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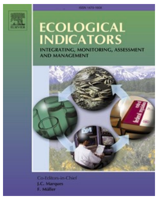

Original Articles

Acoustic beta indices exhibited a weak correlation with both vocal species composition dissimilarity and environmental factors dissimilarity in a subtropical forest

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ABSTRACT

Monitoring biodiversity through analyzing acoustic signals of ecosystems, as well as their relationship with environmental factors has garnered significant attention in fields like landscape ecology and biodiversity conservation. However, validation studies centered around only one of the acoustic diversities, the alpha index, while largely left out the beta one. Therefore, we evaluated the efficacy of acoustic beta indices as proxies of dissimilarity in vocal bird composition, and investigated the relative importance of vegetation characteristics dissimilarity, topographic dissimilarity, and geographical distance on acoustic beta diversity. To get acoustic beta indices of birds, we deployed 16 autonomous acoustic recorders across a biodiversity monitoring platform within a subtropical evergreen broad-leaved forest during bird breeding season. We performed bird species aural identification and investigated the relationship between vocal bird composition dissimilarity and eight acoustic beta indices with Mantel test. In addition, we obtained environmental factors included vegetation characteristics and topography variables through unmanned aerial vehicle light detection and ranging (UAV LiDAR) and from census data of the forest dynamics plots. The relative importance of vegetation characteristics, topography, and geographical distance on acoustic beta diversity was investigated with multiple regressions on distance matrices (MRM) and generalized dissimilarity modelling (GDM). Our results showed that the eight acoustic beta indices were significantly positively related to each other. There was weak correlation between acoustic dissimilarity and vocal bird composition dissimilarity, indicating that acoustic diversity is an independent facet of biodiversity. This study provided the first evidence that the combination of vegetation characteristics dissimilarity, topographic dissimilarity, and geographic distance account for few variation in the acoustic beta indices within the subtropical forest. Notably, vegetation characteristics dissimilarity emerged as relatively more important to the acoustic dissimilarity compared to topographic dissimilarity. Further research examining the relationship between specific acoustic spectral characteristics and potential influencing factors is highly encouraged.

1. Introduction

Biodiversity encompasses diversified aspects such as taxonomy, functionality, and phylogeny (Faith, 1992; Petchey and Gaston, 2006), the measurement of which is fundamental to ecology and conservation research (Pavoine and Bonsall, 2011; Monnet et al., 2014; Webb et al., 2002). With the advancement of automated soundscape recording technology, passive acoustic monitoring (PAM) is now a widely used method for assessing ecosystem status and monitoring vocal animal communities (also known as acoustic community) (Krause and Farina, 2016; Pijanowski et al., 2011). Acoustic diversity has also emerged as a potent indicator of biodiversity (Alcocer et al., 2022; Bradfer-Lawrence et al., 2020; Gasc et al., 2013a). As with other biodiversity components, acoustic diversity indices can be divided into alpha indices (within-group diversity) and beta indices (between-group diversity) (Sueur et al., 2014). The variation patterns and influencing factors of alpha indices across ecosystems have been thoroughly explored (e.g. Dröge et al., 2021; He et al., 2022; Pan, et al., 2024; Sueur et al., 2008a). Yet

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research on acoustic beta diversity is scarce (but see Hayashi et al., 2020; Lawrence et al., 2022).

Acoustic beta indices were proposed to examine acoustic differences between soundscapes across dimensions of time, frequency and amplitude (Depraetere et al., 2012; Gasc et al., 2013b; Sueur et al., 2008a). Although more than ten indices have been proposed since 2008 (Lawrence et al., 2022; Sueur et al., 2008a; Sueur et al., 2014), only a few have been studied. For example, the spectral dissimilarity index (D_f) and the acoustic dissimilarity index (D), which was produced by temporal dissimilarity and spectral dissimilarity (Depraetere et al., 2012; Gasc et al., 2013a; Wilford et al., 2021). The correlation between different acoustic beta indices was few studied (e.g. Lawrence et al., 2022; Lellouch et al., 2014). Among the known indices, some have demonstrated a positive correlation with each other (Gasc et al., 2013a; Lawrence et al., 2022), so ecologists are paying increasing attention to their efficacy as a measurement of biodiversity between acoustic communities. For example, acoustic beta indices were revealed to be related to vocal species composition dissimilarity between acoustic communities, even part of phylogenetic diversity and functional beta diversity (Gasc et al., 2013a; Gasc et al., 2013b; Sueur et al., 2008a). However, Lellouch et al. (2014) claimed that they should not be considered as a proxy of dissimilarity of bird species composition in the field. Instead, he proposed acoustic diversity as a new dimension of biodiversity. Therefore, more empirical studies are needed to explore their efficacy for biodiversity assessment.

The dissimilarity of biodiversity within natural assemblages may be attributed to two primary processes: stochastic processes, including dispersal limitation caused by geographic distance, and deterministic processes, such as niche-based environmental filtering (Hubbell, 2001; Webb et al., 2002). Acoustic dissimilarity may increase with geographic distance, which could be because of growing dissimilarity among vocal species and distance decay of sound (Azaele et al., 2015). However, the Acoustic Adaptation Hypothesis states that vocal animals could adapt to the habitat's physical structure to maximize the propagation of their vocalizations, emphasizing the importance of environmental filtering (Morton 1975). On the other hand, according to the Acoustic Niche Hypothesis (Krause, 1993), vocal organisms may engage in competition for acoustic space and could partition specific temporal and frequency intervals. In one previous research, the acoustic dissimilarity indices showed no correlation with the geographical distances both between and among oil palm plantations and surrounding forests (Hayashi et al., 2020). It indicated that, unlike species composition, the acoustic similarity did not diminish with an increase in geographical distance. At the same time, the soundscape of different habitat types consistently exhibited distinct patterns, which could be resulting from vegetation heterogeneity of the forest ecosystems (Rodriguez et al., 2014). However, the specific importance of respective environmental factor on acoustic beta indices remains largely unknown.

Therefore, this study focused on the relationship between acoustic beta diversity and vocal bird species beta diversity, as well as relative importance of vegetation characteristics dissimilarity, topographic dissimilarity and geographic distance on acoustic beta diversity in forest ecosystem. The expectation was that the majority of acoustic beta indices would show significant relationship between each other, as they were all designed to assess differences in soundscape (Lawrence et al., 2022). Although the acoustic dissimilarity was found to be associated with the number of unshared species among simulated acoustic communities (Sueur et al., 2008a), the soundscape of natural fields and simulated acoustic environments was different. As a result, we also anticipated that the vocal bird species composition dissimilarity calculated with aural identification results would exhibit no correlation with acoustic beta diversity (Lellouch et al. 2014). According to the Acoustic Adaptation Hypothesis, habitat heterogeneity may produce different physical environments for sound propagation (Mullet et al., 2017). We further predicted that vegetation characteristics, rather than geographic distance and topography, play a relatively more important role in explaining acoustic dissimilarity within subtropical evergreen broad-leaved forest.

