Ecological Indicators 142 (2022) 109229

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

The relationship between acoustic indices, vegetation, and topographic characteristics is spatially dependent in a tropical forest in southwestern China

Xuelian He [a,b], Yun Deng [a,b], Anran Dong [c], Luxiang Lin [a,b,d,*]

[a] CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming 650223, China
[b] National Forest Ecosystem Research Station at Xishuangbanna, Menglun, Mengla, Yunnan 666303, China
[c] Guangxi Key Laboratory of Forest Ecology and Conservation, College of Forestry, Guangxi University, Nanning 530004, China
[d] Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China

A R T I C L E I N F O

Keywords:
Acoustic indices
Forest dynamics plot
Spatial scale dependence
Vegetation characteristics
Topography

A B S T R A C T

The soundscape of different habitats can be discriminated by multiple acoustic indices as they have previously been related to vegetation characteristics. However, the relationship between acoustic indices and topography still needs to be thoroughly evaluated, as well as the variance in the relationship at different spatial scales within the same research system. Networks of forest dynamics plots constructed under the same protocol provide an ideal research platform for addressing the above issue. Our study investigated the relationship between acoustic indices, vegetation, and topographic characteristics at two spatial scales. We recorded soundscapes using autonomous recorders across a tropical forest dynamics plot network consisting of 22 plots in Xishuangbanna, Yunnan Province, southwest China. To exclude recordings with geophony and with biotic sounds from non-avian species, especially from cicadas and frogs, the recordings were previewed aurally and visually, with 9110 min of "clear" bird acoustic recordings chosen for final analysis. We assessed the relative importance of tree species richness, six vegetation characteristics, and three topographic characteristics for five acoustic signal complexity indices, and three statistical indices which describe the properties of frequency spectrum, at 25 m and 50 m spatial scales. We found that topographic complexity was the most significant factor influencing acoustic indices. The variation explained by topographic complexity ranged from 13.2 % to 47.2 % for the seven best-fitted models at both spatial scales. Horizontal vegetation characteristics, including tree density and basal area, were also important variables related to acoustic indices. The Acoustic Diversity Index (ADI) and Bioacoustic Index (BIO) were not associated with vegetation or topographic characteristics at either spatial scale. Three out of seven significant relationships between acoustic indices and vegetation or topographic characteristics disappeared as the spatial scale increased from 25 m to 50 m. In contrast, the significant relationship between Acoustic entropy (H), the centroid (CENT) and skewness (SKEW) and topographic complexity remained stable. Our results suggest that both acoustic signal complexity indices and acoustic statistical indices showed a different relationship to vegetation and topographic characteristics in tropical forests, and the strength of these relationship was scale-dependent. This study revealed that topographic complexity might be an effective predictive variable for further ecoacoustic research.

1. Introduction

Ecoacoustics is an interdisciplinary science investigating soundscapes and their association with the environment over various temporal and spatial scales (Pijanowski et al., 2011; Fuller et al., 2015; Farina and Gage, 2017; Dröge et al., 2021). The emerging technology of automatic soundscape recording simultaneously collects extensive data across large areas and long time periods, avoiding observer bias and disturbance to wildlife (Campos-Cerqueira et al., 2016; Shonfeld and Bayne, 2017; Gibb et al., 2019; Do Nascimento et al., 2020; Shamon et al.,

* Corresponding author at: CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming 650223, China.
E-mail addresses: linluxa@xtbg.ac.cn, linluxa@xtbg.ac.cn (L. Lin).

https://doi.org/10.1016/j.ecolind.2022.109229
Received 6 May 2022; Received in revised form 23 July 2022; Accepted 25 July 2022
Available online 1 August 2022
1470-160X/

2021). Despite the data processing challenges (e.g. automated species identification), soundscape monitoring is now being recognized as a cost-effective way to measure biodiversity and assess ecosystem status under environmental change (Wimmer et al., 2013; Gage et al., 2015; Krause and Farina, 2016; Farina and Gage, 2017; Do Nascimento et al., 2020). Although research on soundscapes in terrestrial systems has grown in the last decade, few soundscape studies have been conducted in the wild tropics compared to temperate areas, as sound complexity and biodiversity are higher in the tropical regions than in temperature zones (Myers et al., 2000; Scarpelli et al., 2020).

Multiple acoustic indices have been developed to characterize different facets of soundscapes (Pieretti et al., 2011; Villanueva-Rivera et al., 2011; Depraetere et al., 2012; Gasc et al., 2013; Sueur et al., 2014). Species-specific classification approaches that estimate taxonomic diversity require complex model-training techniques. Compared with it, acoustic indices can be assessed using simple measurements, such as the amplitude, evenness, richness, and heterogeneity of an acoustic community or soundscape. Such metrics are readily accessible on open-source platforms (Sueur et al., 2018a; Villanueva-Rivera and Pijanowski, 2018). Acoustic indices are often used as a method of rapid biodiversity assessment under the assumption that more biodiverse habitats, the more wildlife sounds, and because soundscape can be readily quantified using acoustic metrics (Gage et al., 2001; Qi et al., 2008; Pijanowski et al., 2011; Depraetere et al., 2012; Farina and Gage, 2017).

Previous studies have revealed positive relationships between acoustic indices and faunal species richness (Sueur et al., 2008b; Depraetere et al., 2012; Harris et al., 2016; Bradfer-Lawrence et al., 2020; Dröge et al., 2021). However, this relationship is inconsistent across studies, with some indices showing weak or no associations with faunal diversity (e.g. Gasc et al., 2015; Mammides et al., 2017; Jorge et al., 2018; Moreno-Gómez et al., 2019). The simultaneous use of multiple acoustic indices to obtain complementary soundscape information is recommended (Sueur et al., 2014).

How biophony (biologically produced sounds) varies with vegetation characteristics and topography remains largely unknown (Pijanowski et al., 2011; Farina and Gage, 2017). Relevant research that has investigated the relationships between acoustic indices and vegetation and/or topographic characteristics in forest ecosystems has not yet focused on natural tropical forests in Asia (e.g. Bradfer-Lawrence et al., 2019; Do Nascimento et al., 2020; Mitchell et al., 2020) (Appendix A: Table S1). A few studies (e.g. Myers et al., 2019; Chen et al., 2021; Dröge et al., 2021) have incorporated topography as an environmental variable related to acoustic indices. For example, Chen et al. (2021) found that elevation was the dominant factor influencing acoustic indices. Additionally, the sizes of the study areas where such environmental characteristics have been measured range from 8 m (Turner et al., 2018) to 250 m radius (Machado et al., 2017), potentially rendering comparison between these studies flawed or impossible (Table S1).

