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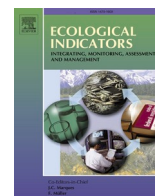
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# The relationship between acoustic indices, elevation, and vegetation, in a forest plot network of southern China

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## ABSTRACT

An emerging method of monitoring biodiversity is through the use of audio recordings, often made by autonomous recording units. Acoustic indices have been developed to estimate animal diversity, especially across human disturbance gradients, and have been shown to often correlate with manual counts of animals. Less work has examined whether acoustic indices can detect finer-scale habitat gradients, such as differences in vegetation within mature forests, especially using long-term vegetation plots. We used autonomous recorders to capture sound predominantly produced by birds in the morning and insects at night across a network of 27 1-ha forest vegetation plots, located between 300 and 1850 m asl in southern China, collecting 38,200 min of sound recordings. Based on the animal diversity literature, we hypothesized that acoustic indices would have strongest relationships with elevation, intermediary relationships with vertical structure (vertical heterogeneity, canopy height and tree density), and the weakest relationships with tree species diversity. Generalized linear mixed models, followed by model averaging, showed that elevation was indeed the strongest of the predictor variables, with the highest mean importance factor. In 6 of 14 models the coefficients had confidence intervals that did not cross zero, and in all such significant relationships acoustic diversity decreased with elevation. Vertical heterogeneity had the second highest mean importance factor, but one of its two significant relationships was negative. The only other significant relationship was a positive one between tree species diversity and the H index. Morning and evening recordings had similar results, despite representing biophony made by different taxa with different acoustic characteristics. However, the seven acoustic indices gave dissimilar results, with the H index having three significant relationships, compared to the ACI, BIO and AR indices that had none. We conclude that autonomous recorders, if analyzed with multiple acoustic indices, can be used to investigate landscape or vegetation-related gradients that may influence animal diversity on long-term vegetation plots.

## 1. Introduction

The current biodiversity crisis may be becoming the world's sixth mass extinction event, due to habitat loss, coupled with defaunation even in those forests that are still standing (Ceballos et al., 2017; Dirzo et al., 2014). Faced with these changes, many methods of remote sensing and large-scale data collection have been advocated to monitor biodiversity and its decline (e.g., Bush et al., 2017). One method in particular that is increasingly applied is the use of acoustic data ("ecoacoustics", Burivalova et al., 2019; Pijanowski et al., 2011; Sueur et al., 2014). Specifically, autonomous recorders can be placed across landscapes for extended periods to collect a massive amount of data on animal communities (Shonfield and Bayne, 2017). The large-scale quality of the data can capture rare species; being remote, the method also captures

animals that could be sensitive to human disturbance (Blumstein et al., 2011; Campos-Cerqueira and Aide, 2016; Celis-Murillo et al., 2009; Obrist et al., 2010; Pérez-Granados et al., 2018). Depending on how the analysis is automated, the method could also be less prone to observer biases than traditional, manual animal counting (Blumstein et al., 2011; Fitzpatrick et al., 2009; Hutto and Stutzman, 2009; Jorge et al., 2018; Shonfield and Bayne, 2017). As costs of equipment decrease, and computing processes become more powerful (Bermant et al., 2019; Metcalf et al., 2020b; Ovaskainen et al., 2018; Stowell et al., 2019; Xie et al., 2015; Zilli et al., 2014), ecoacoustics also promises to be economically more viable than using experts in the field (Darras et al., 2019).

In the future, automated detection of certain species may become commonplace, but currently it remains computationally difficult (see

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OVaskainen et al., 2018; Priyadarshani et al., 2018; Stowell et al., 2019), and therefore most studies of ecoacoustics have used methods that do not require species identification. In particular, researchers have developed various acoustic indices as estimators of biodiversity, based on the fundamental assumption that more diverse communities will produce more diverse soundscapes (Boelman et al., 2007; Bormpoudakis et al., 2013; Depraetere et al., 2012; Kasten et al., 2012; Mitrović et al., 2010; Pieretti et al., 2011; Pijanowski et al., 2011; Sueur et al., 2008; Villanueva-Rivera et al., 2011). The use of these acoustic indices has been tested in various conditions, with some studies finding them to be consistent and sensitive if applied to large datasets of recordings (e.g., Bradfer-Lawrence et al., 2020; Dröge et al., 2021). Yet some researchers have questioned their efficacy in some conditions, like those with human-produced noise (Fairbrass et al., 2017), or in the tropics (Eldridge et al., 2018), or when some taxa like insects dominate over other taxa (Aide et al., 2017; Metcalf et al., 2020a). Other researchers have found some acoustic indices perform better than others under particular conditions (Fuller et al., 2015; Gasc et al., 2015; Mammides et al., 2017; Ross et al., 2020). Also, most studies that have used acoustic indices compare a wide range of habitats from agriculture to mature forests (Bradfer-Lawrence et al., 2020; Do Nascimento et al., 2020; Dröge et al., 2021; Eldridge et al., 2018). Whether acoustic indices can be used to look at finer-scale landscape or vegetation-related gradients, such as differences in vegetation within forests of one disturbance level, is less understood (but see Farina and Pieretti, 2014; Monacchi and Farina, 2019; Pekin et al., 2012). For example, in a literature review of 44 studies that assessed multiple acoustic indices since 2011, only 14 include vegetation data (Table A1), and only three studies (Moreno-Gómez et al., 2019; Hao et al., 2021; Opaev et al., 2021) were conducted exclusively in protected and mature forests.