2. Materials and Methods

2.1. Study area

The Ailao Mountains extend across central Yunnan Province, China (E 100°54′-101° 30′, N 23°44′-24°44′). Within it, there are over 34,000 ha of primary evergreen broadleaf forests conserved in the Ailaoshan National Nature Reserve (Pang et al., 1988). In 2018, a biodiversity monitoring platform comprising 19 1-ha forest dynamics plots was established in the northern region of the Mountains (Yang et al., 2023), following the protocols of Centre for Tropical Forest Science (CTFS) (Condit, 1998). Through it, all trees ≥ 10 cm DBH were mapped, tagged, identified to species, and measured across all plots. The vegetation type of the plot network is subtropical mid-mountain moist evergreen broad-leaved forest. Its composition and structure are dominated by subtropical species, such as *Lithocarpus hancei* (Fagaceae), *Lithocarpus xylocarpus* (Fagaceae), *Schima noronhae* (Theaceae), and *Machilus bombycina* (Lauraceae) (Yao et al., 2023). This study was conducted in 16 1-ha forest dynamics plots within the platform (Fig. 1).

2.2. Data collection

2.2.1. Soundscape monitoring

Song Meter SM4 recorders (Wildlife Acoustics Inc., Maynard, USA) were deployed in the center 20 × 20 quadrat of each forest dynamics plot during bird breeding season from June 1st to August 31st, 2022 (Table S1). The first one-minute recording was collected of each hour, totaling 24 recordings per day. As the current study focused on bird vocalization, the signals were sampled at 24 kHz and a depth of 16 bits quantization. Sound fragments were recorded in wav format and stored on two 16 GB SDHC memory cards in each machine. All recorders were attached to tree trunks at the height of 2.0–2.5 m.

2.2.2. Pre-processing and selection of the recordings

Except for one machine (ID: 6703) which stopped recording since July 2nd, all others functioned the entire three months, collecting 2208 recordings for each of the 15 plots. All recordings were previewed aurally and visually by analyzing their waveforms and spectrograms using Kaleidoscope (v5.4.2) (Wildlife Acoustics Inc., Maynard, USA). As the absence of human disturbance within the research plots, there was few anthrophony recorded. Recordings including geophonic sources (mainly raindrop sounds) and biophony from other animal taxa were deleted.

In order to review bird vocalization pattern, recordings of all the 16 plots on one particular day, June 20th, when the weather was good with no wind or rain, were chosen. The cumulative vocal time of birds and other vocal animal species such as insects and squirrels were accessed separately. That is, if one bird species calls or sings for a duration of 10 s, and another species occurs during that same period, the total cumulative time remains 10 s. Results showed that avian vocalization displayed a typical daily rhythm, characterized by silence from 21:00 to 05:00 with shorted than 1 s vocalization (Fig. S1, Table S2). Bird vocal activity was notably higher during the morning hours from 07:00 to 11:00 and in the afternoon from 16:00 to 17:00. During these periods, The cumulative vocal time of birds exceeded 20 s (19.9 s in 10:00) within a span of 60 s. As a result, we narrowed down to recordings from 07:00 to 11:00 for further analysis. A total of 30 recordings from each plot were selected. The spectrograms of all the selected recordings were relatively “clear”, devoid of sounds from other vocal animal species, as well as distinct raindrops and wind. To eliminate the influence of permanent device background noise, frequencies below 1000 Hz were removed with filter function in the R package seewave from all the one-minute recordings (Sueur et al., 2008b).