Permanent forest dynamics plots have been established worldwide to investigate ecological questions, such as understanding the mechanisms behind species coexistence, forest dynamics, and ecosystem functioning (Hubbell et al., 1999; Anderson-Teixeira et al., 2015; Baker et al., 2017; ForestPlots.net, 2021). The shared census and monitoring protocols of these plots made such biodiversity monitoring platforms an ideal system in which to conduct our research. Here, we investigated the relationship between bird acoustic indices and various environmental factors including vegetation and topographic characteristics in a network of tropical forest dynamics plots in southwest China. We aimed to address the following questions: (1) Do acoustic indices have a stronger relationships with vegetation characteristics, including floristic composition and vegetation structure, than with topographic characteristics? and (2) Do the relationships between acoustic indices and plot-scale vegetation/topographic variables weaken or even disappear as the spatial scale increases?

2. Materials and methods

2.1. Study site

This work was conducted in Xishuangbanna Dai Autonomous Prefecture (21°08′–22°36′ N, 99°56′–101°50′ E) in southwest China, bordering Laos to the south and Myanmar to the southwest. The Xishuangbanna region has a typical monsoon climate with a mean annual temperature of 15.1–21.7 ℃ and mean annual precipitation of 1193–2491 mm (Cao et al., 2006). The region contains the largest and northernmost tropical rain forest in China, and more than 80 % of the flora in this region belongs to tropical genera and 32.8 % are endemic to tropical Asia (Zhu et al., 2006). Nine research sites located within either the Xishuangbanna National Nature Reserve or Nabanhe National Nature Reserve were used in our study (Fig. 1). We selected 1–7 forest dynamics plots per research sites, resulting in a total of 22 plots (Appendix A: Table S2). The minimum distance between research sites was 3900 m and the distance between plots within one site ranged from 250 to 1360 m to avoidance sampling overlapping soundscape. All plots were 1 ha in area except for BBTD (1.44 ha) and BBWW (1.12 ha). The average elevation of the 22 forest plots ranged from 549.96 to 1705.85 m above sea level.

2.2. Soundscape monitoring

2.2.1. Soundscape recordings

Previous survey of this region indicated that bird activity peaks from sunrise to late morning. Song Meter SM4 recorders (Wildlife Acoustics Inc., Maynard, USA) were deployed for at least one month in each plot from June 28th to September 13rd, 2018. Acoustic recordings were collected three times every day from sunrise to late morning (7–10 am) in an intervals of 10 min (i.e. 10-min on, 50-min off) (e.g. Ross et al., 2021) (Appendix A: Table S2). Each weatherproof recorder was equipped with an omni-directional microphone. Signals were sampled at 441 kHz with 16-bits digitization. Sound fragments were recorded in wav format and stored on two 16 GB capacity SDHC memory cards for each machine. All recorders were stationed on tree trunks at the height of 2.5–3.0 m in the center of each forest dynamics plot, except in GMS03, where the recorder was placed 20 m away from the center to avoid sound disturbance from a nearby stream (Appendix A: Fig. S1).

2.2.2. Recording pretreatment

We obtained 3126 files of 10 min recordings in total. Due to the absence of human disturbance within the research sites, we are confident that the significant contributions to the soundscape are geophony and biophony. We aim to relate bird acoustic indices to forest plot-scale environmental variables, to exclude undesired sound from the audio files besides bird, all the recordings were previewed aurally and visually through waveform and spectrogram using Kaleidoscope (v5.4.2) (Wildlife Acoustics Inc., Maynard, USA). As previous studies revealed, geophonic sources, such as rainfall and wind, are common in the rainy season, and recordings also capture biophony from cicadas and frogs in addition to the target bird taxa (Bradfer-Lawrence et al., 2019; Chen et al., 2021) (Appendix A: Fig S2-S4). 911 relatively "clear" bird acoustic recordings were included in the final analysis (Appendix A: Fig. S5; Appendix B).

2.3. Acoustic indices

We calculated eight acoustic indices for each 10-minute recording, including five signal complexity indices, and three statistical indices widely used in ecoacoustic research. Moreover, their relationship with vegetation, topographic characteristics or both combined was revealed by previous studies (Appendix A: Table S1).

The Acoustic Complexity Index (ACI) focuses on the intensity variations in the amplitude between succeeding time frames for a specific