One opportunity for ecoacoustics is to use them on networks of vegetation plots, as these networks represent one of science's largest investments in biodiversity research (e.g. large plots of forestgeo.si.edu; 1-ha plots of rainfor.org, afritrion.org, or tforces.net; Condit, 1995; Malhi et al., 2002). Autonomous technology may be especially suitable technology for vegetation plots because they could help prevent damage from the trampling of observers (Pescott and Stewart, 2014). Vegetation plots span different kinds of landscape or vegetation-related gradients that have strong, weak or intermediate effects on animal communities. For example, some vegetation plots have been constructed over elevational gradients, and elevation can have strong effects on biodiversity, with either linear declines when elevation increases (Lomolino, 2001; Malsch, 2008; Rahbek, 1995; Sergio and Pedrini, 2007), or diversity maximums at mid-elevations (Aliabadian et al., 2008; Colwell and Lees, 2000; McCain, 2005). That vegetation structure itself (e.g. vertical heterogeneity) is also a strong influence on animal diversity is a classical hypothesis in ecology (MacArthur and MacArthur, 1961) with much evidence accumulating over the years (August, 1983; Heidrich et al., 2020; Stein et al., 2014; Tews et al., 2004; Willson, 1974). In contrast, floristic diversity has in general less effect than vegetation structure on animal communities, although there are some cases in which it can influence animal biodiversity (Fleishman et al., 2003; Mac Nally, 1990; Rodewald and Abrams, 2002; Rotenberry, 1985). Given that vegetation plot networks encompass a range of gradients in both the type of gradients (landscape gradient, such as elevation, or vegetation-related gradient) and their strength, we suggest that these networks can be used as testing grounds to understand which kinds of gradients can be detected, and monitored, by acoustic indices. In particular, we were interested to see if tree species richness could influence the acoustic indices, as this information is one of the key kinds of data produced by vegetation plots.

In this study, we deployed autonomous recorders in a network of 27 1-ha vegetation plots in relatively undisturbed forests of Guangxi Zhuang Autonomous Region, that varied over a large (~300 to 1850 m) elevational gradient. Acoustic data was collected in relatively short intervals (10 min periods) and at peaks of the activity period of different

taxa, to avoid signal masking of one taxa by another (Metcalf et al., 2020a). We collected data on landscape and vegetation-related variables, not on animal diversity, but our hypotheses about which variables would be most important rely on the literature linking these variables to animal diversity. We expected that the strongest relationships would be between the acoustic indices and elevation for this regional forest plot network, due to the strong variation in elevation among plots. We expected relationships between the acoustic indices and vertical structure to be of intermediary strength, and relationships with floristic diversity to be weakest, given these general trends in the literature about animal diversity, as discussed above. We also expected that there would be some differences between taxa, with biophony produced by insects more influenced by tree species richness, since insects are often host specific (García-Robledo et al., 2016; Mayhew, 1997; Novotny and Basset, 2005). Finally, we hypothesized that there would be differences between the indices in the strength of their relationships with the explanatory variables, as has been suggested in previous research (Mammides et al., 2017; Moreno-Gómez et al., 2019; Sousa-Lima et al., 2018). In particular, we expected H, ADI and AEI to show the strongest relationships with predictor variables, as these indices correlated most strongly with animal diversity in an earlier study (Mammides et al., 2017), which was also spread across a tropical/subtropical gradient in China.

## 2. Materials and methods

### 2.1. Study site

The study was carried out in seven National Nature Reserves in Guangxi Zhuang Autonomous Region (Fig. 1). The reserves sampled, from south to north, included: Shiwandashan National Nature Reserve (21° 51'N, 107° 59'E; SWSNNR), Damingshan National Nature Reserve (24° 2'N, 110° 9'E; DMSNNR), Dayaoshan National Nature Reserve (23° 37'N, 108° 50'E; DYSNNR), Cenwangaoshan National Nature Reserve (24° 27'N, 106° 22'E; CWLSNNR), Jiuwandashan National Nature Reserve (25° 7'N, 108° 42' E; JWSNNR), Mulun National Nature Reserve (25° 8'N, 107° 59'E; MLNNR), and Huaping National Nature Reserve (25° 36'N, 109° 54'E; HPNNR).

This study was part of a larger project to study the vegetation of these nature reserves. Three to five 1-ha vegetation plots per reserve were created between 2015 and 2017 and are maintained by the College of Forestry, Guangxi University (CoFGXU), with the permission and support of the Guangxi Forest Department. These plots were selected to be in mature forest with little human disturbance, with a large range of elevation both within and between reserves (Table 1).

### 2.2. Vegetation data

CoFGXU made a full inventory of all individuals (>1 cm dbh) of tree species in the vegetation plots, taking information for each tree on its species identity, and its height. Based on these data, we calculated four variables to reflect forest structure and floristics of each plot: (a) canopy height (mean height of tallest 5% of trees), (b) tree density (total number of tree individuals per plot), and metrics of (c) vertical heterogeneity and (d) tree species diversity. The latter two variables were calculated by applying the Shannon-Wiener index to (c) the data on the trees' heights (with trees binned into 20 groups between 0 and the maximum canopy height), and to (d) the data of the different tree species' abundances. Three plots had no data for canopy height. Hence, the final sample number for plots was 27 (see Table 1).