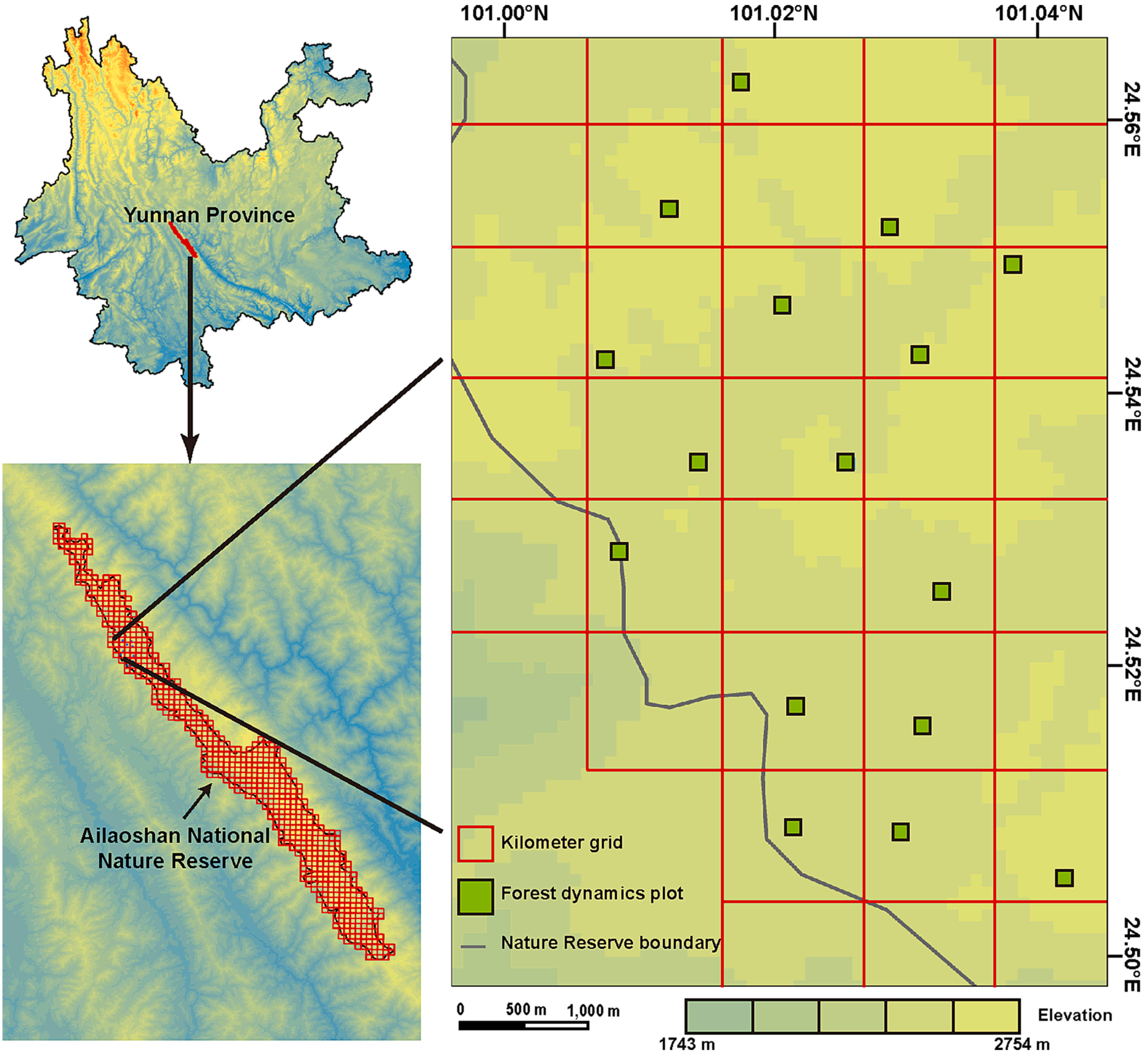


Fig. 1. Distribution map of the 16 forest dynamics plots within north Ailaoshan National Nature Reserve in Yunnan Province, China. The distance between research forest dynamics plots varies from 774 m to 6644 m, while their elevations range from 2414 m to 2642 m.

2.2.3. *Aural identification*

Our group has been doing bird survey in the region since 2021, so we are familiar with local bird vocalization. Aural identification was accomplished through both listening to and visualizing spectrogram of the recordings from each plot. A presence/absence (1/0) matrix was built to record the occurrence of each species within recordings. For bird taxonomy and nomenclature, we followed the HBW and BirdLife Taxonomic Checklist v8 (HBW and BirdLife International, 2023).

2.3. *Acoustic beta diversity*

Eight acoustic beta indices were used in the present study (Table S3). The Mutual information index (I) measured the differences in shape between each pair of cumulative frequency spectra, including variations of increases, decreases, peaks, troughs, and the lengths of flat segments (Cazelles et al., 2004). The Correlation-based dissimilarity index (R) employs a correlation coefficient to estimate the covariation between two frequency spectra (Lellouch et al., 2014). Kolmogorov-Smirnov distance index (D_{KS}) calculated the frequency location of the maximum difference between two cumulative frequency spectra using the Kolomogorov-Smirnov distance (Gasc et al.,2013a). The spectral dissimilarity index (D_f) was obtained by calculating the average of the STFT (Short Time Fourier Transform) of each sound, scaling each average spectra by its integral, and calculating the difference for each frequency bin (Sueur et al., 2008a). The symmetric Kullback-Leibler distance index (D_{KL}) was estimated by calculating the relative entropy between two probability frequency spectra (Gasc et al.,2013a). Log-spectral distance index (D_{LS}) was the log of the difference between two frequency spectra (Sueur, 2018). The symmetric Itakura-Saito distance index (D_{IS}) calculated the dissimilarity of two frequency spectra by calculating the Itakuro-Saito distance (Sueur, 2018). The relative frequency dissimilarity index (S) calculated the relative dissimilarity between minimum and maximum frequency of two frequency spectra (Deecke and Janik, 2006).

Detailed description of the R functions and equations used in calculation are in Table S3. The beta indices return a data matrix of pairwise comparisons between recordings. Based on the 480 recordings, mantel tests was used to explore the relationship between the eight acoustic beta indices with mantel function in the R package vegan (Oksanen et al., 2022). To evaluated the acoustic dissimilarity between forest plots, the mean value of the acoustic beta indices were calculated from 900 pairs of one-minute recordings (30 × 30) taken from each pair of plots.

2.4. Environmental factors

UAV LiDAR data of the study dynamics plots were collected from October 2018 to February 2019 using a Velodyne LiDAR PUCK-16 laser scanner. The point cloud data obtained of each plot were processed in the following procedure: denoising, filtering, and normalizing (more details in Yao et al., 2023). A canopy height model (CHM) of 1 m resolution was derived by normalized point clouds using point-to-raster algorithms. With the normalized point clouds and CHM, we obtained three plot-level lidar-derived metrics to characterize forest structure. Canopy closure (Closure) was measured as the ratio of pixels with a height value of more than 10 m (Zhang et al., 2016). The values ranged from 0 to 1 with higher values indicating a closed canopy. Mean canopy height (Hmean) was defined as the mean value of all cloud points with 1 m resolution. The vertical distribution ratio (VDR) was calculated with the equation: $\mathrm{VDR} = (\mathrm{HTmax}\text{-}\mathrm{HTmed})/\mathrm{HTmax}$, where HTmax and HTmed were the maximum and median values of canopy height within the plot (Goetz et al., 2007) respectively. Areas with more even vertical biomass distribution showed larger values close to 1.

In addition to the three LiDAR-derived metrics, four other vegetation characteristics were calculated based on census data of the forest dynamics plot collected in 2019. The stand basal area (BA) was the sum of stem basal area in each plot. Tree size variation within a plot was calculated by the coefficient of variation of individual DBH (diameter at breast height) (DBHcv). Tree species richness (SR) was the total tree species number within each plot. Tree density (Density) was estimated as the total number of tree individuals recorded within each plot. In all, we obtained seven plot-level vegetation characteristics in each plot.

Four topographic characteristics were obtained per plot. Mean elevation (Elevation) was the mean value of four corners. The slope (Slope) was the mean angular deviation from the horizontal of each of the four triangular planes formed by connecting three of its corners (Harms et al., 2001). Aspect (Aspect) was the orientation of slope, for which both the sine and cosine value were calculated. Topographic complexity (Complex) was calculated with the equation: $\mathrm{complexity} = \mathrm{As}/\mathrm{Ap}$, where as was the total surface area and Ap, the projected area of the plot (Ren et al., 2019).

2.5. Statistical analyses

We used Mantel tests to verify the statistical significance of correlation between acoustic beta indices and species composition dissimilarity for the 480 one-minute recordings. The species dissimilarity was calculated as the Bray-Curtis distance (B-C distance) using the presence/absence vocal bird species composition got from aural identification (Magurran, 1988). B-C distance was assessed with vegdist function in the R package vegan.

The environmental factors, which encompassed vegetation characteristics and topographic variables of the 16 plots, were normalized. Euclidean distance among plots was calculated with dist function in the R package stats (R Core Team, 2024). The geographic distance between each pair of plots was also calculated with the dist function based on the coordinate of the plots.

To distinguish the effects of environmental dissimilarity and geographic distance on acoustic beta indices, multiple regressions on distance matrices (MRM) were used. It involved a multiple regression of a response matrix on any number of explanatory matrices (Lichstein 2007). In this stage, vegetation and topographic characteristics of each forest plot were considered as environmental factors. We used MRM to partition variance in acoustic beta indices between unique contributions of environmental and geographic distances, as well as the combination of them. The significance of regression coefficients was tested with 1,000 permutations. MRM was performed with MRM function in the R package ecodist (Goslee and Urban, 2007).