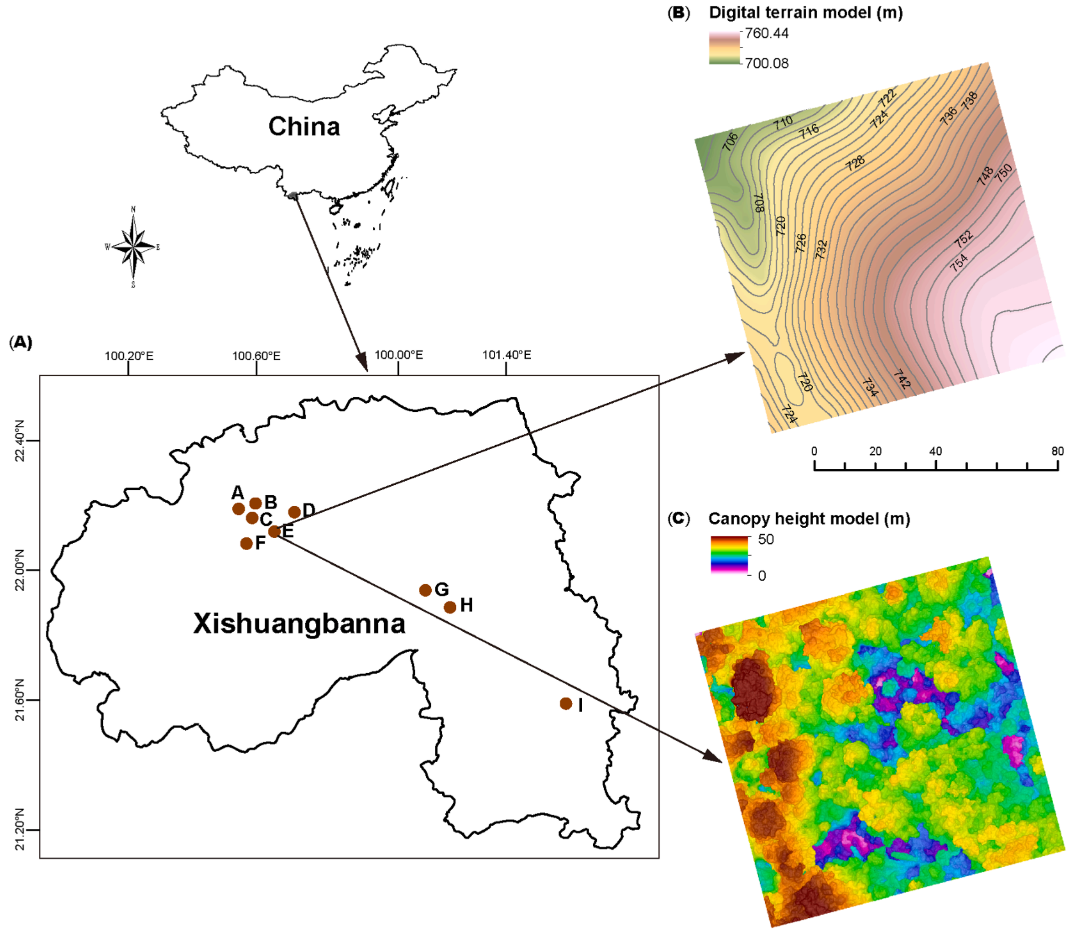

Fig. 1. Location of the nine research sites (A), digital terrain model (DTM) (B) and canopy height model (CHM) (C) of the 1-ha tropical forest dynamics plot CCHS in Xishuangbanna, southwest China.

frequency bin (Pieretti et al., 2011). The Acoustic Diversity Index (ADI) is calculated by dividing the spectral range of the spectrogram into frequency bins and taking the proportion of the signal energy in each bin above a threshold. The ADI is the result of the Shannon index applied to these bins (Villanueva-Rivera et al., 2011). The Acoustic Evenness Index (AEI) is related to the ADI, but uses the Gini coefficient to obtain the distribution of the different frequency bins (Villanueva-Rivera et al., 2011). The Bioacoustic Index (BIO) is calculated as the area under each curve including all frequency bands associated with the dB value that was greater than the minimum dB value for each curve (Boelman et al., 2007). Acoustic entropy (H) quantifies sound intensity variation across time and frequency. It is calculated as the product of the spectral entropy and the temporal entropy of the signal (Sueur et al., 2008b). The minimum frequency for the *ACI* calculation was set to 500 Hz and the maximum frequency to 12 kHz. The minimum frequency for the BIO calculation was set to 500 Hz, as we noticed that the frequency of bird species, such as Megalaimoidea, ranges from 500 to 1800 Hz. Other parameters used in the calculation of the signal complexity indices were set to default values provided in the R package soundecology (Villanueva-Rivera and Pijanowski, 2018).

The statistical indices describe statistical properties of a frequency spectrum, such as mean frequency and median frequency. The three frequency spectrum statistical indices were: median frequency of the upper half of the spectrum (third quartile: TQ), average frequency weighted by amplitude (centroid: CENT), and asymmetry of signals in the spectrum (skewness: SKEW), they were calculated with the R package seewave (Sueur et al., 2008a).

2.3.1. Explanatory variables

2.3.1.1. Vegetation characteristics. Freestanding woody stems $\geq$ 1 cm diameter at 130 cm from the ground (DBH: diameter at breast height) were measured, mapped, tagged, and identified in all plots, following the same standardized census protocol (Condit, 1998). We extracted tree census data of a circle surrounding the autonomous recorders with a 25 m and 50 m radius. In addition to tree species richness, we estimated horizontal and vertical vegetation characteristics for each location. Tree density was estimated as the total number of tree individuals recorded within the selected circular plot. Basal area was calculated as the total area of all living trees at breast height. Tree size variation was estimated as the ratio of the standard deviation to the average DBH value of all living stands within the circular plot.

Vertical vegetation characteristics were obtained based on aerial photogrammetry within a 25 m and 50 m radius of the recorders. The digital surface model (DSM) was surveyed with a Tarot T960 drone (TAROT, Wenzhou, China) equipped with a NEX 5 T camera (SONY Inc., Tokyo, Japan) from 2015 to 2017. We kept the flying height at 160–400 m depending on the elevational range for different forest dynamics plots. The average overlap of orthophotos was over 80 %, with a pixel size of 2.4–5.5 cm. The highest elevation in a 1 m grid was used to build the DSM model in 1 m resolution by SAGA GIS 3.0 (https://www.saga-gis.org). Based on the canopy height model (CHM) derived by subtracting the digital terrain model (DTM) from the DSM, we calculated three vertical vegetation characteristics at both the 25 and 50 m radius scales.

Canopy height was calculated as the mean value of canopy height with 1 m resolution. The vertical distribution ratio (VDR) was calculated with the equation: VDR = (HTmax-HTmed)/HTmax, where HTmax and HTmed are the maximum and median values of canopy height within the circular plot (Goetz et al., 2007; Zhang et al., 2016). Areas with a dense canopy and sparse understory tended to exhibit a low VDR. Areas with a more even vertical biomass distribution showed larger values close to 1. We quantified canopy closure by the percentage of pixels with a height value of more than 10 m (Zhang et al., 2016). The values of canopy closure ranged from 0 to 100 with higher values indicating a closed canopy and lower values indicating an open canopy.

2.3.2. Topography

Three topographic characteristics were obtained for square forest plots of 50 × 50 m and 100 × 100 m at each plot, with the recorders located at the center. Elevation was calculated as the mean elevation of the four corners. The 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; Baldeck et al., 2013). Topographic complexity was calculated with the equation: complexity = As/Ap, where As is the total surface area and Ap is the projected area of the plot (Ren et al., 2019).

2.4. Statistical analyses

The acoustic indices and explanatory variables were all scaled and centered. Moran's I autocorrelation coefficient was calculated using an inverted distance matrix between all plots with the R package ape (Paradis and Schliep, 2019). This was done to check whether the acoustic indices of the 22 sampled plots were spatial independent.

We conducted linear mixed models (LMMs) for the eight acoustic indices to investigate their relationship with the vegetation and topographic characteristics using the R package lme4 (Bates et al., 2015). Within each model, the plot and recording month were treated as random effects. Models were fit independently at the 25 and 50 m scales considering the distance decay of sound in the dense tropical forest and refer to former research (Appendix A: Table S1). The 25 m scale models included all 911 recordings from the 22 plots, while the 50 m scale models included only 20 plots due to the absence of explanatory variables for the GMS03 and BBWW plots, resulting in 828 recordings for the following analyses at the 50 m scale (Appendix A: Table S2 and Appendix B).