The plot network includes ~ 300 to 1850 m gradient in elevation (see Table 1). They also vary in their canopy height (ranging between 5.0 and 18.3 m height), their vertical heterogeneity (between 1.23 and 2.62 SW values), the number of individual trees present (between 518 and 1665 individuals per ha), and the number of tree species represented (between 73 and 183 species per ha; see Table A2 for means and standard

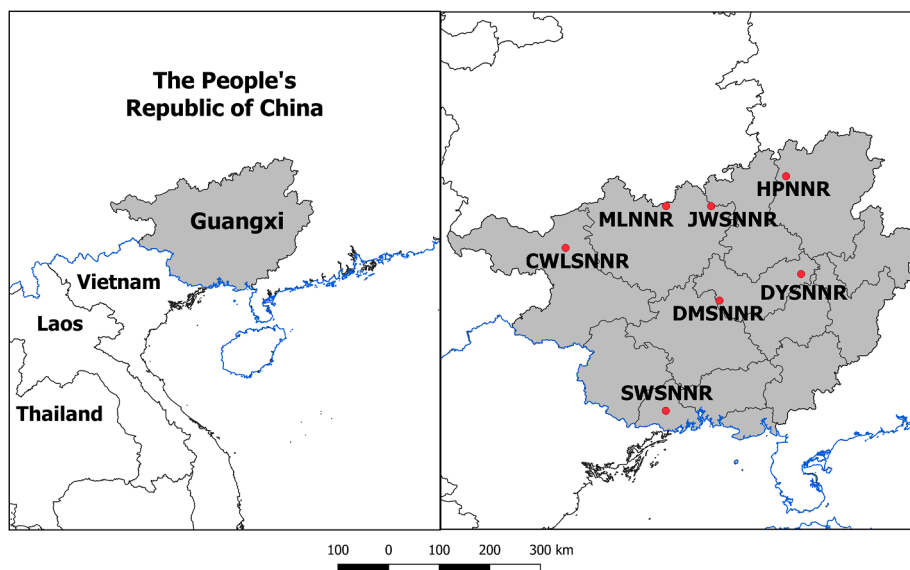


Fig. 1. Location of the seven National Nature Reserves in Guangxi Zhuang Autonomous Region, southwest China.

**Table 1**

Descriptions of the seven National Natural Reserves that were sampled in Guangxi, China, and the dates and extent of the sampling. The reserves are ordered by their latitudes, from north to south.

Reserve name	Plots*	Recording years	Recording dates	Average recording days per plot	Mean elevation (m)	Total recordings
Huaping (HPNNR)	4	2019	05/17–07/07	51	808.8–999	408
Mulun (MLNNR)	5	2017	04/20–06/17	49	368–653	496
Jiuwandashan (JWSNNR)	4	2018	05/09–08/21	94	632.25–1294.75	752
Cenwangaoshan (CWLSNNR)	5	2017	04/08–06/01	54	1365.65–1842.84	544
Dayaoshan (DYSNNR)	1 (of 4)	2017	05/14–07/14	49	1240.33	396
Damingshan (DMSNNR)	3	2016	04/21–07/03	74	535.5–1284	444
Shiwandashan (SWSNNR)	5	2018	05/16–08/08	78	316.75–606.5	780
Total	4 27 (of 30) plots sampled	2019	04/19–08/08	103		829 3820 for main analysis (plus 829 for seasonal and annual consistency analysis)

\*The canopy height and vertical heterogeneity data were missing for three out of four plots in Dayaoshan National Nature Reserve, and hence these plots were not used in the analysis.

deviations of these predictor variables).

### 2.3. Soundscape survey

We conducted a long-term monitoring study to collect the sounds of forest songbirds and insects in the plot network during breeding seasons from mid-April to mid-August, in the years of 2016 through 2019. We used nine autonomous acoustic recorders, Song Meter model SM3, produced by Wildlife Acoustics (Maynard, MA, USA), and equipped with omni-directional microphones.

The Song Meter autonomous recorders were deployed at approximately the center of the plots, and attached to tree trunks with rope at approximately 1.5 m height. They were programmed to record sounds three times per day (starting at 30 min past sunrise, 9 h after sunrise, and 1 h after sunset), each time for ten minutes, selecting these times to capture peak activities levels of birds (daytime) and insects (nighttime). Ten minutes is a common duration for a point count, and thus these results can be usefully compared to traditional surveys (Shonfield and Bayne 2017), and this duration of recordings has been used by previous studies that used autonomous units (Pekin et al., 2012; Ross et al., 2020). Like many regions of the world, bird song in Guangxi in the breeding season tends to peak in the morning, with a second, lesser peak

in the late afternoon (Li et al., 2020; Liu et al., 2019), guiding the timing of the recordings.

The Song Meter autonomous recorders recorded at least 30 consecutive days worth of data at each study site. All recordings were saved in .wav format at a sample rate of 24000 Hz (16 bits). Generally, each plot was only sampled during one year. However, to understand how recordings were influenced by annual variation, and by differences between early (towards April) and late (towards July) seasons, we sampled SWSNNR a second time in 2019, and for a long period (four months). For details of the sampling, see Table 1.

