<i>FS</i>
			<i>FS</i>	0.008*	-
			<i>S</i>	0.011*	0.999
<i>H<sub>t</sub></i>	0.335	2.185			
<i>H</i>	0.0007*	14.3013		<i>FP</i>	<i>FS</i>
			<i>FS</i>	0.013*	-
			<i>S</i>	0.003*	0.910
<i>ACI</i>	0.4807	1.465			
<i>NDSI</i>	0.692	0.737			
<i>AD</i>	0.019*	7.974		<i>FP</i>	<i>FS</i>
			<i>FS</i>	0.105	-
			<i>S</i>	0.034*	0.911
<i>AE</i>	0.015*	8.3935		<i>FP</i>	<i>FS</i>
			<i>FS</i>	0.133	-
			<i>S</i>	0.022*	0.794
<i>BI</i>	0.049 *	6.045		<i>FP</i>	<i>FS</i>
			<i>FS</i>	0.455	-
			<i>S</i>	0.042*	0.545
	<i>P-Value</i>	Chi-Square (df=3)	Post Hoc (by altitude band)		
<i>H<sub>s</sub></i>	0.1395	5.4852			
<i>H<sub>t</sub></i>	0.0006*	17.433		<i>1</i>	<i>2</i>
			<i>2</i>	0.290	-
			<i>3</i>	0.002*	0.035*
			<i>4</i>	0.014*	0.138
<i>H</i>	0.067	7.1759			
<i>ACI</i>	0.001*	16.112		<i>1</i>	<i>2</i>
			<i>2</i>	0.680	-
			<i>3</i>	0.003*	0.005*
			<i>4</i>	0.170	0.420
<i>NDSI</i>	0.0003**	18.919		<i>1</i>	<i>2</i>
			<i>2</i>	0.821	-
			<i>3</i>	0.006*	0.006*
			<i>4</i>	0.023*	0.043*
<i>AD</i>	0.372	3.130			
<i>AE</i>	0.243	4.175			
<i>BI</i>	0.650	1.643			

**Table 3.** Results from the Kruskal-Wallis rank sum significance tests between each habitat type (top) and each altitude band (bottom) for each acoustic index. Results are significant at  $p > 0.05$  (indicated by \*). Results from post-hoc tests (where applicable) comparing each condition using the Tukey approximation are given in the right hand column.

### 3.6 Correlation Analysis

To test the capabilities of the acoustic indices as predictors of the diversity indices, correlation analysis was performed between each acoustic index and each ecological index (Table 4). Only spectral entropy ( $H_s$ ) and total entropy ( $H$ ) were significantly positively correlated with each of the ecological indices, although the weak correlations suggest that little variability is explained by the relationships.

	<i>H<sub>s</sub></i>	<i>H<sub>t</sub></i>	<i>H</i>	<i>ACI</i>	<i>NDSI</i>	<i>AD</i>	<i>AE</i>	<i>BI</i>
<b><i>Richness</i></b>	0.23*	-0.02	0.19*	-0.17	0.05	-0.06	0.05	0.09
<b><i>Shannon &amp; ESN</i></b>	0.25*	-0.04	0.20*	-0.16	0.02	-0.11	0.10	0.07
<b><i>Gini-Simpson &amp; Inv-Simpson</i></b>	0.26*	-0.02	0.19*	-0.17	0.006	-0.06	0.05	0.09

**Table 4.** Spearman's rho rank correlations between acoustic indices and ecological indices. Results are significant at  $p = < 0.05$  (indicated by \*).

## **4 Discussion**

Acoustic indices were applied here for the first time to recordings made in an Andean tropical montane cloud forest of high bird diversity. Point count observations were performed and the results were used to determine how the bird species diversity and composition changed over two environmental gradients of habitat disturbance and altitude. Audio recordings were made simultaneously to the point count observations and acoustic indices were calculated based on the spectral properties of each recording; an assessment of whether these acoustic indices changed along the same gradients of habitat disturbance and altitude was made. Finally, acoustic indices were correlated with the point count data in an attempt to investigate their potential use as biodiversity indicators. Whilst previous efforts have been made to estimate species richness based on individual indices (Boelman et al., 2007; Kasten et al., 2012; Pieretti et al., 2011; Sueur et al., 2008b; Villanueva-Rivera et al., 2011), here they have been investigated together in an attempt to discover which ones correlate best with traditional diversity measures.

### **4.1 Species Composition and Diversity**

Based on point count measures, a turnover in bird community composition was found across sample sites. The DCA (section 3.1) gave axis lengths above 4 standard deviations of species turnover indicating that some species have a unimodal response along the gradient. This pattern of high species turnover is typical of long environmental gradients such as the altitudinal one used in this analysis, where either end of the gradient is unlikely to have any species in common (Bocard et al., 2011). This is particularly prevalent on the Western slope of the Ecuadorian Andes due to a high incidence of endemism and restricted range species, as well as a tendency of montane avifauna to exhibit a high diversity of unique ecological roles within a habitat (Herzog & Kattan, 2011; Poulsen & Krabbe, 1997).

Results of the point counts found mean species richness at its lowest in primary forest and highest in secondary forest (Figure 7); mean species richness of silvopasture was closer to secondary than primary forest, although was not significantly different from either (Table 2).

Both silvopasture and secondary forest sites exhibited a significantly higher mean diversity than primary forest. This result may seem counter intuitive since anthropogenically disturbed or degraded Andean forests are often characterized by lower bird diversity than nearby undisturbed forests (Herzog & Kattan, 2011), however, mature secondary forest has previously been found to harbour greater species diversity than comparable primary forest when abandoned pastures have been allowed to regenerate (O'Dea & Whittaker, 2007; Welford, 2000). Many of the most common species observed in this study were edge-tolerant and are therefore not restricted to a single habitat type. This allows them to move between sites of varying disturbance, which could increase the species richness of intermediate habitats (Da Silva et al., 1996; O'Dea & Whittaker, 2007; Welford, 2000). Welford (2000) also demonstrated that regenerated forest can be utilised by rare or threatened forest interior species, and specifically by range restricted species when primary forest habitat is limited or fragmented (Welford, 2000).