We checked for multi-collinearity of explanatory variables using the R package car (Fox and Weisberg, 2019). Canopy height and canopy closure were excluded from the 25 m scale models. In contrast, canopy height, canopy closure, and species richness were excluded at 50 m scale models due to variance inflation factors exceeding 10.

We used the dredge function from the package MuMIn (Bartoń, 2020), which produces models with all possible combinations of the eight and seven fixed explanatory variables ($2^8 = 256$ and $2^7 = 128$, respectively). The interactions between these fixed variables were not included in consideration of overfitting. Model selection was performed using the corrected Akaike information criteria (AICc; Burnham and Anderson, 2004). Models were considered similar if ΔAICc < 2 (Burnham and Anderson, 2004). We calculated the conditional and marginal R^2 values of the fitted models, and the individual contribution of each fixed effect with the packages MuMIn and r2glmm (Jaeger, 2017).

3. Results

With all recordings at both spatial scales, tree species richness, tree size variation, vertical distribution ratio, slope, and elevation were not related to any acoustic indices in the best-fitted models (Table 1 and Appendix A: Table S3). The conditional R^2 of the fitted models ranged from 0.3466 to 0.7607, while the marginal R^2 of the significant fixed effects of the fitted models ranged from 0.077 to 0.472 (Table 1 and Appendix A: Table S4). Tree density was a vital vegetation characteristic at the 25 m scale, as it was significantly related to ACI and TQ. The basal area was related considerably to ACI at the 25 m and 50 m scales. Topographic complexity was the most crucial topographic factor significantly related to acoustic indices at both the 25 m and 50 m scales. H, CENT, and SKEW had a consistent significant relationships with topographic complexity at both spatial scales. In contrast, the significant relationship between AEI and topographic complexity, and the relationship between ACI/TQ and tree density, disappeared at the 50 m scale. Three out of seven significant relationships between acoustic indices and vegetation and topographic characteristics diminished or even disappeared from 25 m to 50 m.

Moran's I autocorrelation coefficients indicated that our sample plots had an independent sampling unit based on the average value of the acoustic indices (Appendix A: Table S5) for the 22 sample plots (Appendix A: Table S6). However, spatial autocorrelation was found for six out of eight indices with all 911 recordings (Appendix A: Table S6) confirming the conservativeness of the soundscape within the selected

Table 1
The results of LMMs to detect the influence of vegetation and topographic characteristics on acoustic indices with all recordings selected at the 25 m and 50 m scales in tropical forests in Xishuangbanna China. Bolded coefficients represent variables that have a significant effect on the model. R^2C are the conditional R^2 of the fitted models.

25 m scale	Intercept	Species richness	Tree density	Basal area	Size variation	Vertical distribution ratio	Slope	Elevation	Topographic complexity	AIC	R^2C
ACI	−0.1087	-	**0.2731**	**-0.3817**	-	-	-	-	-	1284.216	0.3466
ADI[a]	−0.0738	-	-	-	-	-	-	-	-	1135.015	0.6418
AEI	0.0714	-	-	-	-	-	-	-	**-0.3764**	1026.644	0.715
BIO[a]	−0.0054	-	-	-	-	-	-	-	-	1241.39	0.4553
H	0.0288	-	-	-	-	-	-	-	**0.5611**	871.358	0.7607
TQ	0.0704	-	**-0.3305**	-	-	-	-	-	-	1177.381	0.5325
CENT	0.0000	-	-	-	-	-	-	-	**0.4108**	1095.499	0.6046
SKEW	−0.0228	-	-	-	-	-	-	-	**-0.3879**	1194.92	0.4421
50 m scale	**Intercept**		**Tree density**	**Basal area**	**Size variation**	**Vertical distribution ratio**	**Slope**	**Elevation**	**Topographic complexity**	**AIC**	**R^2C**
ACI	−0.0949		-	**-0.3143**	-	-	-	-	-	1182.5	0.3246
ADI[a]	−0.0935		-	-	-	-	-	-	-	1080.905	0.5979
AEI[a]	0.0482		-	-	-	-	-	-	-	1039.357	0.625
BIO[a]	0.0383		-	-	-	-	-	-	-	1168.67	0.3659
H	0.0248		-	-	-	-	-	-	**0.5197**	854.913	0.7205
TQ[a]	0.0431		-	-	-	-	-	-	-	1109.626	0.4816
CENT	0.0029		-	-	-	-	-	-	**0.3128**	1064.298	0.5277
SKEW	0.0139		-	-	-	-	-	-	**-0.4445**	1086.11	0.4382

[a] : NULL model was top performing model for the acoustic indices.

forest dynamics plot. The Pearson correlation coefficient of the eight and five explanatory variable pairs exceeded 0.6 for the two spatial scales, respectively (Fig. 2).

4. Discussion

Multiple acoustic indices can discriminate the soundscape of different habitat types related to vegetation characteristics (e.g. Fuller et al., 2015; Retamosa Izaguirre et al., 2021; Do Nascimento et al., 2020). However, the relationship between acoustic indices and topography was rare (but see Dröge et al., 2021; Chen et al., 2021), and the variability of this relationship at different spatial scale in the same mature protected forest research system has never been studied. In this study, we investigated the relationship between acoustic indices and vegetation and topographic characteristics in a network of tropical forest dynamics plots at two spatial scales. Our results revealed that topographic complexity and tree density were significantly related to several acoustic indices selected.

4.1. Acoustic indices and vegetation characteristics

The vegetation structure was related to bird species richness (MacArthur, 1964; Batáry et al., 2014., Basile et al., 2021). Our results confirmed a significant relationship between vegetation structure and acoustic indices but not between tree species richness and any acoustic indices. Chen et al. (2021) and Turner et al. (2018) found that tree species richness showed positive and negative relationships with H and AEI, respectively. The selected soundscape could cause a disparity, as recordings containing biophony emitted by other fauna (mainly insects) were excluded from our study.