### 2.4. Manual identification of Geophony, anthrophony and biophony

To identify common background noises and animal sounds on the recordings, we manually listened to six recordings from each of the plots during each of the time periods (27 plots times  $\times$  three times of the day  $\times$  six replicates = 486 recordings). We then scored the first minute of the recording for the presence/absence of geophony, anthrophony and biophony. For geophony, we identified rain, dripping leaves, other types of running water (streams, etc.), thunder, and heavy wind (including tree branches hitting together). For anthrophony, we identified cars, planes, motorbikes, human voices, and the sounds of livestock. Among

animal sounds we listened for birds, tree frogs, cicadas, crickets and katydids.

In this network of mature, undisturbed forest plots, geophony related to weather and water were common (339 detections during the manual listening of first minute of 486 recordings), and anthrophony was relatively rare (60 detections, Table 2). As to biophony, morning recordings were dominated by birds, evening recordings by insects, and the afternoon recordings tended to be a mix of both groups (see Table 2).

2.5. Preparation of recording dataset

Starting with a total dataset of 3820 recordings, we first removed any recordings that did not last 10 min due to technical problems (a total of 5 recordings). As the second step of data cleaning, we used an automated procedure to identify and remove recordings that were affected by rain, given that this was the most identified geophony. Using the dataset of the manually-scored recordings, we identified recordings with and without rain, and then subjected them to the package “hardrain” (Metcalf et al., 2020b) in the R statistical environment (R Core Team, 2020). We calibrated the hardrain algorithm so that misidentifications were <10%. Running hardrain with these settings removed 568 recordings from the dataset. Although heavy wind was not common (see Results), some level of low frequency wind noise was found in most recordings. As wind sound varied in its intensity and frequency, we could find no obvious cut-off to filter it, and therefore decided not to filter. A preliminary analysis that filtered at 500 Hz (similar to Bradfer-Lawrence et al., 2020; Eldridge et al., 2016), gave qualitatively similar results.

Recent research has suggested that sampling be targeted to specific taxa and short-time intervals to avoid “masking” of environmental-acoustic relationships that may differ between taxa or at different times (Metcalf et al., 2020a). Given the results of the manual identification of biophony, we only analyzed the morning and evening recordings to best distinguish bird and insect sounds.

2.6. Acoustic index calculation

We calculated seven acoustics indices for each 10-min recording. The indices included: Acoustic Complexity Index (ACI, Pieretti et al., 2011), Acoustic Diversity Index (ADI) and Acoustic Evenness Index (Villanueva-Rivera et al., 2011), Acoustic Entropy Index (Sueur et al., 2008), Bioacoustic Index (Boelman et al., 2007), and Normalized Difference Soundscape Index (Kasten et al., 2012). These six indices were calculated using the multiple\_sounds function in the ‘soundecology’ package. A seventh index, the Acoustic Richness Index (Depraetere et al., 2012) was calculated using the ‘AR’ function in the ‘seewave’ package. We used the default settings of both packages. These indices have been commonly tested in other studies (see Table A1), and a brief description of these indices’ calculation is summarized in Table A3.

The Song Meter autonomous recorders produce two channel recordings representing the input into the two microphones on opposite sides of the machine. It is inappropriate to use both recordings made at the same time in statistical tests that require independence as an animal close to the recorder will be recorded in both channels. However, rather than throwing out recordings from one channel, we averaged the values of the acoustic indices from the two channels (Turner et al., 2018). This captures the most information, because sometimes a distant animal on one side of the plot may be captured by one of the microphones but not the other.

2.7. Statistical analyses of the acoustic indices

All analyses were conducted in the R Statistical environment, using R version 4.0.3. To prepare for analyses that looked at the relationships between the acoustic indices and the explanatory variables (environmental [elevation], structural [vertical heterogeneity, canopy height, tree density], floristic [tree species richness]), we tested for collinearity

**Table 2** Sources of biophony, geophony, and anthrophony in a sample of 486 recordings. For each plot (n = 27) and time period, we randomly selected six recordings, and manually listened to the first minute of the recording. This minute was scored as to the presence/absence of the sound type, with the categories not being mutually exclusive (i.e. the minute could have many sounds at once). UnID Animal = the sound of an animal that could not be assigned with certainty to one of the other five categories.

Time	Animal Noises (Biophony)					Environmental Noises (Geophony)					Human Noises (Anthrophony)					
	Bird	Frog	Cicada	Cricket	Katydid	UnID Animal	Rain	Dripping Leaves	Thunder	Wind	RunningWater	Cars	Planes	Motor-bike	Human Voice	Domestic Animal
Morning	119	5	29	8	3	35	66	37	3	11	2	3	2		1	
Afternoon	85		88	3		14	60	21	8	8	2	13	10	3	8	5
Evening	2	20		93	13	36	67	37	4	8	5	7	7		1	

among all the potential explanatory variables with the “performance” package (Lüdecke et al., 2021), and found no VIF (variance inflation factor) values above 2. All acoustic indices and explanatory variables were scaled and centered to avoid convergence problems with mixed models.

