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Island biogeography of soundscapes: Island area shapes spatial patterns of avian acoustic diversity

Peng Han[1] | Yuhao Zhao[1] | Yi Kang[1] | Ping Ding[2] | Xingfeng Si[1]

[1]Zhejiang Zhoushan Archipelago Observation and Research Station, Institute of Eco-Chongming, Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China

[2]MOE Key Laboratory of Biosystems Homeostasis & Protection, College of Life Sciences, Zhejiang University, Hangzhou, China

Correspondence
Xingfeng Si, Zhejiang Zhoushan Archipelago Observation and Research Station, Institute of Eco-Chongming, Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China.
Email: sixf@des.ecnu.edu.cn

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Abstract

Aim: The equilibrium theory of island biogeography predicts the positive species–area relationship and the negative species–isolation relationship, resulting in higher species richness on large and close islands. Unlike species richness, soundscape diversity integrates sound from various sources (e.g. biophony, geophony and anthrophony). However, how soundscape diversity varies with island area and isolation still needs to be tested. Here, we explored the island biogeography of bird soundscapes and the determinants of island attributes in shaping bird diversity and soundscape diversity.

Location: Thousand Island Lake, Zhejiang, China.

Taxon: Birds.

Methods: We recorded avian soundscapes by audio recorders and censused bird diversity by line transects on 20 land-bridge islands. We calculated four acoustic indices (acoustic complexity index, bioacoustic index, acoustic evenness index and acoustic entropy index) to assess acoustic richness, evenness and heterogeneity to explore the soundscape diversity of birds. We used multiple linear regressions, spatial autoregressions and piecewise structural equation models to examine the relationships between bird richness and acoustic diversity, and island attributes.

Results: We found positive diversity–area relationships for avian soundscapes. Larger islands had more vocal species and higher habitat diversity, which led to an increment in the richness and unevenness of avian soundscapes on large islands. Acoustic evenness decreased with increasing isolation (distance to the mainland).

Main Conclusions: Soundscapes on large islands are more diverse than those on small islands. Rich acoustic assemblages and heterogeneous habitats promote increased soundscape diversity on islands. Conversely, the lack of vocal contributors, resulting in a decrement in the communication of acoustic signals, can create a lower soundscape diversity on small and remote islands. Our study emphasizes the necessity of examining both species and habitat diversity in island biogeography for better understanding the underlying mechanisms determining biological soundscapes on islands.

KEYWORDS
acoustic index, bird, functional biogeography, island area, island biogeography, isolation, passive acoustic monitoring, soundscape

1 | INTRODUCTION

The equilibrium theory of island biogeography (ETIB) describes a general paradigm on the dynamic equilibrium of island biota based on immigration and local extinction processes (MacArthur & Wilson, 1967). The theory predicts that species richness increases with island area (area effect) and decreases with isolation (isolation effect) (Kohn & Walsh, 1994; MacArthur & Wilson, 1967; Ricklefs & Lovette, 1999). Following these predictions, there is a widespread reduction in species richness on small and remote islands, which may also lead to reduced acoustic signalling if sound-producing species were locally extinct (Krause, 1993; Prugh et al., 2008).

Acoustic signalling (often measured as soundscape diversity) have now received much attention in biogeographical research (Lomolino & Pijanowski, 2021; Robert et al., 2019). One important aspect is that studies have demonstrated that acoustic monitoring is a fast and convenient way to monitor biodiversity because soundscape diversity can act as a proxy for inferring some aspects of biodiversity, such as taxonomic diversity (Buxton et al., 2018; Pieretti et al., 2011; Shamon et al., 2021; Sueur, Pavoine, et al., 2008). However, studies have also questioned the generalization of soundscape diversity representing biodiversity (Fairbrass et al., 2017; Gasc et al., 2015; Ross et al., 2021). Despite the debate, researches focusing on the island biogeography of soundscape diversity are still limited (Lomolino et al., 2015; Pijanowski, 2011; Robert et al., 2019). Here, we assess the avian soundscapes following ETIB in a subtropical land-bridge island system.