Bird species diversity was usually positively influenced by habitat heterogeneity, particularly in forests, as higher complexity in vegetation structure tends to provide more resources and nesting sites (Tews et al., 2004). In our study, tree density was positively correlated to ACI and negatively correlated to TQ in the best models at the 25 m scale. As ACI measures the variation in sound intensity over time and frequency and TQ measures the median frequency of the upper half of the spectrum, we can infer that forests with dense plantations hold complex soundscapes (unevenly distributed sound across frequency and time), and lower frequencies of the upper half of the spectrum. Tree density was previously found to be negatively related to ACI (Turner et al., 2018) and ADI (Hao et al., 2021) or neutral to any selected acoustic indices (Chen et al., 2021). Plot-level tree basal area was negatively associated with ACI in the work by Dröge et al. (2021). We also found that the basal area was negatively related to ACI at both spatial scales in our study. The basal area was positively related to canopy height and canopy closure at both spatial scales (Pearson's $r > 0.62$, Fig. 2). Higher basal area implied bigger trees and mature/old forests located far from the forest borders and disturbances. The negative relationship with ACI indicated evenly distributed sound intensity in the mature tropical forests in the study region. The third horizontal vegetation characteristic, tree size variation, had no relationship with acoustic indices at either scale.

As an essential indicator of habitat heterogeneity, vertical vegetation structure has been found to be closely related to acoustic indices (Pekin et al., 2012; Do Nascimento et al., 2020; Hao et al., 2021). The vertical distribution ratio had no relationship with any acoustic indices. Meanwhile, the model fitting did not include canopy height and canopy closure due to variance inflation factors. The canopy height was highly correlated with the basal area (Pearson's $r > 0.76$ at both spatial scales, Fig. 2). As a result, canopy height could be related to ACI, but further work is needed to confirm this.

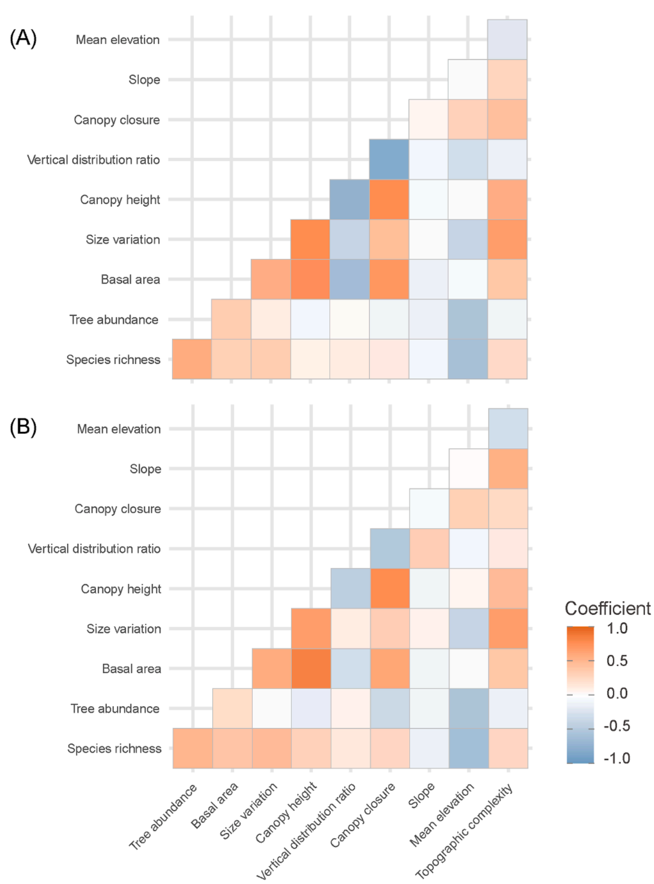

Fig. 2. Pearson correlation coefficient of the 10 vegetation and topographic characteristics at the 25 m (A) and 50 m (B) scales.

4.2. Acoustic indices and topography characteristics

Bird species richness was correlated with multiple factors, such as climate, geometric constraints, and food availability along elevational gradients (McCain, 2009; Price et al., 2014; He et al., 2019). To the best of our knowledge, elevation has been considered a predictor of acoustic indices in a few studies (Appendix A: Table S1), Chen et al. (2021) found that elevation was significantly related to ADI, AEI, and H. In our study, elevation was unrelated to any of the selected acoustic indices. The inconsistency could result from more extensive range of elevation of the forest plots studied by Chen et al. (1526 m) compared with the our study (1078 m), and large latitudinal range of nearly 4° in Chen et al. (21°51′ to 25°36′ N), compared to less than 1° in our study.

Topographic variability, such as slope, convexity, and roughness, are important indicators of habitat heterogeneity. Topography variability has been revealed as a determinant of bird distribution, especially in tropical forests across hilly regions (Davies et al., 2007; Ribon et al., 2021). Landscape-scale topographic roughness negatively affects ACI and BIO in a grassland ecosystem (Shamon et al., 2021). Forest plot-level topographic complexity was first considered in our study. Four out of eight acoustic indices at the 25 m scale and three out of eight acoustic indices at the 50 m scale were significantly related to topographic complexity. Forest plots with high topographic complexity tend to hold soundscapes with little variation in sound intensities across frequency bands at both spatial scales.

The marginal R^2 value of topographic complexity for the seven fitted models ranged from 0.185 to 0.472 (Appendix A: Table S4), indicating that topographic features were a crucial environmental driver of acoustic indices. Linear mixed models without topographic complexity showed a significant relationships between vegetation characteristics and the remaining acoustic indices (Appendix A: Table S7). Slope and SKEW also strongly correlated with the 25 m scale but this relationship disappeared at the 50 m scale. High topographic variability was previously believed to be correlated with high bird diversity. However, as previously discussed, other studies failed to confirm the relationship between measurements of diversity from bird surveys and species identification from an autonomous recording or acoustic indices (e.g. Hutto and Stutzman, 2009; Mammides et al., 2017). Additionally, Mammides et al. (2021) found that higher species richness could lead to higher acoustic evenness. Our research could provide evidence to support this conclusion. Meanwhile, our study may reconfirm the importance of acoustic diversity in the biodiversity assessment (Sueur et al., 2008b; Pijanowski et al., 2011).

4.3. Spatial dependence of the relationship between acoustic indices and vegetation/topography

Sound propagation is affected by several factors such as distance, barriers, and air absorption (Embleton, 1996; Tarrero et al., 2008). It is believed that closed habitats degrade signals more than open habitats. The relationship between vegetation/topography and acoustic indices was investigated at two spatial scales for the first time in dense tropical forest. As expected, nearly half of the significant relationships disappeared with increasing the spatial scale, confirming the scale-dependence of these relationship.