To then investigate the relationship between the soundscape and these explanatory variables, we fitted generalized linear mixed models (GLMMs) for each acoustic index. The response variables were the acoustic indices values, with all the recordings in all the plots included in the dataset. Random factors included plot nested in nature reserve, to control for the clustered placement of the plots throughout Guangxi. Another random factor was the month of the recording (preliminary analyses in which the day of the recording, or the month, was used as a fixed factor did not converge). The full models were:

Acoustic indices (14 separate models, representing each of 7 acoustic indices calculated for morning and evening recordings)  $\sim$  Mean-Elevation + CanopyHeight + TreeDensity + VerticalHeterogeneity + Floristics + (1|Reserve/Plot) + (1|Month)

We did not include interactions because we could not identify any interaction in which we would hypothesize one variable would likely influence the effect of another variable on the acoustic indices.

Models were run using the “*glmmTMB*” package (Magnusson et al., 2020), and the *beta* distribution. We then used the package “*MuMIn*” (Bartoń, 2013) to determine all models with delta corrected Akaike Information Criterion ( $\Delta AIC_c$ )  $< 4$  from the best model, finding the model-averaged standardized coefficients using the ‘full’ method of calculation (Nakagawa and Freckleton, 2011). We consider relationships to be significant if their 95% confidence intervals around the coefficient value did not cross zero. To compare the relative effects of the different predictors, or the relative degree to which variables explained the response variables (the acoustic indices), we report the importance factor (IF) of each variable in each model as calculated by *MuMIn*. IF is a measure of how consistently a variable is included in models with  $\Delta AIC_c < 4$ , although it does not necessarily reflect the variable’s effect size (Galipaud et al., 2014). To provide some summary of IF across models, we simply averaged the IFs for variables/indices, provided they were included in the model averaging ( $\Delta AIC_c < 4$ ).

One problem with these models was that they were slightly affected by spatial autocorrelation. Moran’s *I* values, which vary from 1 to  $-1$ , with 0 indicating no spatial correlation, were small (absolute values  $< 0.01$ ), but significant for 4/14 models (Table A4). A second analysis, using one datapoint per plot, a mean of all the acoustic index values for all recordings, had one advantage: in this analysis only 1/14 models showed significant autocorrelation. This analysis shows very similar results, but has disadvantages (much larger absolute values of Moran’s *I*; less significance for some relationships like those between elevation and the acoustic indices) and is shown in the Supplemental (Table A5).

A final analysis was to understand the annual and seasonal variation of the values obtained by the acoustic indices. To understand how differences between plots in the year and the season they were sampled might have affected results, we investigated variation in the values of the acoustic indices obtained from four Shiwandashan plots, which we sampled in two years (2018, 2019). We also sampled Shiwandashan for four months in 2019, allowing us to divide the 2019 database in half, into early recordings and late ones (the dividing line was June 17). For each of these four plots we conducted Welch’s *t*-tests on ranked data (to deal with unequal variances and non-normality), comparing the value of the acoustic indices in one year or one season to the other year/season. We consider this a measure of within-plot differences due to annual or seasonal variation. We then measured across-plot variation, using similar *t*-tests between each of the four plots and the 26 others used in the main analysis (104 total comparisons). We expected that within-plot differences would be smaller than across-plot differences, which would mean that our results were not strongly affected by year and/or season.

### 3. Results.

Elevation was the most important of the variables influencing the acoustic indices, averaging an importance factor of  $0.66 \pm 0.34$  across the 14 analyses (Table 3). In both the morning and the evening, as elevation increased, ADI and H decreased and AEI increased significantly (the AEI result is consistent with the results from the other indices, since AEI is calculated with the Gini coefficient). For all models, 13/14 had a negative relationship between elevation and acoustic diversity, with the one exception being ACI in the evening. The elevation result for the analysis with one datapoint per plot was similar, but AR showed significant results, and result for ADI was only significant in the morning (Table A5).

There were only a few vegetation variables that had significant relationships with the acoustic indices. Vertical heterogeneity was the second most important explanatory variable in both morning and evening ( $0.41 \pm 0.24$  importance factor averaged across the 14 analyses). However, vertical heterogeneity’s two significant results were in opposite directions: while vertical heterogeneity was positively related with NDSI in the evening, it was negatively related with ADI in the morning (although the confidence interval for this relationship came close to zero, and the effect was not seen in the analyses with one data point per plot, see Table A4). The only other significant relationship between a characteristic of the vegetation and an acoustic index was the relationship in the morning between tree species diversity and H.

Comparing among the indices, H had the highest number of significant relationships (3) and the highest average importance factor both in morning and evening ( $0.51 \pm 0.35$  across 14 analyses). Indices with intermediate importance factors ( $0.40$ – $0.43$ ) included ADI, AEI and NDSI. Indices with the lowest average importance factors were BIO ( $0.30 \pm 0.19$ ), ACI ( $0.24 \pm 0.24$ ) and AR ( $0.21 \pm 0.13$ ), and these indices were not significantly related to any of the predictor variables we tested.

In the analysis of annual and seasonal variation of the four plots in Shiwandashan NNR, we found across-plot differences to be larger than within-plot differences for 6/7 acoustic indices, with the exception being AR (Table A6).