The relative importance of specific vegetation characteristics dissimilarity, topographic dissimilarity, and geographic distance in explaining acoustic beta indices was assessed by generalized dissimilarity modelling (GDM). All the explanation variables were considered as GDM is generally insensitive to collinearity between predictor variables (Ferrier et al., 2007). With the acoustic beta indices served as response variables, we used Akaike's Information Criterion (AIC) for model selection with the lowest AICs as final models (Mokany et al., 2022). The GDM model was implemented with the R package gdm (Ferrier et al., 2007).

3. Results

3.1. Vocal bird species composition dissimilarity and acoustic beta diversity

A total of 75 bird species were recorded by aural identification (Table S4), among them 81 % belonging to Passeriformes. *Yuhina gularis*, *Heterophasia desgodinsi*, and *Minla ignotincta* were the three most frequently recorded bird species in the study area. The dissimilarity in bird composition exhibited weak correlations with all the eight acoustic indices, with the Mantel correlation coefficients ranged from 0.028 to 0.120 (Table 1).

All the eight acoustic beta indices exhibited significant positive correlations with one another. The Mantel correlation coefficients were all higher than 0.50, except for the D_{KL} (Fig. 2).

3.2. Effect of environmental dissimilarity and geographic distance on acoustic beta diversity

The results of the MRM analysis showed that environmental factors accounted for a greater proportion of variation than geography in five out of the eight acoustic beta indices. However, less than 5 % of the variation could be attributed to the combined influence of both environmental and geographical factors (Table 2). The Mantel tests showed that the vegetation characteristics and topographic dissimilarity showed higher relationship for all the acoustic beta indices (Fig. 3). The vegetation characteristics dissimilarity was significantly related with the relative frequency dissimilarity index (S).

GDM was further used to weigh how specific vegetation characteristic dissimilarity, topographic dissimilarity, and geography explains acoustic beta indices. Based on AIC results, we got the best generalized dissimilarity model with two to three variables of vegetation characteristics and topography left for all the indices (Fig. 4 and Table S5). We found that the best fitted GDM models for S included only the canopy height vertical distribution ratio (VDR) and tree size variation (DBHcv) (Fig. 4 and Table S5). Vegetation characteristics dissimilarity explained relatively more deviance compared with the topographic dissimilarity for all acoustic indices.

4. Discussion

Ecoacoustics is a discipline that investigates the ecological role of sound along a broad range of spatial and temporal scales (Sueur and Farina, 2015). Automated species identification from recordings is difficult to get correct results due to the variability of songs and calls of a certain species, as well as frequency overlap caused by simultaneous singing species (Acevedo et al., 2009; Stowell, 2022). On the other hand, acoustic alpha and beta indices have been specifically developed to evaluate the acoustic diversity at acoustic community level without the

Table 1
Mantel correlation coefficients (R) and significant level (*p*) between the eight acoustic beta indices and vocal bird species composition dissimilarity (B-C distance).

B-C distance	I	R	D_{KS}	D_f	D_{KL}	D_{LS}	D_{IS}	S
R	0.120	0.056	0.028	0.044	0.051	0.049	0.054	0.031
p	0.001	0.001	0.057	0.006	0.003	0.003	0.003	0.016

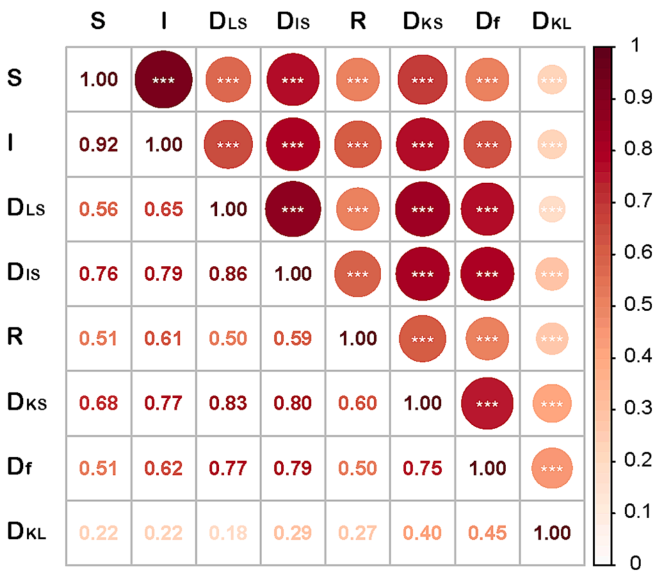


Fig. 2. Mantel correlation coefficients (R) and significant level (*p*) between the eight acoustic beta indices for the 480 one-minute recordings.

Table 2
Results of MRM demonstrating the variation explained by environment (vegetation characteristics and topography together), geography and the combination of them for the eight acoustic beta indices. R^2: the proportion of variation explained.

Index	Type	Environment	Geography	Both
I	R^2	0.018	0.001	0.019
	p	0.551	0.803	0.734
R	R^2	0.009	0.015	0.018
	p	0.439	0.197	0.480
D_{KS}	R^2	0.005	0.009	0.011
	p	0.744	0.490	0.800
D_f	R^2	0.011	0.002	0.017
	p	0.524	0.704	0.645
D_{KL}	R^2	0.002	0.002	0.005
	p	0.817	0.709	0.873
D_{LS}	R^2	0.036	0.003	0.049
	p	0.209	0.655	0.219
D_{IS}	R^2	0.017	0.014	0.045
	p	0.472	0.313	0.349
S	R^2	0.042	0.000	0.046
	p	0.281	0.960	0.371