ADI and BIO showed no relationship with vegetation and topographic characteristics we measured. Similar significant relationships between vegetation and topographic characteristics and ACI and AEI were found at both spatial scales, suggesting that they have a stable correlation with vegetation or topographic characteristics in the tropical forest. Do Nascimento et al. (2020) reported that acoustic statistical indices were better than signal complexity indices at identifying habitat-specific soundscapes for six natural and two human-modified habitats. In our study in an Asian tropical forests, both acoustic statistical and signal complexity indices showed a relationship with vegetation structure at both spatial scales. We inferred that habitat type was also an important driver for the relationship between vegetation characteristics and acoustic indices.

5. Conclusions

Thanks to the availability of plot-scale vegetation characteristics and detailed topographic information, the spatial dependence of the relationship between acoustic indices, vegetation, and topographic characteristics was revealed in the current sudy. Our study system found ACI and TQ to be significantly related to vegetation structure characteristics, thus, the two indices could be used as an indication of deforestation and tropical forest succession in future research. Topographic complexity was another important variable for half of the selected acoustic indices. Forest plots with high topographic complexity tend to hold soundscapes with evenly distributed sound intensity at both spatial scales. Further investigation should be dedicated to fully understanding the mechanisms underlying the correlation between acoustic indices and sound characteristics (Shamon et al., 2021). Our findings indicate the importance of topographic complexity to acoustic indices and that topographic complexity should be considered in future ecoacoustic studies in other ecosystems.

Funding

This study was supported by the National Natural Science Foundation of China (31971443), the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB31000000) and Yunnan Fundamental Research Projects (202001AT070111).

CRediT authorship contribution statement

Xuelian He: Conceptualization, Funding acquisition, Investigation, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Yun Deng:** Data curation, Writing – review & editing. **Anran Dong:** Investigation, Writing – review & editing. **Luxiang Lin:** Funding acquisition, Resources, Methodology, 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.

Data availability

Data will be made available on request.

Acknowledgments

We would like to thank National Forest Ecosystem Research Station at Xishuangbanna, Xishuangbanna National Nature Reserve and Nabanhe National Nature Reserve for providing logistical support. We thank Jiu Ma and Rongzhi Li for assisting this work in the field. We also thank two anonymous reviewers for their valuable comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109229.

References

Anderson-Teixeira, K.J., Davies, S.J., Bennett, A.C., Gonzalez-Akre, E.B., Muller-Landau, H.C., Joseph Wright, S., Abu Salim, K., Almeyda Zambrano, A.M., Alonso, A., Baltzer, J.L., Basset, Y., Bourg, N.A., Broadbent, E.N., Brockelman, W.Y., Bunyavejchewin, S., Burslem, D.F.R.P., Butt, N., Cao, M., Cardenas, D., Chuyong, G.B., Clay, K., Cordell, S., Dattaraja, H.S., Deng, X., Detto, M., Du, X., Duque, A., Erikson, D.L., Ewango, C.E.N., Fischer, G.A., Fletcher, C., Foster, R.B., Giardina, C.P., Gilbert, G.S., Gunatilleke, N., Gunatilleke, S., Hao, Z., Hargrove, W.W., Hart, T.B., Hau, B.C.H., He, F., Hoffman, F.M., Howe, R.W., Hubbell, S.P., Inman-Narahari, F.M., Jansen, P.A., Jiang, M., Johnson, D.J., Kanzaki, M., Kassim, A.R., Kenfack, D., Kibet, S., Kinnaird, M.F., Korte, L., Kral, K., Kumar, J., Larson, A.J., Li, Y., Li, X., Liu, S., Lum, S.K.Y., Lutz, J.A., Ma, K., Maddalena, D.M., Makana, J.-R., Malhi, Y., Marthews, T., Mat Serudin, R., McMahon, S.M., McShea, W.J., Memiaghe, H.R., Mi, X., Mizuno, T., Morecroft, M., Myers, J.A., Novotny, V., de Oliveira, A.A., Ong, P.S., Orwig, D.A., Ostertag, R., den Ouden, J., Parker, G.G., Phillips, R.P., Sack, L., Sainge, M.N., Sang, W., Sri-ngernyuang, K., Sukumar, R., Sun, I.-F., Sungpalee, W., Suresh, H.S., Tan, S., Thomas, S.C., Thomas, D.W., Thompson, J., Turner, B.L., Uriarte, M., Valencia, R., Vallejo, M.I., Vicentini, A., Vrška, T., Wang, X., Wang, X., Weiblen, G., Wolf, A., Xu, H., Yap, S., Zimmerman, J., 2015. CTFS-Forest GEO: a worldwide network monitoring forests in an era of global change. Glob. Chang. Biol. 21 (2), 528–549.

Baker, T.R., Pennington, R.T., Dexter, K.G., Fine, P.V., Fortune-Hopkins, H., Honorio, E.N., Huamantupa-Chuquimaco, I., Klitgård, B.B., Lewis, G.P., de Lima, H.C., Ashton, P., Baraloto, C., Davies, S., Donoghue, M.J., Kaye, M., Kress, W.J., Lehmann, C.E.R., Monteagudo, A., Phillips, O.L., Vasquez, R., 2017. Maximising synergy among tropical plant systematists, ecologists, and evolutionary biologists. Trends. Ecol. Evol. 32 (4), 258–267. https://doi.org/10.1016/j. tree.2017.01.007.

Baldeck, C.A., Harms, K.E., Yavitt, J.B., John, R., Turner, B.L., Valencia, R., Navarrete, H., Davies, S.J., Chuyong, G.B., Kenfack, D., Thomas, D.W., Madawala, S., Gunatilleke, N., Gunatilleke, S., Bunyavejchewin, S., Kiratiprayoon, S., Yaacob, A., Nur Supardi, M.N., Dalling, J.W., 2013. Soil resources and topography shape local tree community structure in tropical forests. Proc. R. Soc. B Biol. Sci. 280 (1753), 20122532. https://doi.org/10.1098/rspb.2012.2532.

Bartoń, K., 2020. MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn.

Basile, M., Storch, I., Mikusiński, G., 2021. Abundance, species richness and diversity of forest bird assemblages - The relative importance of habitat structures and landscape context. Ecol. Indic. 133, 108402 https://doi.org/10.1016/j.ecolind.2021.108402.

Batáry, P., Fronczek, S., Normann, C., Scherber, C., Tscharntke, T., 2014. How do edge effect and tree species diversity change bird diversity and avian nest survival in Germany's largest deciduous forest? For. Ecol. Manag. 319, 44–50. https://doi.org/10.1016/j.foreco.2014.02.004.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Boelman, N.T., Asner, G.P., Hart, P.J., Martin, R.E., 2007. Multi-trophic invasion resistance in Hawaii: bioacoustics, feld surveys, and airborne remote sensing. Ecol. Appl. 17 (8), 2137–2144. https://doi.org/10.1890/07-0004.1.