Generally, the loss of sound-producing species will release acoustic spaces (i.e. the acoustic niche) and alter the overall soundscape diversity on islands. However, for island biota, species richness and soundscape diversity may not be precisely correlated. The potential difference between them may be the result of acoustic data that included non-target information and/or background noises, such as those from insects and amphibians, and wind, water and microphone self-noises (Morrison et al., 2021; Pijanowski et al., 2011; Wilkins et al., 2013). Therefore, more species on an island does not imply higher soundscape diversity. In island biogeography studies, the positive species–area and negative species–isolation relationships are widely reported (MacArthur & Wilson, 1967; Ricklefs & Lovette, 1999). However, how the soundscape diversity varies with island area and isolation remain largely unknown.

Island area can directly affect soundscape diversity through area and target effects. Area effect predicts that large islands have lower extinction rates that support higher species richness (MacArthur & Wilson, 1967). Large island can also attract potential colonists that disperse from the mainland to island (i.e. target effects; Johnson, 1980). If an island supports more species, the intensity of competition among species may also be higher. This process is known as 'acoustic niche competition', which may tend to diverge in three dimensions (time, amplitude and frequency) in the vocalization of assemblages on large islands (Krause, 1993; Villanueva-Rivera, 2014; Wells, 2010). For example, amphibians and birds have spatial or temporal differentiations of sound frequencies (Halfwerk & Slabbekoorn, 2009; Villanueva-Rivera, 2014). The acoustic signals of species within communities will occupy species-specific frequency bands to reduce the overlap of signals, which will lead to increased soundscape diversity (Burivalova et al., 2019; Morrison et al., 2021). In addition, island area can also affect soundscape diversity indirectly. Larger islands should have more heterogenous habitats (MacArthur & Wilson, 1967; Stracey & Pimm, 2009), which provide a wide range of acoustic spaces. Specifically, high environmental heterogeneities on islands can provide organisms with more available resources, which may lead to decreased interspecific competition. As biological competition for acoustic spaces decreases, species may evolve a wider range of acoustic niches (Krause, 1993; Robert et al., 2019). Thus, diverse habitats can exhibit high soundscape diversity. As a result, we can observe a positive soundscape diversity–area relationship but it is important to disentangle the direct and indirect (e.g. through habitat diversity) effects of island area on soundscape diversity (Figure 1a).

The geographical distance between island and source pool (e.g. the mainland or nearby islands) is another essential factor that affect the soundscape on islands (i.e. distance effect; Fahrig, 2013; MacArthur & Wilson, 1967; Robert et al., 2019). However, in previous studies, only the acoustic differences between continents and islands were compared (Morinay et al., 2013; Robert et al., 2021).

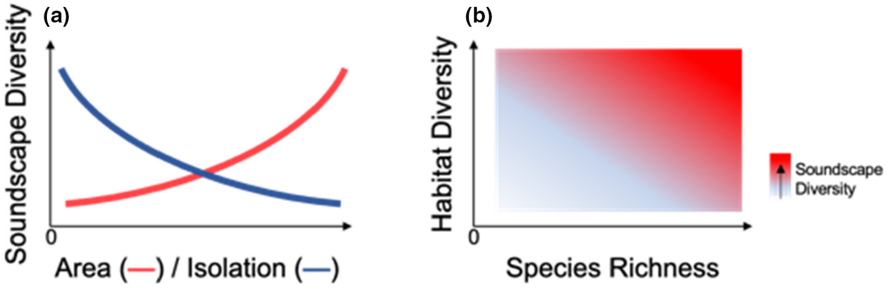

FIGURE 1 Conceptual models illustrating the relationship between island area/isolation and soundscape diversity (a), and possible patterns of soundscape diversity constructed by species richness and habitat diversity (b). According to the equilibrium theory of island biogeography, we predict that soundscape diversity should increase with island area and decrease with isolation. Conversely, species richness and habitat diversity positively shape the soundscape on islands. Colours in (a) indicate island attributes. In (b), the redder color indicates a higher diversity of soundscapes.