### 4. Discussion

Acoustic indices have been successfully used to distinguish between habitats that have been disturbed at different levels by human beings (Benocci et al., 2020; Bradfer-Lawrence et al., 2020; Do Nascimento et al., 2020). In this study, we wanted to explore their utility in studying protected and mature forests on long-term vegetation plots, to see what kind of landscape or vegetation-related gradients might be found to be related to the acoustic indices. We found that three acoustic indices that are similar in how they are calculated (H, ADI and AEI) showed significant and consistent negative relationships with elevation, which varied strongly across the forest plot network. In contrast, we were unable to detect many relationships between the acoustic indices and characteristics of the vegetation. However, we do not know whether this is because vegetation did not alter biophony, or whether it did, but the acoustic indices failed to capture such effects. Here we compare the landscape/vegetation-related variables in their influence on the acoustic indices, before reversing the analysis and comparing model fit among the acoustic indices themselves.

#### 4.1. Explanatory variables

As we did not measure animal diversity on these plots at the species level, we cannot evaluate the accuracy of the acoustic indices. However, we will argue that relationships between the acoustic indices and the landscape and vegetation-related variables likely reflect the consequences of these variables acting on animal diversity. Therefore, here we will compare our results to what has been found previously about how these variables influence animal diversity.

**Table 3**

The results of GLMM and model averaging describing the relationship between the seven acoustic indices and the five explanatory variables using the full dataset of all recordings. We show results both from morning and evening; only variables that were included in at least one model with  $\Delta AICc < 4$  are shown in the table. The values represent standardized coefficients (Coef) and standard errors (SE), calculated by the full averaging method, as well as importance factors (IF). Bolded and shaded variables represent those for which the 95% confidence intervals (CI) did not cross zero.

Index	Environmental Variable			Vegetation Structural Variables						Floristic Variable			Mean IF for Index			
	Elevation			Canopy Height			Tree Density			Vertical Heterogeneity				Tree Species diversity		
	Coef	CI 2.5%	IF	Coef	CI 2.5%	IF	Coef	CI 2.5%	IF	Coef	CI 2.5%	IF		Coef	CI 2.5%	IF
	SE	CI 97.5%		SE	CI 97.5%		SE	CI 97.5%		SE	CI 97.5%			SE	CI 97.5%	
<b>MORNING</b>																
ACI	-0.03	-1.23	0.13	-0.75	-1.88	0.83	0.003	-0.96	0.12	0.03	-0.67	0.14	0.01	-0.81	0.12	<i>0.27 ± 0.31</i>
	0.20	0.76		0.57	0.08		0.18	1.02		0.19	1.15		0.16	0.98		
ADI	<b>-1.88</b>	<b>-2.80</b>	<b>1.00</b>	0.11	-0.34	0.28	-0.04	-1.23	0.13	<b>-0.80</b>	<b>-1.86</b>	<b>0.85</b>	0.09	-0.33	0.28	<i>0.51 ± 0.39</i>
	<b>0.47</b>	<b>-0.95</b>		0.27	1.14		0.20	0.59		<b>0.55</b>	<b>-0.02</b>		0.24	1.01		
AEI	<b>1.70</b>	<b>0.76</b>	<b>1.00</b>	-0.17	-1.25	0.37	0.02	-0.70	0.09	0.55	-0.10	0.70	-0.09	-1.12	0.23	<i>0.48 ± 0.37</i>
	<b>0.48</b>	<b>2.64</b>		0.33	0.33		0.16	1.19		0.52	1.66		0.24	0.37		
AR	-0.03	-0.57	0.16	0.02	-0.26	0.08	-0.07	-0.64	0.28	0.13	-0.11	0.45	0.01	-0.29	0.14	<i>0.22 ± 0.15</i>
	0.10	0.24		0.08	0.47		0.16	0.13		0.20	0.71		0.06	0.49		
BIO	-0.23	-1.92	0.35	-0.03	-1.30	0.13	-0.42	-2.02	0.49	0.24	-0.57	0.34				<i>0.33 ± 0.15</i>
	0.49	0.58		0.21	0.80		0.59	0.32		0.50	1.94					
H	<b>-1.94</b>	<b>-2.94</b>	<b>0.96</b>	-0.05	-1.25	0.24	-0.10	-1.40	0.28	-0.17	-1.37	0.35	<b>1.20</b>	<b>0.32</b>	<b>1.00</b>	<i>0.57 ± 0.38</i>
	<b>0.51</b>	<b>-0.94</b>		0.28	0.86		0.32	0.67		0.35	0.41		<b>0.53</b>	<b>2.18</b>		
NDSI	-1.15	-2.64	0.85				-0.24	-1.95	0.31	0.87	-0.26	0.73	-0.01	-0.79	0.11	<i>0.50 ± 0.35</i>
	0.77	-0.07					0.49	0.41		0.82	2.64		0.12	0.62		
<i>Mean IF for Variable</i>			<i>0.64 ± 0.40</i>			<i>0.32 ± 0.27</i>			<i>0.24 ± 0.14</i>			<i>0.51 ± 0.26</i>			<i>0.31 ± 0.34</i>	
<b>EVENING</b>																
ACI	0.10	-0.28	0.27	0.15	-0.57	0.15	0.02	-0.56	0.18							<i>0.20 ± 0.06</i>
	0.24	1.04		0.02	0.82		0.15	0.78								
ADI	<b>-1.99</b>	<b>-3.00</b>	<b>1.00</b>	0.17	-0.64	0.15	-0.02	-1.17	0.14	-0.06	-1.04	0.19	-0.01	-0.73	0.14	<i>0.32 ± 0.38</i>
	<b>0.51</b>	<b>-0.99</b>		0.03	1.00		0.20	0.87		0.20	0.38		0.13	0.57		
AEI	<b>1.91</b>	<b>0.87</b>	<b>1.00</b>	-0.03	-1.09	0.15	0.06	-0.68	0.16	0.07	-0.45	0.19	0.02	-0.59	0.14	<i>0.33 ± 0.38</i>
	<b>0.53</b>	<b>2.96</b>		0.19	0.66		0.25	1.38		0.22	1.16		0.14	0.85		
AR	-0.09	-0.58	0.38	0.01	-0.25	0.09	-0.03	-0.46	0.21	0.03	-0.24	0.20	-0.003	-0.37	0.08	<i>0.19 ± 0.12</i>
	0.16	0.10		0.05	0.39		0.09	0.21		0.10	0.50		0.05	0.31		
BIO	-0.83	-2.72	0.66	-0.03	-1.42	0.16	-0.07	-1.78	0.08	0.28	-0.66	0.32	-0.06	-1.21	0.16	<i>0.28 ± 0.23</i>
	0.85	0.21		0.18	0.81		0.32	0.91		0.61	2.43		0.22	0.51		
H	<b>-1.48</b>	<b>-2.32</b>	<b>0.61</b>	-0.01	-0.93	0.20	-0.01	-0.92	0.20	-0.09	-1.04	0.29	0.38	-0.11	1.00	<i>0.46 ± 0.35</i>
	<b>0.42</b>	<b>-0.65</b>		0.20	0.86		0.19	0.79		0.24	0.44		0.42	1.37		
NDSI	-0.77	-2.84	0.82	-0.01	-1.39	0.08	-0.26	-2.26	0.29	<b>1.63</b>	<b>0.26</b>	<b>0.61</b>	-0.03	-1.21	0.10	<i>0.38 ± 0.33</i>
	0.88	0.29		0.18	1.04		0.55	0.47		<b>1.10</b>	<b>3.70</b>		0.17	0.54		
<i>Mean IF for variable</i>			<i>0.68 ± 0.29</i>			<i>0.14 ± 0.04</i>			<i>0.18 ± 0.07</i>			<i>0.30 ± 0.16</i>			<i>0.27 ± 0.36</i>	