The three entropy indices ( $H$ ,  $H_t$  and  $H_s$ ) and the *NDSI* were the only indices found to significantly correlate with species composition in the ordination of species and acoustic indices (Figure 6, but see section 3.4.2). These indices could therefore be used to identify changes in community composition.

Constrained ordination of the environmental gradients found that altitude has a stronger influence on the species composition than habitat type. This was characterised by a reduction in species richness with increasing altitude, with a drop in both species richness and diversity at approximately 2000m. Although no single cause can account for all observed species richness patterns, altitude has been widely noted as one of the best predictors, wherein the decrease in species richness with increasing elevation is a well-documented phenomenon (Herzog & Kattan, 2011; Romdal & Grytnes, 2007). This trend is due to a combination of factors such as decreasing temperature and ecosystem productivity and increasing precipitation with increasing altitude (Kessler et al., 2001; McCain, 2005; McCain & Grytnes, 2010). The species-area effect, which predicts a positive relationship between land area and number of species, is also a possible driver of species richness patterns where land area decreases with increasing elevation on a mountain (Romdal & Grytnes, 2007). Richness of the Andean slopes has previously

been found characterized by a hump-shaped relationship of altitude and species richness, with diversity peaks between 1000m and 2000m (Kattan & Franco, 2004). So it is possible that the Santa Lucia Reserve (SLR) is exhibiting a mid-altitudinal hump and that the lack of observations at altitudes lower than 1420m resulted in truncated sampling (McCain & Grytnes, 2010).

It is important to note that a higher number of silvopasture sites were sampled at lower altitudes, and high altitudes consist predominantly of primary forest, therefore although the effect of altitude on diversity is stronger than habitat type, the results observed are probably exacerbated by a combination of the environmental conditions.

## **4.2 Acoustic Indices**

### ***NDSI***

The *NDSI* values are calculated between -1 and +1, where +1 is indicative of a habitat with no anthrophony. The mean values calculated for this index are between 0.69 and 0.74 for habitat types and between 0.59 and 0.81 for altitude bands, which indicates low occurrence of anthropogenic noise. This is to be expected in the SLR due to low human population density and no industrial presence (Personal communication, Dr Mika Peck, April 15<sup>th</sup>, 2015). No significant difference in *NDSI* values were found between habitat types, however, the *NDSI* values were significantly lower in the two lowest than in the two highest altitude bands (Table 3). As there is a low human presence in the SLR it may be intuitive to suggest that lower *NDSI* values were due to geophony at lower altitudes. Geophony is a soundscape property that can occupy a range of frequency bands throughout a recording, so although a band pass filter was used to correct for noises from generators and aeroplanes below 1kHz, geophonic sounds between 1-2kHz (the band in which anthrophony is expected to occur) would still affect the result of this index.

### ***AD & AE***

Acoustic Diversity (*AD*) appears to show a trend of increasing value and concomitantly, Acoustic Evenness (*AE*) appears to show a trend of decreasing values with increasing habitat disturbance (Figure 8); these values were significant at  $p=0.019$  (*AD*) and  $p=0.015$  (*AE*). Post hoc tests revealed that *AE* values for

silvopasture were significantly higher (the amplitude envelope of the signal was more even) than in both primary and secondary forest sites (Table 3). This result is representative of the lower observed species richness in silvopasture sites and is in accordance with the initial findings made by Villanueva-Rivera et al. (2011) during the development of this index. An opposite trend was revealed by post hoc tests on the *AD* index, in which silvopasture sites gave significantly lower mean values; again this is in accordance with the preliminary findings of the original study (Villanueva-Rivera et al., 2011).

### ***BI***

The Bioacoustic Index (*BI*) is based on the calculation of the area under the mean frequency spectrum (minus the value of the lowest bin). The preliminary study by Boelman et al. (2007), which evaluated the use of the *BI*, found that values strongly positively correlated with counts from an ornithological survey (Boelman et al., 2007). However, the analysis made here found that mean *BI* values were significantly lower in silvopasture sites than in both primary and secondary forest sites; as the mean species richness was higher in Silvopasture sites this result contradicts original findings for this index (Boelman et al., 2007). In order to demonstrate why this index is not appropriate as a measure of biodiversity, mean frequency spectrums from sites with identical ecological values that gave values at either end of the range of calculated *BI* values, are plotted in Appendix 3. Despite the clear differences in frequency properties between the two recordings, the point counts at these sites identified the same number of species. Noë was able to identify 10 species in both FP 64 and FS 18, however the Dusky Bush-tanager (*Chlorospingus semifuscus*), a bird with a repeated, high frequency call dominates the recording in FP 64 whereas the sound of a river can be heard throughout the recording in FS 18. The amplitude of the dominating frequency bins is similar in the two recordings, however since the *BI* is calculated as a product of frequency (Hz) and amplitude (dB), the recording with the dominant high frequency gives a higher value. We can therefore say that the *BI* can give a representation of the actual vocalisation behaviour of avifauna in a site, however its oversensitivity to particularly noisy species renders it inappropriate for use as a biodiversity measure.



### ***ACI***

Although strongly associated with primary sites on the ordination biplot (Figure 6), the Acoustic Complexity Index (*ACI*) values were only found significantly different among altitude bands (Table 3). Mean values increase with increasing altitude (Figure 8). Band 1 & 2 were found significantly different from band 3, however band 4 was not found significantly different to any other band due to a high variability in values. The *ACI* should give a higher value with an increased prevalence of birdsong within a recording, assuming a more complex variability within the intensities registered (Pieretti et al., 2011). Given the observed species richness, we would expect the *ACI* to be higher in lower altitude bands, however a negative correlation between *ACI* and richness (Table 4) shows this to be the opposite. The cause of this trend is unclear, however, considering the results of the *NDSI*, we see that this may be due to geophonic noise disturbance in lower altitudes, which is often characterised by more constant intensity values (Pieretti et al., 2011). Alternatively, birds calling at low altitudes may be doing so with less frequency variations, although confirmation of this would require investigation further than the scope of this paper.