These studies found that the vocalization frequency of bird assemblages was lower on islands than in the mainland, yet the acoustic performance of some assemblages (such as acoustic complexity) did not change (Robert et al., 2019). However, to the best of our knowledge, there is no research testing how island isolation modifies the soundscape patterns. It is well known that distance to the mainland (a common measure of isolation) determines the colonization probability of species from continental species pool to an island (Morinay et al., 2013; Robert et al., 2021). With reduced colonization rates, species diversity declines as islands become more isolated (MacArthur & Wilson, 1967). Therefore, the lack of major acoustic contributors may impoverish the soundscapes (MacDonald et al., 2021; Morand, 2000). In addition, only species with high dispersal abilities could reach remote islands (Diamond, 1975; Gillespie & Baldwin, 2010), causing remote islands to possess more similar species composition. The similar species composition in turn can lead to homogenization of soundscape (i.e. similar vocal fauna) on these remote islands (Burivalova et al., 2019; Rappaport et al., 2022). However, for islands surrounded by many other islands far from the mainland, the turnover process of soniferous populations migrating from one island to another may be beneficial for maintaining soundscape diversity (Blumstein & Daniel, 2005; MacArthur & Wilson, 1967; MacDonald et al., 2021). Hence, it is possible for these islands to produce a high diversity of soundscapes because of the high connections between surrounding islands. Therefore, we can predict that soundscape diversity will be lower on remote islands than on less isolated islands (Figure 1a).

Land-bridge islands (i.e. islands that used to be connected to the mainland that were subsequently isolated by rising water) have similar climatic conditions. They may contain various environmental features (e.g. vegetation structure, water conditions and climatic dynamics) that modify the natural soundscape. In addition, these islands were formed within a relatively short period, ensuring that the evolution of acoustic assemblages had negligible effects on results (Farina et al., 2011; Newmark, 1987; Wu et al., 2004). Therefore, land-bridge islands are considered as natural laboratories for studying island biogeography (Whittaker & Fernández-Palacios, 2007). In this study, we chose island soundscapes dominated by bird vocalizations because birds, the common taxa in the studies of ETIB, are also the dominant vocal species on habitat islands (Searcy et al., 2006; Terborgh et al., 1997). It is worth noting that although birds have rich characteristics in the expression of acoustic signals, the acoustic index reflecting the soundscape diversity of birds may be also driven by other vocalization taxa, such as insects and amphibians, and geophony (e.g. wind and rain). Currently, low-cost portable automatic recording devices allow us to simultaneously monitor natural sounds on multiple islands (Morrison et al., 2021; Pijanowski et al., 2011; Shamon et al., 2021). We thus used passive acoustic technology to record bird sounds on 20 land-bridge islands of varying sizes, aiming to ask how island attributes and bird species diversity affect island soundscape diversity. Specifically, we address the following questions: (1) Does soundscape diversity increase with island area and decrease with isolation (distance to the mainland) (Figure 1a)? (2) Despite the effects of island area and isolation, do other island attributes (e.g. habitat diversity) directly or indirectly influence soundscape diversity? (3) How do island attributes and bird diversity jointly affect the soundscape diversity (Figure 1)?

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out in the Thousand Island Lake, eastern China (29°22′–29°50′N, 118°34′–119°15′E). The Lake was formed due to the construction of the Xin'anjiang Dam for the hydropower project. The lake area is approximate 58,000 ha, and there are 1078 islands larger than 0.25 ha when the water level fluctuates to the highest (108 m). This region is in the subtropical monsoon climate zone with hot and humid summers and cold and dry winters. Natural secondary Masson pine forests (*Pinus massoniana*) dominate the islands, and each island contains varying degrees of open habitat and has more than 80% forest coverage (Wu et al., 2004). Since 2002, continuous research of avian ecology has been carried out, including bird diversity and community assembly (Si et al., 2014; 2017), laying a foundation for exploring bird assemblage acoustics.

We selected 20 islands covering the area and isolation gradients in this lake system (Figure 2 and Table S1). The area of selected islands varies from 0.53 to 143.19 ha, and island isolation (distance from the edge of the focal island to the mainland coast) varies from 21.85 to 3712.31 m. Except occasional sounds from local boats in the fishing season, the selected islands are free from human voices, away from road traffic, and factory noises, which provide a purer environment for natural sound (animal sounds) research.