#### 4.1.1. Elevation

Most of the acoustic indices supported the idea that the complexity of animal biophony decreases with elevation at the regional level. This result is consistent with much research on elevational gradients in tropical or subtropical regions in which animal diversity declines with increasing elevation (Peters et al., 2016; Rahbek, 2004). There is some variation in the exact shape of the elevation/diversity relationship. In many cases, like what is implied by our results, there is a linear decrease (Lomolino, 2001; Malsch, 2008; Rahbek, 1995; Sergio and Pedrini, 2007; Whittaker and Niering, 1975). But in other cases, diversity can peak at mid elevations <https://github.com/citation-style-language/schema/raw/master/csl-citation.json> (Aliabadian et al., 2008; Colwell and Lees, 2000; McCain, 2005; Szewczyk and McCain, 2016). A recent comparative study of many taxa across an elevational gradient on Mt. Kilimanjaro has shown that both bird and insect diversity rapidly decline across elevation, although some insect taxa show non-linear, complex relationships (Peters et al. 2016).

In the case of our study, elevation is colinear with latitude: more southern reserves are closer to the sea and hence lower in elevation. In fact, Shiwandashan, the most southernly of the reserves is classified as a tropical forest, whereas all other forests are classified as subtropical (Chen, 2007; Zeng and Liu, 1974). This latitudinal collinearity may be one factor for why elevation was a particularly strong effect in this study.

#### 4.1.2. Vegetational characteristics

Field ecologists have shown for a century that the structure of vegetation affects the composition of fauna (Dunlavy, 1935). A classical theory in ecology about vegetation structure is that greater heterogeneity in vertical structure leads to higher animal, and particularly bird, diversity (MacArthur and MacArthur, 1961). Other studies also support this idea (August, 1983; Heidrich et al., 2020; Stein et al., 2014; Willson, 1974). In support of the hypothesis that vertical heterogeneity is an especially strong predictor of biodiversity, we found that it was the factor with the second highest mean importance factor, influencing the biophony in both morning and evening recordings. However, the two significant relationships between the acoustic indices and vertical heterogeneity that we found went in opposite directions (NDSI positive, ADI negative).

The negative relationship between vertical heterogeneity and ADI was unexpected, not only because of the usual positive impact of vertical heterogeneity on animal diversity, and hence biophony, but because in earlier research ADI has been found to correlate with the vertical structural complexity of the forest, as estimated through LIDAR data (Pekin et al. 2012). As to the relationship with NDSI, higher NDSI values are indicative of lower levels of human activity. Although in this forest plot network all the plots are relatively undisturbed, some of them still are fairly close to areas traveled by humans and light levels of extraction could have occurred in the past, possibly leading to lower vertical heterogeneity, less diversity, and hence less complex biophony.