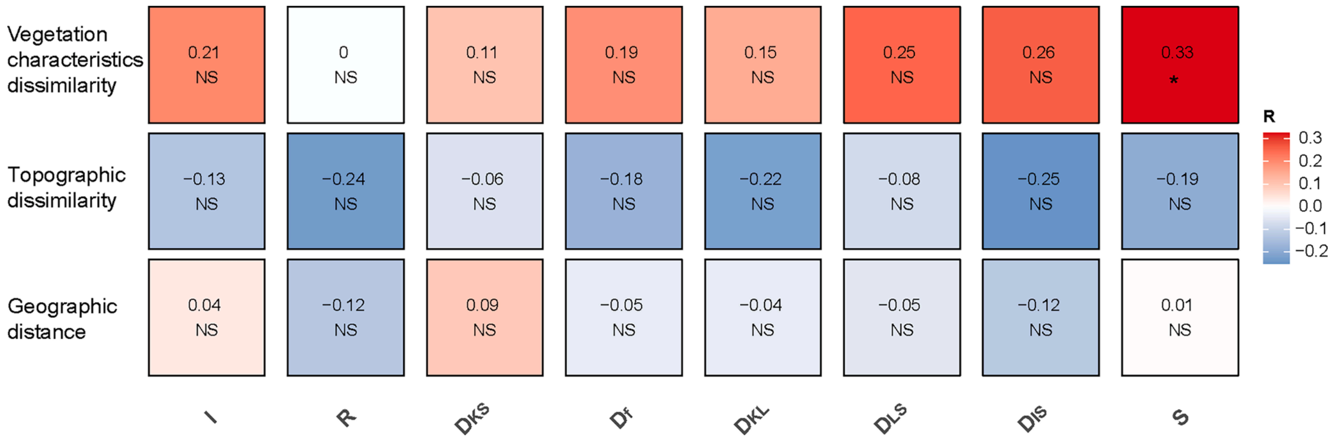
need for species identification (Lawrence et al., 2022; Sueur et al., 2008a). As anticipated, the eight acoustic beta indices were significantly positively related to each other. There was a weak correlation observed between the beta diversity of vocal bird species, as determined through aural identification, and the acoustic beta indices. Moreover, the characteristics of vegetation and topographic dissimilarity generally exhibited a higher correlation with acoustic beta indices than geographic dissimilarity, though the combination of them explained few variation of acoustic beta indices. Vegetation characteristics dissimilarity was relatively more important than topographic dissimilarity for acoustic dissimilarity.

In natural ecosystems, sounds produced by non-human organisms (biophony) constitute the primary component of the soundscape. Biophony could exhibit diverse temporal patterns depending on specific life cycle or biological event. In this subtropical forest, avian vocalizations, unlike those of other vocal animals, displayed a typical daily rhythm characterized by silence during the period from 21:00 to 05:00. As previous studies have indicated that acoustic indices performed better when applied during ecologically relevant periods (Metcalf et al., 2021), we focused on the soundscape in birds' breeding season, which spans from April to early August in the study area. Furthermore, recordings from 7:00 to 11:00, a period during which birds were vocally active, were selected as reliable comparisons.

After the acoustic indices were proposed, biologists were trying to decide how well acoustic diversity represents biodiversity, with a particular focus on avian species. (e.g. Alcocer et al., 2022; Mammides et al., 2017; Myers et al., 2019). Yet what was more investigated was the relationship between biodiversity metrics and acoustic alpha diversity, with beta largely understudied. Acoustic alpha indices did show a low positive correlation with animal diversity, but it was inconsistent, vulnerable to various factors that may affect their performance (Alcocer et al., 2022; Eldridge et al., 2018; Pan et al., 2024; Sethi et al., 2023). Among the limited researches on acoustic beta indices, the acoustic dissimilarity index (D) was found linked to the number of unshared species between simulated acoustic communities (Sueur et al., 2008a). Additionally, the frequency spectral dissimilarity index (D_f) was suggested as a tool to detect acoustic differences between sites characterized by varying species assemblages within a Pacific island (Gasc et al., 2013b). However, the correlation between other beta indices and species composition dissimilarity requires further investigation with additional empirical data.

Automated identification of vocal animal species from recordings could be unreliable due to the complexity of real-world field data. Further technical challenges come from the difficulty of optimizing the identification through machine learning, which, itself, is to be perfected (Kumar et al., 2024; Ovaskainen et al., 2018). By comparison, identification done by human experts seems more reliable in spite of more time-consuming. More than 210 bird species were recorded from 2021 to 2023 in the study region, from which 75 vocal species were assembled into the acoustic community in this study. All the acoustic beta indices calculated from field recordings showed weak correlation with vocal bird composition dissimilarity in the present subtropical forest. On the other hand, the acoustic beta indices were significantly positively related as former studies showed (Gasc et al., 2013a; Lawrence et al., 2022; Lellouch et al., 2014), confirming their similar function to determine how much two acoustic communities dissimilarity.

Unlike conclusions drawn from field data evidence, the acoustic beta indices derived from simulated acoustic communities exhibited a correlation with the number of unshared species, or with species compositional dissimilarity among these simulated communities (Lellouch et al., 2014; Sueur et al., 2008a). This could be because of the significant differences between real (field) and simulated acoustic communities. As the songs and calls of specific species usually exhibited distinct spectrogram characteristics, both can be utilized for species aural identification. Nevertheless, one typical song from each species is used to construct the simulated choruses (e.g. Sueur et al., 2008a). In addition, though spectral frequency is typically confined to a specific range for a certain species, the duration of vocalizations may vary in the field, which may affect acoustic diversity. Moreover, the distance from vocal individuals to recorders could influence sound pressure level and, consequently, influencing the acoustic dissimilarity indices (Sueur et al.,



	I	R	D_{KS}	D_f	D_{KL}	D_{LS}	D_{IS}	S
Vegetation characteristics dissimilarity	0.21 NS	0 NS	0.11 NS	0.19 NS	0.15 NS	0.25 NS	0.26 NS	0.33 *
Topographic dissimilarity	−0.13 NS	−0.24 NS	−0.06 NS	−0.18 NS	−0.22 NS	−0.08 NS	−0.25 NS	−0.19 NS
Geographic distance	0.04 NS	−0.12 NS	0.09 NS	−0.05 NS	−0.04 NS	−0.05 NS	−0.12 NS	0.01 NS

Fig. 3. Mantel correlation coefficients (R) between the eight acoustic beta indices and vegetation characteristics dissimilarity, topographic dissimilarity, and geographic distance of the 16 forest dynamics plots. NS: $p > 0.05$, *: $p < 0.05$.