### ***H<sub>s</sub>***

With values ranging from 0.78 to 0.92, Sueur's spectral entropy index (*H<sub>s</sub>*) approaches the top end of its maximum value of 1 for all sites; indicating heterogeneity of frequencies within the soundscape of the Santa Lucia Reserve (Sueur et al., 2008b). A significant difference across habitat types was found for this index, where mean *H<sub>s</sub>* values were significantly lower in primary forest than in both secondary forest and silvopasture (Figure 8). Mean spectral entropy is highest in secondary forest sites, where a higher diversity of species was observed. This result is consistent with the original findings by Sueur et al. (2008b), and is potentially caused by the partitioning of frequency bands by several species, in accordance with the Acoustic Niche Hypothesis (Sueur et al., 2008b; Pijanowski et al., 2011b). The obstruction of sound waves by trees can cause distortion to patterns in bird song, so in the tropics many birds vocalise using pure tones that pass through the environment relatively uninfluenced (Beckers et al., 2003; Slater, 1999). Therefore, it is possible that pure tones are present in the SLR (which would produce low spectral entropy values), although the partitioning of

frequency bands registers as high heterogeneity within each amplitude envelope, producing high  $H_s$  values (Sueur et al., 2008b).

### **$H_t$**

The bar plot in Figure 8 shows that mean  $H_t$  values increase with increasing habitat disturbance, although this difference is not significant. Mean  $H_t$  values significantly increased ( $p= 0.0006$ ) with increasing altitude; this is contrary to the expected pattern in which  $H_t$  values are predicted to decrease where there are fewer species (Sueur et al., 2008b). However, all sites except FP 11 (which has a value of 0.87) give  $H_t$  values higher than 0.93, therefore approaching the very top end of their maximum values. This indicates high heterogeneity of amplitude modulations within each recording and little variation between recordings. The unexpected correlation found here between  $H_t$  values and species richness highlights an issue with the entropy index: although high values can be produced from loud continuous birdcall, they may also be generated from a spectrum with a sustained signal, such as in the presence of human noise or continuous running water (Sueur et al., 2008b). A manual auditory inspection of the recordings revealed that those with the highest  $H_t$  values ( $H_t = >0.990$ ) all contained consistent sounds of running water, therefore it is not possible to determine whether  $H_t$  could be used to predict species richness in this study.

### **$H$**

The total entropy ( $H$ ) was found significantly different ( $p=0.0007$ ) across habitat types, although was not significant ( $p=0.067$ ) across altitude bands. As a product of the two,  $H$  is very sensitive to the results of  $H_s$  and  $H_t$ . On a habitat gradient, both  $H_s$  and  $H_t$  gave lower mean values where there was lower species richness and high values with high richness. Despite  $H_t$  not producing a significant result, the two positive correlations resulted in a significant positive correlation of  $H$  values and species richness. This is consistent with the expected result (Sueur et al., 2008b). On an altitudinal gradient, mean  $H_s$  values corresponded to the patterns of species richness (although not significantly), while mean  $H_t$  values were significantly higher ( $p=0.0006$ ) where lower species richness was observed for reasons previously discussed. The opposition of the correlations led to a non-significant result for  $H$  values across altitude bands. This highlights the observation by Sueur et al. (2008b), that whilst total entropy shows potential for use as a species

diversity indicator, the reliability of this index can be reduced by geophony or anthrophony (Sueur et al., 2008b).

### **4.3 Correlation Analysis**

$H_s$  and  $H$  were the only two indices found to significantly correlate with all ecological indices in the correlation analysis (Table 4); moreover these correlations were weak. Sueur et al. (2008b) developed the  $H$  index as a product of both spectral and temporal indices ( $H_s$  and  $H_t$ ), and only the  $H$  index was used to test the species richness of a community. We would suggest therefore that the  $H$  index is the only reasonable index to use as a measure of diversity.

### **4.4 Limitations and Considerations**

#### **The use of indices**

One aim of this study was to evaluate whether acoustic indices could be used as a proxy for biodiversity measurements obtained from traditional point count methods. However, a number of issues concerning the use of indices were identified.

A problem associated with the ecological indices, is that they take into account the species richness and the abundance distribution of these species, without necessarily taking into account the overall species composition of a habitat, consequently, they may not always be effective to accurately determine the 'health' of a habitat, as a pristine habitat may host more rare species or more indicator species than its degraded counterparts (Magurran, 2004).

The use of acoustic indices to obtain biodiversity measures can be problematic because they provide an overall summary of the frequency or amplitude modulations of a recording, under the general assumption that more species at a site will lead to a recording with increased heterogeneity of spectral properties. In reality, vocalisations of organisms are hugely variable and as shown in the example in Appendix 3, a single vocalising organism can dominate the acoustic spectrum, thereby affecting the accuracy of the calculations.

The acoustic indices also do not take into account the presence of non-vocalising species, and can be affected by the distance between the sound source and the microphone (Hobson et al., 2002; Pieretti et al., 2011); a point count observation would report these species but the vocalisations would have a disproportionate impact on the amplitude or frequency modulations registered in the recording and their presence could be overlooked (Haselmayer & Quinn, 2000). The position of the  $H_t$  arrow on the biplot constrained by acoustic indices appears to show a correlation with sites FP 47 – FP 50, these sites were strongly associated with Andean cock of the Rock (*Rupicola peruvianus*) which is an uncommon to fairly locally common species found in and near forested gorges and ravines in the foothills, they have a wide elevational range occurring from as low as 600m up to 2500m (Ridgley & Greenfield, 2001). *R. peruvianus* is known to exhibit Lekking behaviour, in which congregations of birds vocalise loudly for hours at a time. By dominating the spectrum, incidences such as these would be likely to have a strong effect on the acoustic index values produced, which may cause a problem if attempting to conduct a fully automated analysis of the recordings.

### **Study methods**

This study aimed to capture the soundscape of the sites during the dawn chorus, however there is slight temporal variation (between 6am and 8am) among recordings. Light availability has been found largely responsible for dictating precise timing events of the dawn chorus in the tropics; physical traits such as eye size and ecological determinants such as canopy foraging height of different birds species have been found to have an effect on the timing of chorus vocalisations throughout communities (Berg et al., 2006; Pickrell, 2002). Temperature has also been found to have an effect on this timing (Bruni & Mennill, 2015); as the study sites are situated along an altitudinal gradient, with varying temperatures and light availability, it is possible that the ten minute recording period could have picked up an inconsistent representation of the dawn chorus.

In order to more accurately assess how the acoustic indices behave according to either habitat type or altitude, one of these environmental conditions should have been kept constant throughout the data collection. Considering the stronger affect that altitude had on community composition, it may have been rational to maintain a constant habitat type and work along only an altitudinal gradient.