Floristics – i.e. the diversity of plant species – is also another factor that can influence biophony by affecting animal diversity, and it was an especially focus of our research because it is difficult to measure without vegetation plots. Although not as widespread as the connection between vertical heterogeneity and diversity, there are instances, particularly in temperate and relatively species-poor communities, where tree species richness has been shown to be important to birds (Rodewald and Abrams, 2002; Rotenberry, 1985). However, it was surprising to find a relationship between tree species richness and the complexity of biophony of birds, not insects, given that insects tend to more host-specific (Novotny and Basset, 2005). Follow-up research should investigate what bird species are present to ensure that there truly is a relationship between bird diversity and tree species richness, and if so, to understand it in more depth (e.g., is this trend found in frugivores, or in other guilds as well?).

We found no relationship between the acoustic indices and other

characteristics of the vegetation, such as canopy height and tree density. Further, despite the very different characteristics of their vocalizations, we saw no large differences between birds (morning) and insect (evening) sounds. We should acknowledge as to the latter finding that there were some insect sounds in among the morning recordings (see Table 2), particular cicadas, which could have confounded such a comparison, and have been known to mask bird song (Aide et al. 2017).

Finally, as to the general paucity of relationships between vegetation and the acoustic indices, it might be because differences in the vegetation added relatively little to a baseline strongly influenced by elevation. Networks of plots with less elevational or latitudinal variance will be necessary to truly understand how vegetation affects soundscapes. Indeed, most studies that have looked for vegetational effects on acoustic indices with such designs have found them (e.g. Pekin et al. 2012, Hao et al. 2021). However, only a few (e.g., Hao et al., 2021; Ng et al., 2018; Turner et al., 2018) have examined tree species richness or diversity because of the difficulty of obtaining this information, and none have used a previously established plot network.

#### 4.2. Comparisons among the acoustic indices

Of the seven commonly used acoustic indices examined in our study, H (Sueur et al., 2008) had the strongest relationships to the explanatory factors. ADI and AEI (Villanueva-Rivera et al., 2011), and NDSI (Kasten et al., 2012) together had the next strongest relationships. ADI, AEI and H all divide sound files into multiple frequency bands and derive a measurement of the diversity of these bands, and their results are often correlated (Ross et al., 2020). The result that H, ADI and AEI were among the indices with the strongest relationships examined is similar to that of Mammides et al. (2017), who found these to be among the indices that best predicted animal diversity, and also worked on a tropical to subtropical gradient of sites in China.

ACI, AR and BIO had the poorest model fits in our results. This may be partially related to how they dealt with seasonal variation, as they tended to have relatively more within-plot variation compared to across-plot variation. Specifically, AR was the highest index in this ratio, and BIO the next highest. As a ranked index, comparisons between AR in different datasets might also give spurious results (Sueur et al., 2020). For example, loud cicada sounds might make AR results in late summer quite different from those in early spring, explaining the strong seasonal change that we observed. These qualities might be why AR is infrequently used in acoustic index research (only four studies of 44 used it, Table A1).

Our results emphasize the necessity of using multiple acoustic indices. For example, ACI is a very commonly used index – used in 33 of the 44 studies summarized in Table A1 – and it is often found by the authors of these studies to be among the most effective, or most sensitive, indices (in 17 studies). But in this research, it was the one index that had a positive (though not significant) relationship with elevation. Hence, our results would have been very different if we did not use multiple indices.

#### 4.3. Conclusions and future directions

Here we conducted one of the first studies of long-term vegetation plots that attempted to correlate tree data to acoustic indices, as calculated from autonomously-captured recordings. Elevation was clearly the dominant factor influencing acoustic indices across the plot network. There were few significant relationships found between the acoustic indices and the characteristics of the vegetation at the plot level, perhaps because of the dominance of elevation. Recordings made of different taxa at different times (morning recordings dominated by bird song and evening recordings dominated by insect sounds) gave quite similar results. But among the different indices there were some that found multiple significant relationships (like H) and others that found none (like ACI, BIO and AR), which emphasizes that future studies are wise to use a

variety of indices to assess their results.

What future do autonomous recordings have for long-term vegetation plots? As we have argued before, the technology suits the conditions of these plots, as it can reduce observer disturbance. Perhaps the most valuable data that these plots gather is about tree species diversity, and the acoustic indices can give us some data on how such diversity affects biophony. Indeed, in this study we saw an unexpected relationship between tree species diversity and the H index in morning recordings (mostly representing bird sounds) that needs to be explored further with animal species identification on this plot network. Research using autonomous recordings and acoustic indices on the worlds' many vegetation plot networks at 1 ha (e.g., rainfor.org, afrifron.org, or tforces.net) or larger areas (e.g., forestgeo.si.edu), could understand how generally vegetation-related factors influence biophony, especially in the case of plot networks that do not have much elevational and latitudinal variation. We hope therefore that autonomous recording can be added to the procedures regularly used on long-term vegetation plots.

## 5. Data availability statement

The full dataset of the values of the acoustic indices for all the recordings without heavy rain is included in the Supplementary data.

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## CRedit authorship contribution statement

**You-Fang Chen:** Formal analysis, Writing – original draft, Writing – review & editing. **Yinghua Luo:** Conceptualization, Funding acquisition, Project administration, Data curation, Writing – review & editing. **Christos Mammides:** Formal analysis, Writing – review & editing. **Kun-Fang Cao:** Funding acquisition, Project administration, Writing – review & editing. **Shidan Zhu:** Funding acquisition, Project administration, Writing – review & editing. **Eben Goodale:** Conceptualization, Funding acquisition, Supervision, Formal analysis, Writing – original draft, Writing – review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107942>.

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