2.2 | Data collection

2.2.1 | Sampling design

We set up transects on study islands to collect soundscapes. To ensure that the number of transect lines was proportional to the natural logarithm of island area, we set up one to four transect lines for each island (e.g. four transects for islands with area > 100 ha, two transects for islands with area between 10 and 100 ha, and one transect for the islands with area < 10 ha) (Schoereder et al., 2004), and we set one to two recording points on each transect. We used the *AudioMoth v1.1.0* detector (Hill et al., 2018) to record the soundscape during birds breeding season on study islands from 4th May to 10th May 2021. The climatic conditions such as precipitation and temperature were relatively stable during the sampling period. On islands larger than 10 ha, we placed two recorders on each transect: one inside the island and the other near the edge of island (the distance from the shore to avoid mixing effects from marginal habitats). The recorders inside the same island were separated more than 150 m apart to avoid overlapped recordings between the devices.

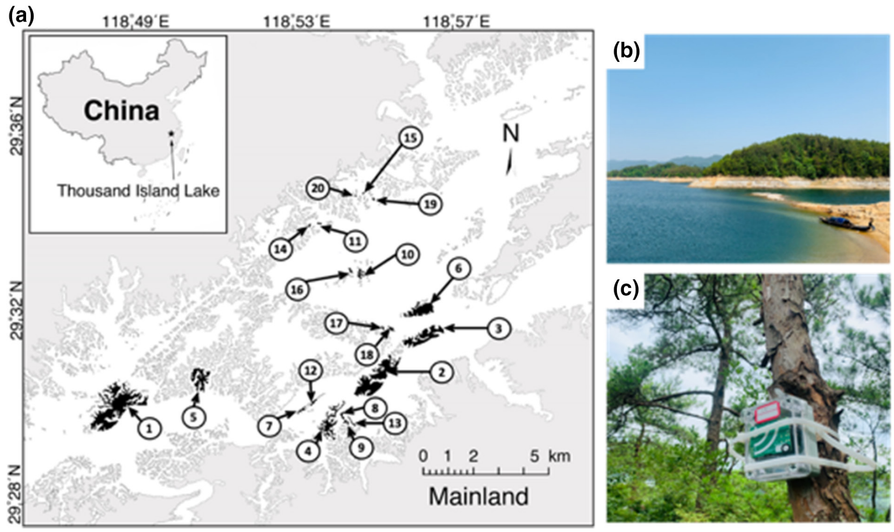

FIGURE 2 (a) Map of the Thousand Island Lake in Zhejiang Province, eastern China. The research sites (20 islands) are numbered in order of decreasing island area and filled in black; the rest of the islands and mainland parts are filled in light grey, while the water surface is filled in white. (b) The landscape of the lake. (c) Photo of the acoustic recorder.

Each recorder was mounted on trees within a suitable waterproof box at a height of 170 cm above ground (Figure 2c). Recorders were set for 48 kHz sampling rate and medium gain level (30.6 dB). All audio files are saved in mono-channel 16-bit WAV format on the 32GB Micro SD cards (SanDisk U1; Hill et al., 2018). The recorders were recording continuously for 3 h at dawn (approximately 05:00–08:00 AM; Bradfer-Lawrence et al., 2020). In this study, we set a total of 46 recorders on 20 islands, resulting in 1260 one-minute recordings per recorder. We manually split the recordings into minutes (i.e. each hour was split into 60 min) and excluded recordings that contained non-target sounds (e.g. boat sounds and thunderstorms) during the analysis.

2.2.2 | Island attributes

We selected four island parameters to assess the composition and variation of the island soundscape diversity. We considered island area (A), distance to the mainland (DM) and distance to the nearest island (DN) (Table S2). To explore the impact of habitat types on island soundscapes, we measured the number of vegetation types on each island, which was defined as *habitat diversity*. Habitat diversity of each island can represent the heterogeneity of the island habitats. In this study, we classified the habitats into seven categories: (1) conifer forest, (2) broadleaf forest, (3) coniferous-broad mixed forests, (4) bamboo groves, (5) shrubs, (6) grasses and (7) farmlands (Zhang et al., 2008). All island attribute parameters were obtained from Si et al. (2014), while habitat diversity was obtained from Wang et al. (2010). More detailed descriptions of each variable are found in Tables S1 and S2.