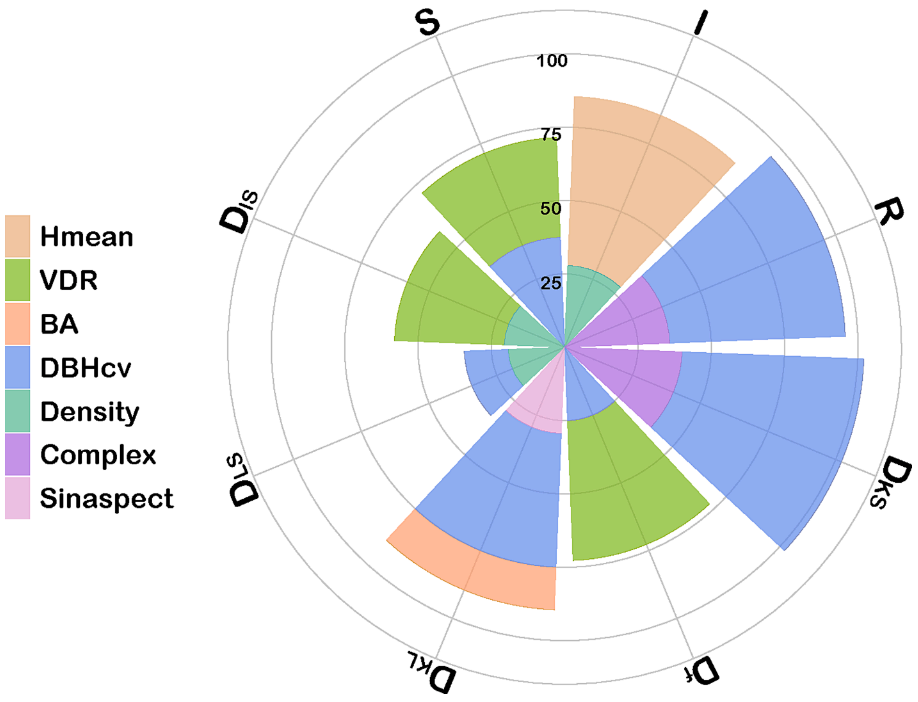


Fig. 4. The relative importance (%) of predictor variables results from the best fitted GDM model of eight acoustic beta indices. The radius of each specific arc represents the corresponding relative importance value. Hmean: mean canopy height; VDR: canopy height vertical distribution ratio; BA: stand basal area; DBHcv: tree size variation; Density: tree density; Complex: topographic complexity; Sinaspect: aspect (sine).

2014). They may all serve as potential explanations for why the acoustic dissimilarity between filed recordings cannot be a proxy of vocal species composition dissimilarity. As a result, it supported that acoustic diversity is an independent facet of biodiversity (Lellouch et al., 2014).

The effect of environmental factors such as vegetation and topographic characteristics on acoustic alpha diversity has been studied since last decade (e.g. Bradfer-Lawrence et al., 2019; Do Nascimento et al., 2020; Pekin et al., 2012). In terrestrial ecosystem, different habitat types always showed unique acoustic signature resulting from the vegetation heterogeneity. For example, in tropical forests, horizontal vegetation characteristics and topographic complexity were found to be important variables related to acoustic alpha diversity (He et al., 2022). On the other hand, although acoustic beta diversity was recognized as related to vegetation condition (BioCondition scores in Ng et al., 2018) or heterogeneity in forest ecosystems (Rodriguez et al., 2014), the relative importance of environmental factors, including vegetation characteristics and topography, on the diversity has yet to be investigated. Acoustic dissimilarity was generally found to be less related with geographic distance, indicating an absence of distance decay in acoustic similarity (Hayashi et al., 2020). Furthermore, this finding confirmed that dispersal limitation is not an underlying mechanism for acoustic dissimilarity.

Habitat structure was considered as an important factor shaping the evolution of vocal signals, especially for birds (Boncoraglio and Saino, 2007). The Acoustic Adaptation Hypothesis even predicts that birds tend to adjust their vocal signals to enhance transmission and minimize song degradation. For example, lower frequencies and narrower frequency ranges occur more frequently in densely vegetated habitat (Blumenrath and Dabelsteen, 2004; Morton 1975). Here in the subtropical forest, the dissimilarity on vegetation characteristics exhibited a more important impact compared to habitat topographic dissimilarity, though the combination of them explained few variation for all the acoustic indices.

Vegetation structure heterogeneity may produce different physical environments for sound propagation, and support different acoustic communities, indicated the importance of environment filtering on the acoustic dissimilarity.

5. Conclusions

Well-recorded local scale vegetation characteristics and UAV LiDAR data of forest dynamics plots available made the current biodiversity monitoring platform ideal for our research. As anticipated, we observed a significant positive correlation between the eight acoustic beta indices. However, there was weak correlation between acoustic dissimilarity and vocal bird composition dissimilarity, indicating that acoustic diversity is a distinct facet of biodiversity. The relative importance of vegetation characteristics dissimilarity, topographic dissimilarity, and geographic distance on acoustic beta diversity were weighed for the first time. The combination of the them explained few variation of acoustic beta indices, and the characteristics of vegetation and topographic dissimilarity generally exhibited weak correlation with acoustic beta indices. Vegetation characteristics dissimilarity emerged as relatively more important to the acoustic dissimilarity compared to topographic dissimilarity. More empirical studies that examine the correlation between specific acoustic characteristics and potential influencing factors is highly encouraged.

CRediT authorship contribution statement

Hexiang Wang: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Xuelian He:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Zhiliang Yao:** Writing – review & editing, Formal analysis, Data curation. **Bin Wang:** Writing – review & editing, Data curation. **Yiting Jiang:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Luxiang Lin:** Writing – review & editing, Resources, Methodology, Funding acquisition.

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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.2025.113266.

Data availability

Data will be made available on request.

References

Acevedo, M.A., Corrada-Bravo, C.J., Corrada-Bravo, H., Villanueva-Rivera, L.J., Aide, T. M., 2009. Automated classification of bird and amphibian calls using machine learning: A comparison of methods. Ecol. Inform. 4, 206–214. https://doi.org/10.1016/j.ecoinf.2009.06.005.

Alcocer, I., Lima, H., Moreira Sugai, L.S., Llusia, D., 2022. Acoustic indices as proxies for biodiversity: a meta-analysis. Biol. Rev. 97, 2209–2236. https://doi.org/10.1111/brv.12890.

Azaele, S., Maritan, A., Cornell, S.J., Suweis, S., Banavar, J.R., Gabriel, D., Kunin, W.E., 2015. Towards a unified descriptive theory for spatial ecology: predicting biodiversity patterns across spatial scales. Methods Ecol. Evol. 6, 324–332. https://doi.org/10.1111/2041-210X.12319.

Blumenrath, S.H., Dabelsteen, T., 2004. Degradation of great tit (*Parus major*) song before and after foliation: implications for vocal communication in a deciduous forest. Behaviour 141, 935–958. http://www.jstor.org/stable/4536177.

Boncoraglio, G., Saino, N., 2007. Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. Funct. Ecol. 21, 134–142. https://doi.org/10.1111/j.1365-2435.2006.01207.x.

Bradfer-Lawrence, T., Bunnefeld, N., Gardner, N., Willis, S.G., Dent, D.H., 2020. Rapid assessment of avian species richness and abundance using acoustic indices. Ecol. Indic. 115, 106400. https://doi.org/10.1016/j.ecolind.2020.106400.

Bradfer-Lawrence, T., Gardner, N., Bunnefeld, L., Bunnefeld, N., Willis, S.G., Dent, D.H., 2019. Guidelines for the use of acoustic indices in environmental research. Methods Ecol. Evol. 10, 1796–1807. https://doi.org/10.1111/2041-210x.13254.

Cazelles, B., 2004. Symbolic dynamics for identifying similarity between rhythms of ecological time series. Ecol. Lett. 7, 755–763. https://doi.org/10.1111/j.1461-0248.2004.00629.x.

Condit, R., 1998. Tropical Forest Census: Plots Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots. Springer, Berlin.