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., Zamora-Gutierrez, V., 2019. Guidelines for the use of acoustic indices in environmental research. Methods Ecol. Evol. 10 (10), 1796–1807.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociol. Meth. Res. 33 (2), 261–304. https://doi.org/10.1177/0049124104268644.

Campos-Cerqueira, M., Aide, T.M., Jones, K., 2016. Improving distribution data of threatened species by combining acoustic monitoring and occupancy modelling. Methods Ecol. Evol. 7 (11), 1340–1348. https://doi.org/10.1111/mee3.2016.7.issue-1110.1111/2041-210X.12599.

Cao, M.X., Zou, M., Warren, M., Zhu, H., 2006. Tropical forests of Xishuangbanna. China. Biotropica. 38 (3), 306–309. https://doi.org/10.1111/j.1744-7429.2006.00146.x.

Chen, Y., Luo, Y., Mammides, C., Cao, K., Zhu, S., Goodale, E., 2021. The relationship between acoustic indices, elevation, and vegetation, in a forest plot network of southern China. Ecol. Indic. 129, 107942 https://doi.org/10.1016/j.ecolind.2021.107942.

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

Davies, R.G., Orme, C.D.L., Storch, D., Olson, V.A., Thomas, G.H., Ross, S.G., Ding, T.S., Rasmussen, P.C., Bennett, P.M., Owens, I.P.F., Blackburn, T.M., Gaston, K.J., 2007. Topography, energy and the global distribution of bird species richness. Proc. R. Soc. B. 274, 1189–1197. https://doi.org/10.1098/rspb.2006.0061.

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 (1), 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.

Embleton, T.F., 1996. Tutorial on sound propagation outdoors. J. Acoust. Soc. Am. 100 (1), 31–48. https://doi.org/10.1121/1.415879.

Farina, A., Gage, S.H., (Eds.) 2017. Ecoacoustics: The ecological role of sounds. Wiley. Doi: 10.1002/9781119230724.

ForestPlots.net, Blundo, C., Carilla, J., Grau, R., Malizia, A., Malizia, L., Osinaga-Acosta, O., Bird, M., Bradford, M., Catchpole, D., Fordd, A., Graham, A., Hilbert, D., Kemp, J., Laurance, S., Laurance, W., Ishida, F.Y., Marshall, A., ... Tran, H.D., 2021. Taking the pulse of Earth's tropical forests using networks of highly distributed plots. Biol. Conserv. 260, 108849.

Fox, J., & Weisberg, S., 2019. An R Companion to Applied Regression, Third Edition. Thousand Oaks CA: Sage. URL: https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Fuller, S., Axel, A.C., Tucker, D., Gage, S.H., 2015. Connecting soundscape to landscape: Which acoustic index best describes landscape configuration? Ecol. Indic. 58, 207–215. https://doi.org/10.1016/j.ecolind.2015.05.057.

Gage, S.H., Napoletano, B.M., Cooper, M.C., 2001. Assessment of ecosystem biodiversity by acoustic diversity indices. J. Acoust. Soc. Am. 109 (5), 2430. https://doi.org/10.1121/1.4744597.

Gage, S.H., Joo, W., Kasten, E.P., Fox, J., Biswas, S., 2015. In: Acoustic Observations in Agricultural Landscapes, in the Ecology of Agricultural Ecosystems: Long-Term Research on the Path to Sustainability. Oxford University Press, New York, pp. 360–377.

Gasc, A., Sueur, J., Jiguet, F., Devictor, V., Grandcolas, P., Burrow, C., Depraetere, M., Pavoine, S., 2013. 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., Pavoine, S., Lellouch, L., Grandcolas, P., Sueur, J., 2015. Acoustic indices for biodiversity assessments: analyses of bias based on simulated bird assemblages and recommendations for field surveys. Biol. Conserv. 191, 306–312. https://doi.org/10.1016/j.biocon.2015.06.018.

Gibb, R., Browning, E., Glover-Kapfer, P., Jones, K.E., Börger, L., 2019. Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. Methods Ecol. Evol. 10 (2), 169–185.

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 (3), 254–263. https://doi.org/10.1016/j.rse.2006.11.016.

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.

Harris, S.A., Shears, N.T., Radford, C.A., Reynolds, J., 2016. Ecoacoustic indices as proxies for biodiversity on temperate reefs. Methods Ecol. Evol. 7 (6), 713–724.

Hao, Z., Wang, C., Sun, Z, Zhao, D., Sun, B., Wang, H., van den Bosch, C.K., 2021. Vegetation structure and temporality influence the dominance, diversity, and composition of forest acoustic communities. For. Ecol. Manage. 482, 118871. https://doi.org/10.1016/j.foreco.2020.118871.

He, X., Wang, X., DuBay, S.H., Reeve, A., Alström, P., Ran, J., Liu, Q., Wu, Y., 2019. Elevational patterns of bird species richness on the eastern slope of Mt. Gongga, Sichuan Province, China. Avian Res. 10, 1. https://doi.org/10.1186/s40657-018-0140-7.

Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S. J., Loo de Lao, S., 1999. Light gap disturbances, recruitment limitation and tree diversity in a Neotropical forest. Science 283, 554–557. https://doi.org/10.1126/science.283.5401.554.

Hutto, R.L., Stutzman, R.J., 2009. Humans versus autonomous recording units: a comparison of point-count results. J. Field Ornithol. 80 (4), 387–398. https://doi.org/10.1111/j.1557-9263.2009.00245.x.

Jaeger, B., 2017. R2glmm: computes R squared for mixed (multilevel) models. R package version, 0.1.2.

Jorge, F.C., Machado, C.G., da Cunha Nogueira, S.S., Nogueira-Filho, S.L.G., 2018. The effectiveness of acoustic indices for forest monitoring in Atlantic rainforest fragments. Ecol. Indic. 91, 71–76. https://doi.org/10.1016/j.ecolind.2018.04.001.

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.

MacArthur, R.H., 1964. Environmental factors affecting bird species diversity. Am. Nat. 98 (903), 387–397. http://www.jstor.org/stable/2459142.

Machado, R.B., Aguiar, L., Jones, G., 2017. Do acoustic indices reflect the characteristics of bird communities in the savannas of Central Brazil? Landsc. Urban Plan. 162, 36–43. https://doi.org/10.1016/j.landurbplan.2017.01.014.

Mammides, C., Goodale, E., Dayananda, S.K., Luo, K., 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.