For comparison, we also conducted bird assemblage surveys on 20 study islands in May 2021 to compare the relationship between bird species diversity and acoustic indices in this system. Bird surveys began half an hour after dawn (around 6 AM) and end at around 11 AM. Surveyors walked each transect at a constant speed of 1–2 km/h during each survey and recorded all birds observed or heard within 50 m of the transect. To remove the systematic survey biases, the same surveyor did not walk the same transect more than twice. A total of nine surveys per each transect were made during the sampling period. Surveys were only done during clear, windless days (Bibby et al., 2000).

2.3 | Data analysis

2.3.1 | Soundscape diversity

To determine the acoustic frequency range for soundscape analyses, we sampled 100 one-minute acoustic recordings (five recordings per island). The amplitude peaks of the soundscape were assessed by plotting the average spectrogram. We found that frequencies between 1.5 and 8 kHz were typical for the vocalizations of birds in our island system (Figure S4). To test whether it was appropriate to use a 1-min recording duration as the normalized length in the soundscape analysis, we ran a sensitivity analysis to test multiple recording durations (30-s, 1-, 5- and 10-min duration). As shown in Figures S5 and S6, the results were quantitively similar, so we used the length of 1 min in the following analyses (Figures S5 and S6). Due to the rapid development of soundscape analyses, a variety of indicators have been proposed. Therefore, we selected four commonly used acoustic metrics for sound clips in this frequency range (frequencies between 1.5 and 8 kHz) to represent the soundscape (Table S7; Shamon et al., 2021; Towsey, 2017; Towsey et al., 2014; Zhao et al., 2019): acoustic complexity index (ACI) (Pieretti et al., 2011), bioacoustic index (BI) (Boelman et al., 2007), acoustic evenness index (AEI) (Villanueva-Rivera et al., 2011) and acoustic entropy index (H) (Sueur, Pavoine, et al., 2008). These four indicators are designed to reflect the richness (ACI and BI), evenness (AEI) and heterogeneity (H) of island soundscapes (Morrison et al., 2021).

ACI measures the variability of sound intensities, which is calculated as the absolute difference between two adjacent values of intensity in a single frequency bin and the sum of all the absolute differences in 1 min of sonograms (Pieretti et al., 2011). BI measures the variation in amplitude over different frequency ranges by spectrogram computing the area above a decibel threshold (Boelman et al., 2007). High values of the ACI and BI indicate high levels of vocal activities in bird assemblages. Low ACI and BI values arise when there are almost no avian vocalizations, although sometimes near-silent recordings have background noises (i.e. insect noise and wind sounds). AEI calculates the island soundscape evenness by the Gini coefficient, with high values representing bird assemblages producing various sounds at different durations and frequencies (Villanueva-Rivera et al., 2011). Low AEI values represent low variations in sound intensity among frequency bands, which may be due either to the absence of sound activity or to the soundscape with great acoustic saturation produced by bird assemblages on islands. H is the multiplication of time entropy index and spectral entropy index, which reflects the heterogeneity of acoustic signal in time and frequency domains (Sueur, Pavoine, et al., 2008). H ranges from 0 to 1, with the highest value indicating random noises across all frequency bands or complete silence and the lowest value indicating a pure tone (i.e. sounds with only one vibrational frequency).

2.3.2 | Sampling completeness

We randomly selected 10 one-minute recordings from each island and assembled a subset of 200 one-minute recordings. At least two well-trained ornithologists who are familiar with the birds in this system were asked to identify bird species manually and the frequency of their appearances was recorded by each segment. Furthermore, we used these data to assess the completeness of avian soundscapes on each island. Coverage-based rarefaction and extrapolation sampling curves were calculated using the *iNEXT* function in the 'iNEXT' package in R software to assess the sampling completeness of each island (Figure S1; Hsieh et al., 2016).

2.3.3 | Statistical inference

We used Moran's *I* to test spatial autocorrelation (Table S4), and found AEI and BI were spatially autocorrelated (Diniz-Filho et al., 2003). We thus used spatial simultaneous autoregressive models (the function *errorsarlm* in R package 'spatialreg') to test the relationships between island soundscape diversity (AEI and BI) and island attributes (area and distance to the mainland). Meanwhile, we tested the relationship between island soundscape diversity and bird species richness through traditional field surveys by Pearson's correlations (Table S5 and Figure S3).