Another potential issue with the data collection method of this study was the recording technique. In order to allow simultaneous collection of sound recordings and point count data, data collection was made *in situ* using a hand held recorder. This recorder was found to be sensitive to anthropogenic noises created by the field observer such as coughs and rustling due to movements. And although efforts were made to eliminate these sounds from the recordings it is unlikely that these were all identified and removed. This set of anthropogenic noises would have been exceptionally close to the microphone so they would have given high amplitude values and may have had a disproportionate effect on the generation of certain indices, for example this would have impacted the *BI* index which is highly sensitive to amplitude differences. Nevertheless, justification of this recording technique could be realized due to its potential for use with citizen science. Local community engagement programs or global online collaborations such as 'Record the Earth' (Record the Earth, 2016), in which handheld recorders or mobile phones provide a cheap and accessible method of data collection, are increasingly widespread and common (Dickinson et al., 2010; Sekercioglu, 2012; Towsey & Planitz, 2011). By using a comparable data collection method, it is possible to see how the acoustic indices could be applied to data collected by a citizen scientist. Further, this would allow multiple replications of recordings in a habitat, which was non-feasible in this study due to time constraints.

### **Using bird sounds as a proxy for biodiversity**

The indices have shown some ability to predict species richness of birds throughout the sample area; however, attempting to use this information as a proxy of diversity for all taxa, this method may encounter some problems (Carignan & Villard, 2002; Gregory & Strien, 2010; Peck et al., 2014). Different taxonomic groups have been shown to exhibit different patterns of species distribution due to life-history traits (Mena et al., 2011); whilst reptiles and bats are shown to exhibit higher species richness at lower altitudes, birds display a mid-altitudinal range and small mammal distributions are rarely related to elevational conditions (McCain & Grytnes, 2010; Mena et al., 2011). Further, in the Tropical Andes, endemism in birds is exceptionally high, (Herzog & Kattan, 2011), however the biogeographic 'island' characteristics of the Andes supports a high prevalence of endemism in other taxa such as plants, fungi, lichen, small mammals

and insects, most of which are under sampled and have distributions which are affected by a varied range of mechanisms (Jørgenson et al., 2011; Larsen et al., 2011; Mena et al., 2011). It is therefore difficult to accurately proximate total diversity based on the diversity of a single taxon. Despite this, from a conservation perspective, the use of birds as indicators of habitat disturbance and land use change has been demonstrated as a cost effective and efficient procedure (Peck, 2014; Caro, 2010).

## 5 Conclusions

The study concludes that the acoustic indices, spectral entropy ( $H_s$ ) and total entropy ( $H$ ), can provide an indication of bird species richness within a montane cloud forest of the Ecuadorian Andes, based on their correlation with traditional ecological indices, although the correlation is weak. We would, however, suggest that  $H$  is the only index that could be used as a reasonable proxy for biodiversity rather than both of these indices because  $H_s$  is not necessarily intended for use on its own. The three entropy indices ( $H$ ,  $H_s$ , and  $H_t$ ) and the  $NDSI$  were found to detect changes in bird species composition and could therefore prove useful for analysis of communities and assist in making recommendations for prioritising conservation efforts. In order to confirm these results, it may be useful to control certain factors of the study method, such as the habitat type.

As a recommendation, the use of handheld recorders for soundscape studies should be minimised, as these require *in situ* observational effort, which can affect the quality of recordings and thus the ability to obtain accurate index values. Nevertheless, the use of this recording method could provide an indication concerning the efficiency of acoustic indices applied to recordings made by non-experts in a citizen science program.

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	Richness	Shannon	Gini-Simpson	ESN	Inverse-Simpson
<b>Primary Forest</b>	.4209 ± .213	.5837 ± .206	.7555 ± .208	.3827 ± .222	.3621 ± .227
<b>Secondary Forest</b>	.5543 ± .191	.7164 ± .182	.8641 ± .134	.5271 ± .192	.5055 ± .194
<b>Silvopasture</b>	.5294 ± .187	.7217 ± .219	.8826 ± .208	.5105 ± .184	.4963 ± .179

	Richness	Shannon	Gini-Simpson	ESN	Inverse-Simpson
<b>Band 1</b>	.5329 ± .234	.6965 ± .227	.8456 ± .196	.5073 ± .228	.4828 ± .224
<b>Band 2</b>	.5444 ± .194	.7087 ± .180	.8527 ± .181	.5086 ± .204	.4869 ± .211
<b>Band 3</b>	.3053 ± .200	.4804 ± .228	.6930 ± .206	.2780 ± .193	.2649 ± .185
<b>Band 4</b>	.2868 ± .127	.4936 ± .184	.7132 ± .203	.2697 ± .139	.2634 ± .149

### Appendix 1.1

Mean of each ecological index calculation for habitat type (top) and altitude band (bottom). Index values are normalised between 0 and 1

	<i>H<sub>s</sub></i>	<i>H<sub>t</sub></i>	<i>H</i>	<i>ACI</i>	<i>NDSI</i>	<i>AD</i>	<i>AE</i>	<i>BI</i>
<b>FP</b>	.620 ± .216	.849 ± .156	.589 ± .232	.182 ± .190	.692 ± .270	.737 ± .239	.462 ± .254	0.354 ± .194
<b>FS</b>	.765 ± 0.203	.876 ± .076	.742 ± .178	.192 ± .160	.744 ± .229	.851 ± .161	.345 ± .202	0.311 ± .206
<b>S</b>	.753 ± .212	.901 ± .080	.747 ± .211	.171 ± .067	.711 ± .180	.854 ± .189	.314 ± .219	0.249 ± .249

	<i>H<sub>s</sub></i>	<i>H<sub>t</sub></i>	<i>H</i>	<i>ACI</i>	<i>NDSI</i>	<i>AD</i>	<i>AE</i>	<i>BI</i>
<b>Band 1</b>	.641 ± .266	.841 ± .237	.552 ± .251	.115 ± .112	.635 ± .280	.727 ± .245	.460 ± .281	.421 ± .230
<b>Band 2</b>	.722 ± .198	.867 ± .099	.669 ± .214	.196 ± .188	.711 ± .250	.778 ± .222	.422 ± .238	.307 ± .168
<b>Band 3</b>	.637 ± .174	.870 ± .088	.718 ± .245	.196 ± .129	.805 ± .152	.863 ± .172	.315 ± .191	.310 ± .230
<b>Band 4</b>	.612 ± .299	.921 ± .072	.694 ± .194	.221 ± .133	.595 ± .206	.838 ± .220	.322 ± .282	.231 ± .166