Mammides, C., Goodale, E., Dayananda, S.K., Luo, K., Chen, J., 2021. On the use of the acoustic evenness index to monitor biodiversity: A comment on "Rapid assessment of avian species richness and abundance using acoustic indices" by Bradfer-Lawrence et al. (2020) [Ecological Indicators, 115, 106400]. Ecol. Indicat. 126, 107626.

McCain, C.M., 2009. Global analysis of bird elevational diversity. Glob. Ecol. Biogeogr. 18, 346–360. https://doi.org/10.1111/j.1466-8238.2008.00443.x.

Mitchell, S.L., Bicknell, J.E., Edwards, D.P., Deere, N.J., Bernard, H., Davies, Z.G., Struebig, M.J., 2020. Spatial replication and habitat context matters for assessments of tropical biodiversity using acoustic indices. Ecol. Indic. 119, 106717 https://doi.org/10.1016/j.ecolind.2020.106717.

Moreno-Gómez, F.N., Bartheld, J., Silva-Escobar, A.A., Briones, R., Márquez, R., Penna, M., 2019. Evaluating acoustic indices in the Valdivian rainforest, a biodiversity hotspot in South America. Ecol. Ind. 103, 1–8. https://doi.org/10.1016/j.ecolind. 2019.03.024.

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.

Myers, N., Mittermeier, R., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501.

Paradis, E., Schliep, K., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35 (3), 526–528.

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. Landscape Ecol. 27 (10), 1513–1522. https://doi.org/10.1007/s10980-012-9806-4.

Pieretti, N., Farina, A., Morri, D., 2011. A new methodology to infer the singing activity of an avian community: The Acoustic Complexity Index (ACI). Ecol. Indic. 11, 868–873. https://doi.org/10.1016/j.ecolind.2010.11.005.

Pijanowski, B.C., Farina, A., Gage, S.H., Dumyahn, S.L., Krause, B.L., 2011. What is soundscape ecology? An introduction and overview of an emerging new science. Landscape Ecol. 26 (9), 1213–1232. https://doi.org/10.1007/s10980-011-9600-8.

Price, T.D., Hooper, D.M., Buchanan, C.D., Johansson, U.S., Tietze, D.T., Alström, P., Olsson, U., Ghosh-Harihar, M., Ishtiaq, F., Gupta, S.K., Martens, J., Harr, B., Singh, P., Mohan, D., 2014. Niche filling slows the diversification of Himalayan songbirds. Nature 509, 222–225. https://doi.org/10.1038/nature13272.

Qi, J., Gage, S.H., Joo, W., Napoletano, B., Biswas, S., 2008. Soundscape characteristics of an environment: A new ecological indicator of ecosystem health. In: W. Ji (Ed.). In Wetland and Water Resource Modeling and Assessment. CRC Press, New York, NY, USA. pp. 201-211.

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 (8), 1155–1167. https://doi.org/10.1111/geb.12922.

Retamosa Izaguirre, M.I., Sequeira, D.S., Barrantes-Madrigal, J., Parallada, M.S., Ramírez-Alán, Ó., 2021. Vegetation, bird and soundscape characterization: A case study in Braulio Carrillo National Park, Costa Rica. Biota Colomb. 22, 57–73. https://doi.org/10.21068/C2021.V22N01A04.

Ribon, R., Dos Santos, L., De Marco, P., Marini, M., 2021. Topography as a determinant of bird distribution in secondary Atlantic Forest fragments. J. Trop. Ecol. 37 (5), 228–234. https://doi.org/10.1017/S0266467421000328.

Ross, S.-J., Friedman, N.R., Yoshimura, M., Yoshida, T., Donohue, I., Economo, E.P., 2021. Utility of acoustic indices for ecological monitoring in complex sonic environments. Ecol. Indic. 121, 107114 https://doi.org/10.1016/j.ecolind.2020.107114.

Scarpelli, M.D., Ribeiro, M.C., Teixeira, F.Z., Young, R.J., Teixeira, C.P., 2020. Gaps in terrestrial soundscape research: it's time to focus on tropical wildlife. Sci. Total Environ. 707, 135403 https://doi.org/10.1016/j.scitotenv.2019.135403.

Shamon, H., Paraskevopoulou, Z., Kitzes, J., Card, E., Deichmann, J.L., Boyce, A.J., McShea, W.J., 2021. Using ecoacoustics metrices to track grassland bird richness across landscape gradients. Ecol. Indic. 120, 106928 https://doi.org/10.1016/j.ecolind.2020.106928.

Shonfeld, J., Bayne, E.M., 2017. Autonomous recording units in avian ecological research: current use and future applications. Avian. Conserv. Ecol. 12, 14. https://doi.org/10.5751/ACE-00974-120114.

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., Pavoine, S., Hamerlynck, O., Duvail, S., Reby, D., 2008b. Rapid acoustic survey for biodiversity appraisal. PLoS One 3 (12), e4065.

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

Tarrero, A.I., Martín, M.A., González, J., Machimbarrena, M., Jacobsen, F., 2008. Sound propagation in forests: a comparison of experimental results and values predicted by the Nord 2000 model. Appl. Acoust. 69, 662–671. https://doi.org/10.1016/j.apacoust.2007.01.007.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x.

Turner, A., Fischer, M., Tzanopoulos, J., Farina, A., 2018. Sound-mapping a coniferous forest-Perspectives for biodiversity monitoring and noise mitigation. PLoS One 13 (1), e0189843.

Villanueva-Rivera, L.J., Pijanowski, B.C., Doucette, J., Pekin, B., 2011. A primer of acoustic analysis for landscape ecologists. Landscape Ecol 26 (9), 1233–1246.

Villanueva-Rivera, L., Pijanowski, B., 2018. Soundecology: Soundscape Ecology. R package version 1.3.3. https://CRAN.R-project.org/package=soundecology.

Wimmer, J., Towsey, M., Planitz, B., Williamson, I., Roe, P., 2013. Analysing environmental acoustic data through collaboration and automation. Futur. Gener. Comput. Syst. 29, 560–568. https://doi.org/10.1016/j.future.2012.03.004.

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. Conservat. 198, 60–69. https://doi.org/10.1016/j.biocon.2016.03.027.

Zhu, H., Cao, M., Hu, H.B., 2006. Geological history, flora, and vegetation of Xishuangbanna, Southern Yunnan, China. Biotropica 38 (3), 310–317. https://doi.org/10.1111/J.1744-7429.2006.00147.x.