The nonlinear relationships between island soundscape diversity and explanatory variables were analysed through the generalized additive models (GAMs, Figure S7). Moreover, most GAM results indicated linear relationships between the four acoustic indices and island area/isolation (Figure S7). We thus used two types of models (type 1: multiple linear regression model; type 2: spatial simultaneous autoregressive model) with multiple explanatory variables ($\log_{10}(A)$, DM, DN and habitat diversity). Based on the Akaike information criterion (AIC) values, we made multi-model inference and evaluated ΔAIC for all possible combinations of predictors. Moreover, we calculated the importance of variables in models with ΔAIC <2 (Table S6). We made model selections to obtain the most parsimonious model (the one with the lowest AIC value) and determine the most optimal model (Anderson, 2008).

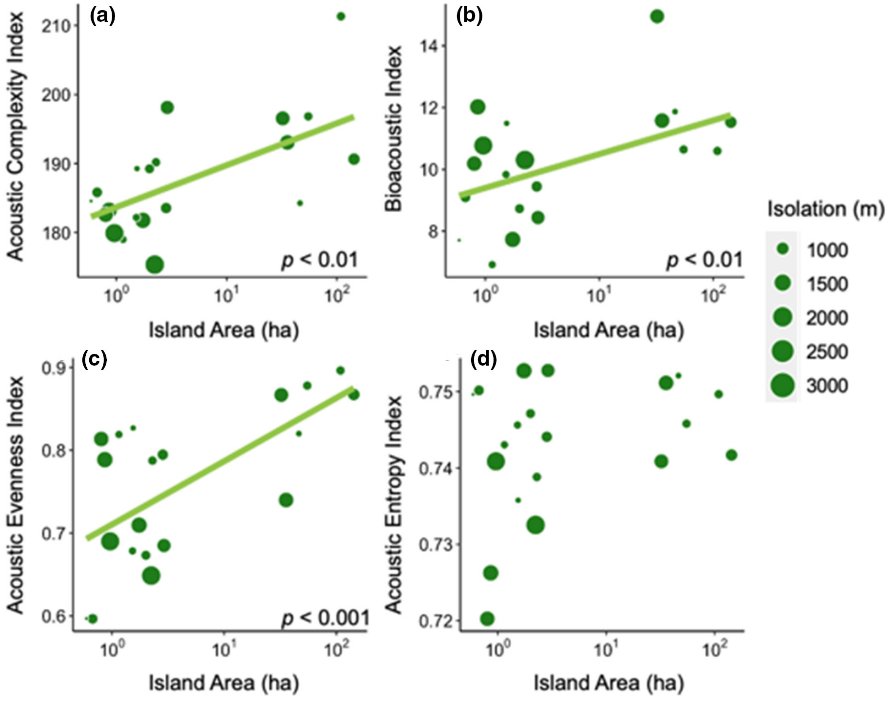

FIGURE 3 Relationship between soundscape diversity (measured by four acoustic indices) and island area and isolation. (a) The acoustic complexity index (ACI; $p < 0.01$) per island; (b) the bioacoustic index (BI; $p < 0.01$) per island; (c) the acoustic evenness index (AEI; $p < 0.001$) per island; (d) the acoustic entropy index (H) per island ($p = 0.18$). The green line is fitted model from linear regressions. Results of *p* values from linear regression models (ACI and H) and spatial autocorrelation models (AEI and BI). Point size is related to distance of island from the mainland.

Finally, we used piecewise structural equation modelling (*Piecewise* SEM) (Lefcheck, 2016) to explore direct and indirect paths among island attributes, bird species richness and soundscape diversity on islands. For SEM, we first considered a complete model containing all reasonable paths, and then sequentially eliminated unimportant paths. We used Fisher's *C* statistic and AIC to evaluate the fit of the model structure and the quality of the model.

All analyses were conducted in R version 4.1.2 (R Core Team, 2013), with packages, 'car' (Fox et al., 2012), 'glmulti' (Calcagno & de Mazancourt, 2010), 'mgcv' (Wood & Wood, 2015), 'MuMIn' (Barton & Barton, 2015), 'spdep' (Bivand et al., 2015), 'spatialreg' (Bivand & Piras, 2019), 'piecewiseSEM' (Lefcheck, 2016), 'soundecology' (Villanueva-Rivera et al., 2018), 'seewave' (Sueur, Aubin, et al., 2008) and 'terra' (Hijmans et al., 2022).