## Appendix 1.2

Mean of each acoustic index calculation for habitat type (top) and altitude band (bottom). Index values are normalised between 0 and 1

Point	Altitude (m)	Richness	Shannon	Simpson	ESN	INV
FP_01	1846	11	2.398	0.909	11.000	11.000
FP_02	1817	13	2.565	0.923	13.000	13.000
FP_03	1832	11	2.342	0.898	10.402	9.800
FP_05	1769	11	2.313	0.893	10.106	9.323
FP_06	1737	18	2.822	0.934	16.803	15.207
FP_07	1531	13	2.488	0.907	12.041	10.714
FP_08	1472	11	2.303	0.889	10.009	9.000
FP_09	1420	6	1.735	0.815	5.670	5.400
FP_11	1752	13	2.523	0.916	12.469	11.842
FP_12	1747	16	2.690	0.925	14.725	13.364
FP_13	1724	9	1.952	0.824	7.044	5.667
FP_14	1693	11	2.172	0.844	8.772	6.429
FP_15	1665	14	2.484	0.900	11.994	10.000
FP_16	1636	5	1.609	0.800	5.000	5.000
FP_17	1630	2	0.693	0.500	2.000	2.000
FP_18	1958	16	2.617	0.917	13.688	12.042
FP_19	1941	13	2.282	0.861	9.792	7.218
FP_21	1865	9	2.146	0.876	8.549	8.067
FP_23	1890	13	2.359	0.885	10.579	8.727
FP_24	1861	13	2.425	0.893	11.308	9.323
FP_25	1849	15	2.623	0.920	13.777	12.500
FP_26	1821	11	2.307	0.891	10.041	9.143
FP_27	1773	9	2.146	0.876	8.549	8.067
FP_28	1760	9	2.133	0.875	8.443	8.000
FP_30	2000	8	1.936	0.833	6.928	6.000
FP_32	2055	6	1.633	0.778	5.117	4.500
FP_33	2076	6	1.581	0.741	4.860	3.857
FP_34	2125	3	1.055	0.640	2.872	2.778

## Appendix 2.1

Altitude values and ecological indices for Primary Forest sites: Richness (Species Richness), Shannon (Shannon entropy), Simpson (Gini-Simpson), Effective Species Number (ESN), Inverse-Simpson (INV).

Point	Altitude (m)	Richness	Shannon	Simpson	ESN	INV
FP_35	1865	7	1.889	0.84	6.614	6.231
FP_36	1805	10	2.243	0.888	9.421	8.909
FP_37	1803	16	2.718	0.93	15.157	14.286
FP_44	1867	6	1.792	0.833	6	6
FP_45	1794	6	1.748	0.816	5.742	5.444
FP_46	1808	14	2.599	0.922	13.454	12.8
FP_47	1825	14	2.448	0.886	11.564	8.805
FP_48	1834	13	2.103	0.795	8.192	4.881
FP_49	1848	7	1.025	0.439	2.788	1.782
FP_50	1846	8	1.049	0.429	2.854	1.75
FP_51	2145	11	2.155	0.85	8.626	6.667
FP_52	2149	5	1.471	0.74	4.353	3.846
FP_53	2214	5	1.594	0.793	4.924	4.84
FP_54	2244	5	1.494	0.75	4.456	4
FP_55	2274	6	1.735	0.815	5.67	5.4
FP_56	2306	2	0.693	0.5	2	2
FP_57	2292	5	1.468	0.744	4.341	3.903
FP_58	2272	7	1.73	0.786	5.64	4.667
FP_59	2309	4	1.277	0.694	3.586	3.267
FP_60	2358	8	1.973	0.84	7.192	6.25
FP_61	2389	11	2.352	0.899	10.503	9.941
FP_63	2426	6	1.733	0.813	5.657	5.333
FP_64	2448	10	2.272	0.893	9.698	9.308
FP_65	2469	7	1.748	0.78	5.743	4.545
FP_66	2491	3	0.95	0.56	2.586	2.273
FP_68	2524	9	2.138	0.875	8.485	8
FP_69	2494	6	1.677	0.79	5.349	4.765
FP_70	2495	6	1.667	0.781	5.299	4.571
FP_71	2508	8	2.02	0.86	7.537	7.118



Point	Altitude (m)	Richness	Shannon	Simpson	ESN	INV
FS_01	1893	14	2.616	0.924	13.676	13.235
FS_02	1880	8	1.907	0.819	6.735	5.538
FS_03	1868	12	2.485	0.917	12.000	12.000
FS_05	1809	3	1.099	0.667	3.000	3.000
FS_06	1733	16	2.631	0.915	13.881	11.756
FS_07	1718	16	2.442	0.878	11.496	8.214
FS_08	1683	14	2.511	0.905	12.311	10.526
FS_09	1658	13	2.513	0.914	12.338	11.636
FS_10	1632	12	2.244	0.862	9.427	7.230
FS_12	1896	8	1.866	0.806	6.464	5.158
FS_13	1938	13	2.476	0.907	11.896	10.800
FS_16	1959	17	2.813	0.938	16.666	16.200
FS_17	2000	11	2.342	0.898	10.402	9.800
FS_18	1887	10	2.272	0.893	9.698	9.308
FS_19	1859	9	2.164	0.880	8.706	8.333
FS_20	1821	11	2.352	0.899	10.503	9.941
FS_21	1770	16	2.690	0.925	14.725	13.364
FS_22	1739	9	2.164	0.880	8.706	8.333
FS_23	1697	9	2.197	0.889	9.000	9.000
FS_24	1654	13	2.425	0.893	11.308	9.323
FS_25.1	1619	19	2.886	0.941	17.924	16.892
FS_25.2	1619	9	2.095	0.861	8.123	7.200
FS_26	2098	3	1.040	0.625	2.828	2.667
FS_27	2123	13	2.415	0.895	11.190	9.524
FS_28	2129	7	1.834	0.820	6.261	5.556
FS_29	2321	12	2.395	0.900	10.965	9.966