Deecke, V.B., Janik, V.M., 2006. Automated categorization of bioacoustic signals: Avoiding perceptual pitfalls. J. Acoust. Soc. Am. 119, 645–653. https://doi.org/10.1121/1.2139067.

Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S., Sueur, J., 2012. Monitoring animal diversity using acoustic indices: Implementation in a temperate woodland. Ecol. Indic. 13, 46–54. https://doi.org/10.1016/j.ecolind.2011.05.006.

Do Nascimento, L.A., Campos-Cerqueira, M., Beard, K.H., 2020. Acoustic metrics predict habitat type and vegetation structure in the Amazon. Ecol. Indic. 117, 106679. https://doi.org/10.1016/j.ecolind.2020.106679.

Dröge, S., Martin, D.A., Andriafanomezantsoa, R., Burivalova, Z., Fulgence, T.R., Osen, K., Rakotomalala, E., Schwab, D., Wurz, A., Richter, T., Kreft, H., 2021. Listening to a changing landscape: Acoustic indices reflect bird species richness and plot-scale vegetation structure across different land-use types in north-eastern Madagascar. Ecol. Indic. 120, 106929. https://doi.org/10.1016/j.ecolind.2020.106929.

Eldridge, A., Guyot, P., Moscoso, P., Johnston, A., Eyre-Walker, Y., Peck, M., 2018. Sounding out ecoacoustic metrics: Avian species richness is predicted by acoustic indices in temperate but not tropical habitats. Ecol. Indic. 95, 939–952. https://doi.org/10.1016/j.ecolind.2018.06.012.

Ferrier, S., Manion, G., Elith, J., Richardson, K., 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Divers. Distrib. 13, 252–264. https://doi.org/10.1111/j.1472-4642.2007.00341.x.

Gasc, A., Sueur, J., Jiguet, F., Devictor, V., Grandcolas, P., Burrow, C., Depraetere, M., Pavoine, S., 2013a. Assessing biodiversity with sound: Do acoustic diversity indices reflect phylogenetic and functional diversities of bird communities? Ecol. Indic. 25, 279–287. https://doi.org/10.1016/j.ecolind.2012.10.009.

Gasc, A., Sueur, J., Pavoine, S., Pellens, R., Grandcolas, P., 2013b. Biodiversity sampling using a global acoustic approach: contrasting sites with microendemics in New Caledonia. PloS One 8, e65311. https://doi.org/10.1371/journal.pone.0065311.

Goetz, S., Steinberg, D., Dubayah, R., Blair, B., 2007. Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. Remote Sens. Environ. 108, 254–263. https://doi.org/10.1016/j.rse.2006.11.016.

Goslee, S.C., Urban, D.L., 2007. The ecodist package for dissimilarity-based analysis of ecological data. J. Stat. Softw. 22, 1–19. https://doi.org/10.18637/jss.v022.i07.

Harms, K.E., Condit, R., Hubbell, S.P., Foster, R.B., 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. J. Ecol. 89, 947–959. https://doi.org/10.1111/j.1365-2745.2001.00615.x.

Hayashi, K., Erwinsyah, L.V.D., Yamamura, K., 2020. Acoustic dissimilarities between an oil palm plantation and surrounding forests: Analysis of index time series for beta-diversity in South Sumatra. Indonesia. Ecol. Indic. 112, 106086. https://doi.org/10.1016/j.ecolind.2020.106086.

HBW and BirdLife International, 2023. Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world. Version 8 . http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v8_Dec23.zip/(accessed December 2023).

He, X., Deng, Y., Dong, A., Lin, L., 2022. The relationship between acoustic indices, vegetation, and topographic characteristics is spatially dependent in a tropical forest in southwestern China. Ecol. Indic. 142, 109229. https://doi.org/10.1016/j.ecolind.2022.109229.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.

Krause, B.L., 1993. The Niche Hypothesis. The Soundscape Newsl. 6, 6–10.

Krause, B., Farina, A., 2016. Using ecoacoustic methods to survey the impacts of climate change on biodiversity. Biol. Conserv. 195, 245–254. https://doi.org/10.1016/j.biocon.2016.01.013.

Kumar, S.A., Verma, M., Kumar, V., Kumar, G., 2024. Identification of Bird Species Through Audio Signal Processing Using Neural Network. In: Bhattacharya, A., Dutta, S., Dutta, P., Samanta, D. (Eds.), Innovations in Data Analytics. Springer, Singapore, pp. 437–447.

Lawrence, B.T., Hornberg, J., Haselhoff, T., Sutcliffe, R., Ahmed, S., Moebus, S., Gruehn, D., 2022. A widened array of metrics (WAM) approach to characterize the urban acoustic environment; a case comparison of urban mixed-use and forest. Appl. Acoust. 185, 108387. https://doi.org/10.1016/j.apacoust.2021.108387.

Lellouch, L., Pavoine, S., Jiguet, F., Glotin, H., Sueur, J., 2014. Monitoring temporal change of bird communities with dissimilarity acoustic indices. Methods Ecol. Evol. 5, 495–505. https://doi.org/10.1111/2041-210x.12178.

Lichstein, J.W., 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. Plant Ecol. 188, 117–131. https://doi.org/10.1007/s11258-006-9126-3.

Magurran, A.E., 1988. Ecological diversity and its measurement. Princeton University Press, Princeton.

Mammides, C., Goodale, E., Dayananda, S.K., Kang, L., Chen, J., 2017. Do acoustic indices correlate with bird diversity? Insights from two biodiverse regions in Yunnan Province, south China. Ecol. Indic. 82, 470–477. https://doi.org/10.1016/j.ecolind.2017.07.017.

Metcalf, O.C., Barlow, J., Devenish, C., Marsden, S., Berenguer, E., Lees, A.C., 2021. Acoustic indices perform better when applied at ecologically meaningful time and frequency scales. Methods Ecol. Evol. 12, 421–431. https://doi.org/10.1111/2041-210x.13521.

Mokany, K., Ware, C., Woolley, S.N.C., Ferrier, S., Fitzpatrick, M.C., 2022. A working guide to harnessing generalized dissimilarity modelling for biodiversity analysis and conservation assessment. Glob. Ecol. Biogeogr. 31, 802–821. https://doi.org/10.1111/geb.13459.

Monnet, A.-C., Jiguet, F., Meynard, C.N., Mouillot, D., Mouquet, N., Thuiller, W., Devictor, V., 2014. Asynchrony of taxonomic, functional and phylogenetic diversity in birds. Glob. Ecol. Biogeogr. 23, 780–788. https://doi.org/10.1111/geb.12179.

Morton, E.S., 1975. Ecological Sources of Selection on Avian Sounds. Am. Nat. 109, 17–34. https://doi.org/10.1086/282971.