3 | RESULTS

We recorded 57,960 one-minute segments across all islands. We randomly selected 420 one-minute recordings from each recording point, resulting in a subset of 17,640 one-minute recordings that were used to assess soundscape diversity. A total of 24 species were recorded in traditional transect surveys and a total of 26 species in soundscape recordings (Table S3).

3.1 | Effects of island attributes on island soundscape diversity

The ACI (Figure 3a, $t = 3.69$, $p < 0.01$), the BI (Figure 3b, $z = 2.68$, $p < 0.01$) and the AEI (Figure 3c, $z = 3.32$, $p < 0.001$) all increased significantly with island area. However, the acoustic entropy index (Figure 3d, $t = 1.41$, $p = 0.18$) did not show a clear trend with island area (Figure 3). In addition, the AEI decreased significantly with isolation (distance to the mainland) (Figure S2c, $z = -2.12$, $p < 0.05$). However, there were no clear relationships between the ACI (Figure S2a, $t = -1.44$, $p = 0.17$), the acoustic entropy index (Figure S2d, $t = 0.99$, $p = 0.35$), the BI (Figure S2b, $z = 0.44$, $p = 0.66$) and island isolation (distance to the mainland).

In addition to analysing the effects of island area and isolation (distance to the mainland), we also considered other island attributes (e.g. habitat diversity) and added them to the models. With the increase in habitat diversity ($t = 4.39$, $p < 0.001$), the ACI increased significantly ($R^2 = 0.55$). Island area remains the main explanatory factor, while the BI and the AEI increased significantly with island area (BI, $z = 3.79$, $p < 0.001$; AEI, $z = 3.32$, $p < 0.001$) increases. The AEI did not find a good fitting model with island attributes (Table 1).

3.2 | Relationship between island attributes, bird species richness and soundscape diversity

The best piecewise structural equation model for forecasting soundscape diversity contains island attributes (i.e. island area, isolation and habitat diversity), bird richness and soundscape diversity (i.e. four acoustic indices) (Fisher's $C = 35.56$, $df = 30$, $p = 0.22$; Figure 4). Island area both had direct and indirect positive effects on bird soundscape diversity. Island area positively affected the AEI ($p = 0.003$, Figure 4). Furthermore, island area positively affected the ACI ($p < 0.001$, Figure 4) of islands by positively affecting habitat diversity ($p < 0.001$, Figure 4). Island area indirectly affects the BI ($p = 0.004$, Figure 4) of islands by impacting the species richness ($p < 0.001$, Figure 4) of birds. In contrast, we found a trend of adverse effects of isolation (i.e. distance to the mainland) on island soundscape diversity but was not significant (Figure 4).

TABLE 1 Results of multiple linear regression models and spatial autocorrelation models explain soundscape diversity in terms of island area (log10 *x*; A), distance to the mainland (DM), distance to the nearest island (DN) and island habitat diversity (*t* value scores are from multiple linear regression models; *z* value scores are from spatial autocorrelation models, see Table S2 for a detailed description of each variable).

Soundscape diversity	Model parameter	Estimate	*SE*	*t* value	*z* value	*p* value	AIC	R^2
Acoustic Complex Index	(Intercept)	166.992	4.943	33.784		<0.001	130.5	0.547
	Habitat diversity	**5.230**	1.221	4.385		**<0.001**		
	DM	−0.003	0.002	−1.809		0.088		
Bioacoustic Index	(Intercept)	8.285	0.855		24.186	<0.001	80.6	
	Log_{10}(A)	**1.419**	0.378		**3.788**	**<0.001**		
	DM	$9*10^{-4}$	$4*10^{-4}$		2.100	0.05		
Acoustic Evenness Index	(Intercept)	0.720	0.030		24.186	<0.001	−44.6	
	Log_{10}(A)	**0.065**	0.020		**3.316**	**<0.001**		
Acoustic Entropy Index	(Intercept)	0.751	0.004	194.47		<0.001	−132.5	0.190
	DN	$-2*10^{-4}$	$7.45*10^{-5}$	−2.34		**<0.05**		

P-values in bold are significant ($p < 0.05$).