Point	Altitude (m)	Richness	Shannon	Simpson	ESN	INV
S_01	1801	14	2.558	0.913	12.907	11.560
S_02	1830	9	2.138	0.875	8.485	8.000
S_03	1883	14	2.580	0.920	13.192	12.448
S_04	1831	13	2.428	0.895	11.339	9.529
S_05	1622	11	2.342	0.898	10.402	9.800
S_06	1598	13	2.513	0.914	12.338	11.636
S_07	1565	13	2.540	0.918	12.680	12.250
S_10	1921	11	2.338	0.898	10.364	9.783
S_11	1940	14	2.437	0.893	11.440	9.308
S_12	1968	11	2.209	0.872	9.105	7.806
S_14	1968	13	2.476	0.907	11.897	10.704
S_15.1	1946	11	2.305	0.888	10.020	8.909
S_15.2	1946	9	2.164	0.880	8.706	8.333
S_16	1947	13	2.513	0.914	12.338	11.636
S_17	1929	7	1.748	0.792	5.744	4.800
S_18	1916	10	2.303	0.900	10.000	10.000
S_19	1929	5	1.561	0.778	4.762	4.500
S_20	1896	11	2.369	0.903	10.691	10.286
S_21	1862	5	1.561	0.778	4.762	4.500
S_22	1824	8	2.043	0.864	7.715	7.364
S_23	1824	9	1.946	0.805	7.000	5.121
S_24	2010	13	2.507	0.913	12.268	11.560
S_25	1975	15	2.686	0.930	14.672	14.222
S_26	1939	13	2.428	0.895	11.339	9.529
S_27	1917	10	2.205	0.876	9.068	8.048

### Appendix 2.1. (Cont.)

Altitude values and ecological indices for Secondary Forest (Left) and Silvopasture (Right) sites: Richness (Species Richness), Shannon (Shannon entropy), Simpson (Gini-Simpson), Effective Species Number (ESN), Inverse-Simpson (INV).

Point	H <sub>s</sub>	H <sub>t</sub>	H	ACI	NDSI	AD	AE	BI
FP_01	0.840	0.970	0.815	15348.463	0.331	1.952	0.451	3.279
FP_02	0.870	0.961	0.836	14737.454	0.928	1.734	0.561	9.305
FP_03	0.835	0.964	0.805	14887.145	0.410	1.738	0.571	5.198
FP_05	0.895	0.988	0.884	14498.853	0.566	2.204	0.229	3.088
FP_06	0.902	0.980	0.884	14550.165	0.799	2.031	0.392	5.351
FP_07	0.862	0.990	0.853	14599.726	0.350	2.291	0.075	3.152
FP_08	0.778	0.992	0.772	14761.459	-0.305	2.272	0.120	2.812
FP_09	0.781	0.991	0.774	14753.212	-0.129	2.115	0.319	2.908
FP_11	0.902	0.874	0.788	14659.920	0.796	2.011	0.421	3.503
FP_12	0.881	0.972	0.857	14548.164	0.777	1.643	0.610	7.808
FP_13	0.861	0.976	0.840	14959.220	0.470	2.162	0.278	2.642
FP_14	0.892	0.985	0.878	14863.694	0.819	2.253	0.134	3.354
FP_15	0.889	0.980	0.871	14696.587	0.626	1.893	0.492	5.085
FP_16	0.860	0.992	0.852	14491.016	0.278	2.302	0.008	4.188
FP_17	0.857	0.989	0.848	14561.794	0.294	2.257	0.136	4.991
FP_18	0.895	0.980	0.877	14819.900	0.874	2.247	0.185	5.095
FP_19	0.846	0.956	0.809	15519.094	0.993	1.977	0.439	6.346
FP_21	0.915	0.983	0.899	14705.094	0.724	2.269	0.144	1.857
FP_23	0.829	0.959	0.795	14662.706	0.634	1.939	0.455	2.281
FP_24	0.908	0.985	0.894	14772.230	0.369	2.284	0.095	2.132
FP_25	0.892	0.974	0.869	14517.289	0.831	1.710	0.575	6.967
FP_26	0.851	0.969	0.824	14656.666	0.624	2.082	0.359	3.654
FP_27	0.888	0.976	0.867	15238.253	0.598	2.181	0.272	3.747
FP_28	0.839	0.988	0.829	15063.964	0.275	2.229	0.195	2.682
FP_30	0.889	0.972	0.864	15636.460	0.852	2.078	0.372	5.321
FP_31	0.904	0.980	0.886	15707.530	0.813	2.291	0.086	2.476
FP_32	0.882	0.965	0.851	15572.410	0.913	2.222	0.212	5.508
FP_33	0.834	0.970	0.809	14925.770	0.346	2.130	0.325	1.802
FP_34	0.906	0.983	0.891	14751.520	0.688	2.049	0.383	3.335