Mullet, T.C., Farina, A., Gage, S.H., 2017. The acoustic habitat hypothesis: an ecoacoustics perspective on species habitat selection. Biosemiotics 10, 319–336. https://doi.org/10.1007/s12304-017-9288-5.

Myers, D., Berg, H., Maneas, G., 2019. Comparing the soundscapes of organic and conventional olive groves: A potential method for bird diversity monitoring. Ecol. Indic. 103, 642–649. https://doi.org/10.1016/j.ecolind.2019.04.030.

Ng, M.-L., Butler, N., Woods, N., 2018. Soundscapes as a surrogate measure of vegetation condition for biodiversity values: A pilot study. Ecol. Indic. 93, 1070–1080. https://doi.org/10.1016/j.ecolind.2018.06.003.

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Antoniazi Evangelista H. B., FitzJohn R., Friendly M., Furneaux B., Hannigan G., Hill M.O., Lahti L., McGlinn D., Ouellette M.-H., Ribeiro Cunha E., Smith T., Stier A., Ter Braak C.G.F., Weedon, J. (2022). Vegan: Community ecology package. R Package Version 2.6-2. https://CRAN.R-project.org/package=vegan.

Ovaskainen, O., de Camargo, U.M., Somervuo, P., 2018. Animal Sound Identifier (ASI): software for automated identification of vocal animals. Ecol. Lett. 21, 1244–1254. https://doi.org/10.1111/ele.13092.

Pan, W., Goodale, E., Jiang, A., Mammides, C., 2024. The effect of latitude on the efficacy of acoustic indices to predict biodiversity: A meta-analysis. Ecol. Indic. 159, 111747. https://doi.org/10.1016/j.ecolind.2024.111747.

Pang, J.H., Fan, J.R., Qiu, X.Z., Qian, D.R., Li, R.L., Li, X.W., Sun, M.S., 1988. The vegetation of the Ailao Mountains (in Chinese with English abstract). In: Xu, Y.C., Jiang, H.Q. (Eds.), Comprehensive Survey of Ailaoshan Nature Reserve. Yunnan Ethnic Press, Kunming, pp. 63–171.

Pavoine, S., Bonsall, M.B., 2011. Measuring biodiversity to explain community assembly: a unified approach. Biol Rev. 86, 792–812. https://doi.org/10.1111/j.1469-185X.2010.00171.x.

Pekin, B.K., Jung, J., Villanueva-Rivera, L.J., Pijanowski, B.C., Ahumada, J.A., 2012. Modeling acoustic diversity using soundscape recordings and LIDAR-derived metrics of vertical forest structure in a neotropical rainforest. Landsc. Ecol. 27, 1513–1522. https://doi.org/10.1007/s10980-012-9806-4.

Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H., Pieretti, N., 2011. Soundscape Ecology: The Science of Sound in the Landscape. Bioscience 61, 203–216. https://doi.org/10.1525/bio.2011.61.3.6.

R Core Team (2024). Stats: The R Stats Package. R package version 4. 4. 1. https://www.R-project.org.

Ren, H., Keil, P., Mi, X., Ma, K., Hao, Z., Ye, W., Lin, L., Valencia, R., Fletcher, C.D., Thomas, D.W., Howe, R.W., Lutz, J., Bourg, N.A., Su, S.-H., Sun, I.F., Zhu, L., Chang, L.-W., Wang, X., Du, X., Kenfack, D., Chuyong, G.B., Jetz, W., 2019. Environment- and trait-mediated scaling of tree occupancy in forests worldwide. Glob. Ecol. Biogeogr. 28, 1155–1167. https://doi.org/10.1111/geb.12922.

Rodriguez, A., Gasc, A., Pavoine, S., Grandcolas, P., Gaucher, P., Sueur, J., 2014. Temporal and spatial variability of animal sound within a neotropical forest. Ecol Inform. 21, 133–143. https://doi.org/10.1016/j.ecoinf.2013.12.006.

Sethi, S.S., Bick, A., Ewers, R.M., Klinck, H., Ramesh, V., Tuanmu, M.-N., Coomes, D.A., 2023. Limits to the accurate and generalizable use of soundscapes to monitor biodiversity. Nat. Ecol. Evol. 7, 1373–1378. https://doi.org/10.1038/s41559-023-02148-z.

Stowell, D., 2022. Computational bioacoustics with deep learning: a review and roadmap. Peerj 10, e13152. https://doi.org/10.7717/peerj.13152.

Sueur, J., 2018. Sound analysis and synthesis with R. Springer, Cham.

Sueur, J., Aubin, T., Simonis, C., 2008a. Seewave, a free modular tool for sound analysis and synthesis. Bioacoustics 18, 213–226. https://doi.org/10.1080/09524622.2008.9753600.

Sueur, J., Farina, A., 2015. Ecoacoustics: the ecological investigation and interpretation of environmental sound. Biosemiotics 8, 493–502. https://doi.org/10.1007/s12304-015-9248-x.

Sueur, J., Farina, A., Gasc, A., Pieretti, N., Pavoine, S., 2014. Acoustic indices for biodiversity assessment and landscape investigation. Acta Acust. Acust. 100, 772–781. https://doi.org/10.3813/aaa.918757.

Sueur, J., Pavoine, S., Hamerlynck, O., Duvail, S., 2008b. Rapid acoustic survey for biodiversity appraisal. PloS One 3, e4065.

Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. Annu. Rev. Ecol. Syst. 33, 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448.

Wilford, D.C., Miksis-Olds, J.L., Martin, S.B., Howard, D.R., Lowell, K., Lyons, A.P., Smith, M.J., 2021. Quantitative Soundscape Analysis to Understand Multidimensional Features. Front. Mar. Sci. 8, 672336. https://doi.org/10.3389/fmars.2021.672336.

Yang, X., Yao, Z., Wang, B., Wen, H., Deng, Y., Cao, M., Zhang, Z., Tan, Z., Lin, L., 2023. Driving effects of forest stand structure of a subtropical evergreen broad-leaved forest on species composition variation: From local to regional scales. Biodivers. Sci. 31, 22139. https://doi.org/10.17520/biods.2022139.

Yao, Z., Yang, X., Wang, B., Shao, X., Wen, H., Deng, Y., Zhang, Z., Cao, M., Lin, L., 2023. Multidimensional beta-diversity across local and regional scales in a Chinese subtropical forest: The role of forest structure. Ecol. Evol. 13, e10607. https://doi.org/10.1002/ece3.10607.

Zhang, J., Hu, J., Lian, J., Fan, Z., Ouyang, X., Ye, W., 2016. Seeing the forest from drones: Testing the potential of lightweight drones as a tool for long-term forest monitoring. Biol. Conserv. 198, 60–69. https://doi.org/10.1016/j.biocon.2016.03.027.