Point	H <sub>s</sub>	H <sub>t</sub>	H	ACI	NDSI	AD	AE	BI
FP_35	0.892	0.979	0.873	14969.020	0.608	2.162	0.275	2.982
FP_36	0.890	0.978	0.870	14991.670	0.773	2.038	0.391	4.822
FP_37	0.897	0.985	0.884	14604.770	0.447	2.191	0.235	4.635
FP_44	0.825	0.991	0.817	14583.091	-0.275	2.199	0.234	4.256
FP_45	0.820	0.991	0.812	14631.657	-0.131	2.289	0.086	3.575
FP_46	0.843	0.977	0.824	14629.544	0.399	1.820	0.531	3.180
FP_47	0.874	0.988	0.864	14583.480	0.476	2.215	0.212	3.608
FP_48	0.885	0.988	0.874	14529.907	0.315	2.296	0.059	4.289
FP_49	0.841	0.986	0.829	14563.488	-0.056	1.632	0.597	4.399
FP_50	0.872	0.988	0.862	14493.836	0.639	2.253	0.169	3.554
FP_51	0.856	0.956	0.818	15424.220	0.989	2.137	0.320	5.301
FP_52	0.861	0.957	0.825	15606.930	0.987	1.826	0.521	3.483
FP_53	0.885	0.975	0.863	14649.610	0.857	1.971	0.449	6.094
FP_54	0.841	0.985	0.828	14861.760	0.099	1.428	0.683	3.231
FP_55	0.862	0.988	0.851	14597.760	0.185	2.285	0.098	3.728
FP_56	0.852	0.984	0.838	14721.730	0.206	2.132	0.305	3.016
FP_57	0.867	0.970	0.840	15257.705	0.979	2.195	0.262	4.554
FP_58	0.884	0.972	0.860	15021.721	0.952	2.288	0.094	2.951
FP_59	0.847	0.934	0.791	16061.600	0.997	1.895	0.491	6.849
FP_60	0.883	0.967	0.854	15234.148	0.980	2.212	0.237	4.115
FP_61	0.859	0.958	0.824	15093.728	0.956	2.027	0.402	2.974
FP_63	0.914	0.980	0.896	14791.407	0.768	2.132	0.329	2.622
FP_64	0.852	0.955	0.814	17035.463	0.995	2.141	0.316	7.015
FP_65	0.835	0.957	0.798	15834.292	0.991	2.103	0.335	5.683
FP_66	0.790	0.955	0.755	15750.249	0.994	1.913	0.476	3.616
FP_68	0.895	0.962	0.861	15122.286	0.926	1.859	0.513	3.344
FP_69	0.890	0.987	0.879	14641.738	0.369	2.291	0.084	1.711
FP_70	0.841	0.960	0.807	14793.892	0.843	2.090	0.340	1.850
FP_71	0.903	0.983	0.888	14584.809	0.785	1.624	0.619	3.928

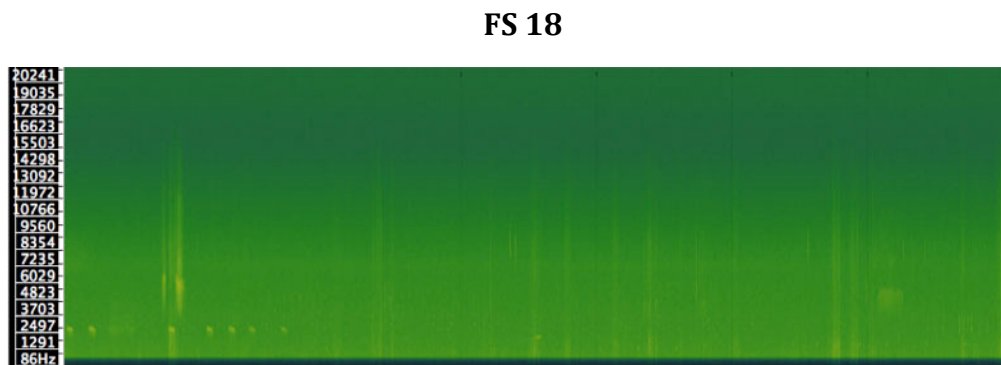
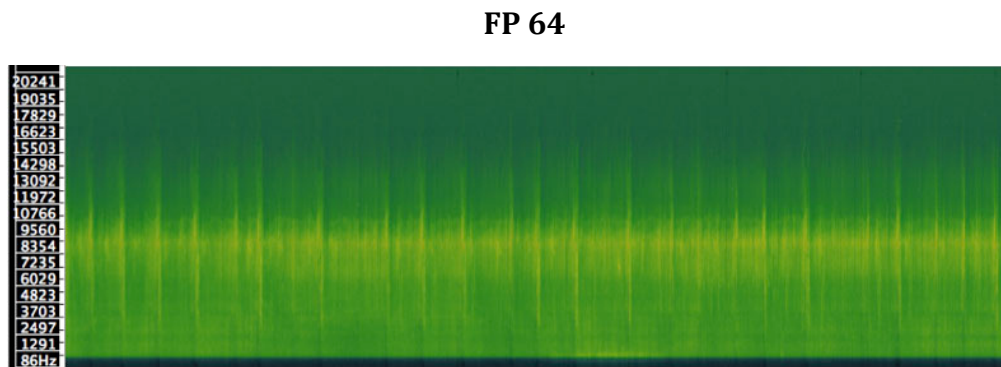
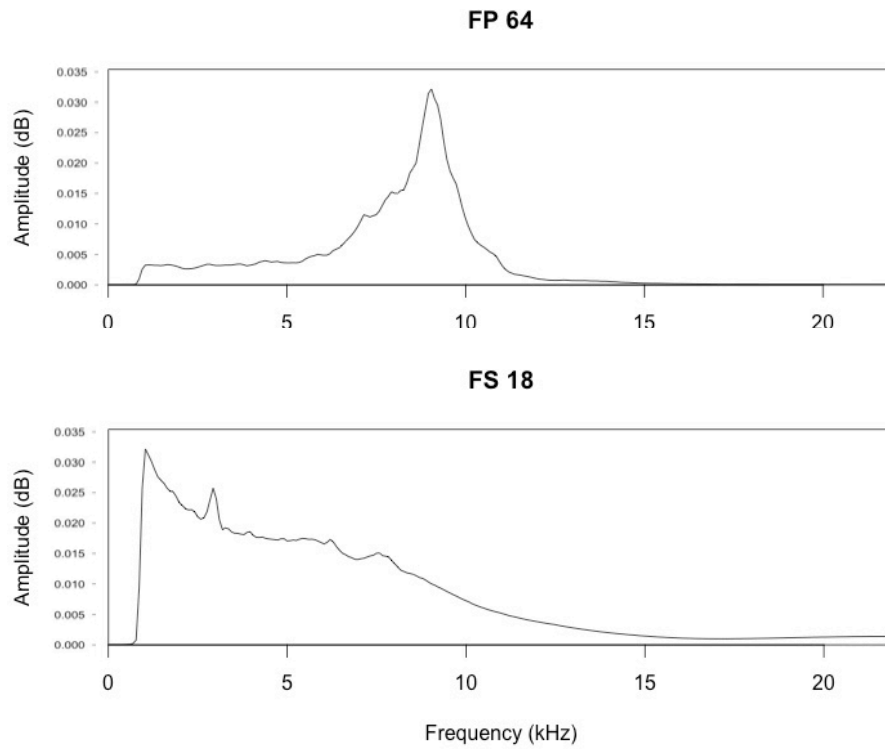
## Appendix 2.2

Acoustic index values for Primary Forest: Spectral Entropy (H<sub>s</sub>), Temporal Entropy (H<sub>t</sub>), Total Entropy (H), Acoustic Complexity Index (ACI), Normalized Soundscape Diversity Index (NDSI), Acoustic Diversity Index (AD), Acoustic Evenness Index (AE), Bioacoustic Index (BI)

Point	H <sub>s</sub>	H <sub>t</sub>	H	ACI	NDSI	AD	AE	BI
FS_01	0.871	0.980	0.854	15405.064	0.171	2.136	0.318	4.082
FS_02	0.863	0.981	0.847	15655.011	0.091	2.269	0.128	4.181
FS_03	0.893	0.983	0.878	15091.994	0.291	2.233	0.197	2.739
FS_05	0.891	0.983	0.876	14776.829	0.811	2.252	0.163	2.459
FS_06	0.894	0.986	0.881	14609.853	0.713	2.164	0.291	2.485
FS_07	0.864	0.990	0.855	14506.006	0.567	2.290	0.082	1.702
FS_08	0.895	0.987	0.884	14633.282	0.469	2.285	0.096	3.497
FS_09	0.891	0.980	0.873	14520.496	0.129	1.977	0.436	2.161
FS_10	0.894	0.980	0.876	14863.190	0.782	2.290	0.074	2.136
FS_12	0.907	0.984	0.893	14595.280	0.666	2.290	0.079	2.258
FS_13	0.907	0.984	0.893	14648.293	0.710	2.131	0.320	2.413
FS_16	0.890	0.972	0.865	15239.451	0.860	2.258	0.166	5.494
FS_17	0.907	0.982	0.890	14695.770	0.774	2.274	0.134	3.323
FS_18	0.920	0.984	0.905	14721.769	0.836	2.262	0.160	1.411
FS_19	0.897	0.977	0.877	14486.656	0.634	1.775	0.552	5.538
FS_20	0.900	0.976	0.878	14809.677	0.889	2.177	0.274	4.608
FS_21	0.876	0.957	0.838	15629.492	0.986	2.053	0.386	5.177
FS_22	0.912	0.974	0.889	14838.252	0.442	2.207	0.237	3.332
FS_23	0.913	0.980	0.894	14769.139	0.095	1.849	0.490	3.139
FS_24	0.861	0.985	0.848	14703.876	0.602	2.078	0.367	4.959
FS_25.1	0.873	0.961	0.840	15268.499	0.978	2.199	0.252	2.687
FS_25.2	0.908	0.972	0.882	14894.682	0.929	2.278	0.125	4.593
FS_26	0.863	0.973	0.840	15471.944	0.914	2.278	0.125	2.908
FS_27	0.899	0.963	0.866	15367.894	0.940	2.260	0.154	4.485
FS_28	0.846	0.965	0.816	15267.467	0.989	2.220	0.226	5.464
FS_29	0.819	0.962	0.788	15933.918	0.992	1.985	0.432	9.149

Point	H <sub>s</sub>	H <sub>t</sub>	H	ACI	NDSI	AD	AE	BI
S_01	0.908	0.985	0.894	15001.891	0.659	2.261	0.162	2.847
S_02	0.901	0.986	0.889	14662.396	0.524	2.257	0.149	3.660
S_03	0.905	0.984	0.890	14604.199	0.509	2.261	0.144	3.200
S_04	0.907	0.988	0.896	14623.173	0.613	2.289	0.081	1.762
S_05	0.879	0.979	0.860	14959.248	0.894	2.081	0.327	6.871
S_06	0.879	0.982	0.863	14687.009	0.714	2.130	0.306	5.276
S_07	0.863	0.990	0.854	14691.152	0.395	2.223	0.202	2.054
S_10	0.900	0.972	0.875	14839.559	0.935	2.290	0.089	4.112
S_11	0.863	0.964	0.832	15267.566	0.985	2.027	0.407	4.686
S_12	0.911	0.979	0.891	15177.272	0.802	2.293	0.078	2.145
S_14	0.804	0.949	0.763	14823.009	0.449	1.648	0.559	1.919
S_15.1	0.916	0.978	0.896	14971.774	0.854	2.198	0.250	2.703
S_15.2	0.908	0.985	0.894	14777.086	0.571	2.275	0.118	3.543
S_16	0.902	0.974	0.878	14847.803	0.867	2.167	0.270	4.022
S_17	0.908	0.981	0.891	14966.673	0.796	2.178	0.270	2.500
S_18	0.885	0.978	0.865	14956.599	0.746	2.226	0.201	3.098
S_19	0.890	0.984	0.875	14821.677	0.465	2.285	0.093	1.175
S_20	0.872	0.982	0.857	15054.588	0.016	1.756	0.561	3.371
S_21	0.831	0.975	0.810	15024.846	0.190	2.098	0.355	2.646
S_22	0.861	0.991	0.853	14942.756	0.409	2.287	0.083	1.726
S_23	0.868	0.988	0.858	15276.013	0.705	2.281	0.092	4.603
S_24	0.901	0.987	0.889	14749.180	0.625	2.293	0.069	1.420
S_25	0.902	0.986	0.889	14783.165	0.458	2.271	0.124	2.448
S_26	0.861	0.965	0.831	15769.770	0.637	2.024	0.411	5.337
S_27	0.901	0.986	0.889	14792.542	0.748	2.278	0.107	2.864

**APPENDIX 2.2. (Cont.)** Acoustic Index values for Secondary Forest (Left) and Silvopasture (Right): Spectral Entropy (H<sub>s</sub>), Temporal Entropy (H<sub>t</sub>), Total Entropy (H), Acoustic Complexity Index (ACI), Acoustic Diversity Index (ADI), Normalized Soundness Diversity Index (NDSI), Acoustic Diversity Index (ADI), Acoustic Evenness Index (AE), Bioacoustic Index (BI).



Site	BI Value	Richness	Shannon	Simpson	ESN	INV
FP 64	7.0146	10	2.2719	0.982	9.698	1.019
FS 18	1.4106	10	2.2719	0.982	9.698	1.019

## Appendix 3

(top) Mean frequency spectrums for two sites of identical ecological value according to traditional indices. (centre) Waveform spectrograms for eight minutes recording time of each site. (bottom) Index values for each site.