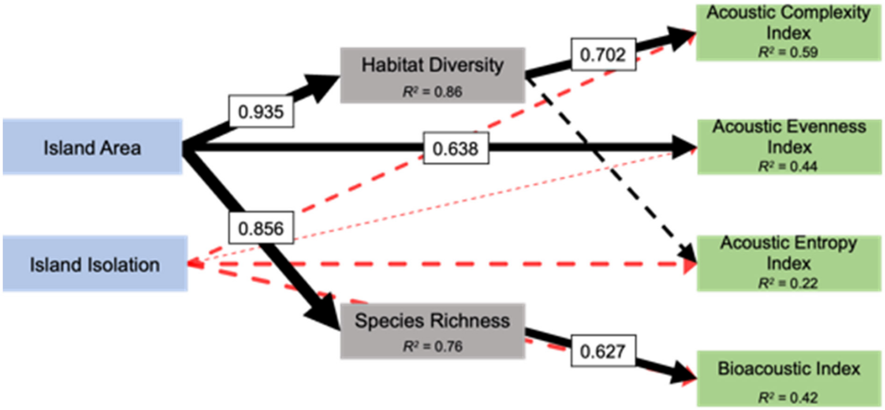

FIGURE 4 Piecewise structural equation modelling showing the relationships between island attributes, bird species richness and soundscape diversity (acoustic indices: ACI, BI, AEI, H). Arrows indicate one-way relationships between variables. Black solid arrows represent significantly positive ($p < 0.05$) pathways. Red solid arrows represent significantly negative ($p < 0.05$) pathways. Dashed lines indicate non-significant pathways. The R^2 of the model is given in the box for the response variable, and the path coefficients are shown in the boxes connecting each path. The width of the path is proportional to the strength of the relationship. Fisher's $C = 35.56$ with $p = 0.22$ and on 30 degrees of freedom.

4 | DISCUSSION

In this study, we found that the avian soundscape diversity increased with island area in a subtropical land-bridge island system. Specifically, these results supported the following predictions: (a) Positive diversity–area relationships for island soundscape diversity (Figures 3 and 4). The soundscape on a larger island exhibited higher richness and unevenness (Figure 3). (b) A negative soundscape evenness–isolation relationship (Figure 4 and Figure S2). (c) Habitat diversity and species diversity were essential factors in influencing the island soundscape (Table 1 and Figure 4). Overall, these results illustrated the variation of soundscape diversity across islands partially supported the ETIB. Nevertheless, by disentangling the direct and indirect effects of island area on soundscapes, we showed that similar positive soundscape diversity–area patterns may depend on the richness of soniferous species and habitat diversity on islands.

It is a general consensus on an ecological pattern of the positive species diversity–area on islands (Chase et al., 2019; Matthews et al., 2019; Whittaker et al., 2017). Similarly, our study also found a positive diversity–area relationship for the island soundscape diversity pattern in this land-bridge island system. Our results showed that larger islands tended to have higher soundscape richness (higher ACI and BI) and lower evenness (higher AEI). On smaller islands, the reason for the high soundscape evenness (lower AEI) is the lack of major vocal contributors in species-poor sites. Therefore, the sound intensity was even over the entire frequency band (Bradfer-Lawrence et al., 2020; Krause, 1993; Luypaert et al., 2022). For example, the major contributors in this study are Japanese Tit (*Parus minor*) and Chestnut Bulbul (*Hemixos castanonotus*). During our systematically aural screening of the extracted audio, the sounds of these two species were mainly captured on large islands. Although there are positive correlations between these acoustic indices and bird richness (Shamon et al., 2021; Sueur et al., 2014; Sueur, Pavoine, et al., 2008), bird-dominated soundscapes may be more moderate than observed bird diversity across islands. For example, monotonic sound signals emitted by species can greatly enhance the acoustic complexity and amplitude of barren soundscapes on small islands. Moreover, birds are also more likely to generate a high-amplitude soundscape through the chorus during morning songs on larger islands (Marín-Gómez & MacGregor-Fors, 2021), but acoustic communications may mask each other, thereby reducing the slope of the increase in soundscape diversity. On the other hand, the changes in vocal species richness are caused by the area difference between islands, which mean large islands often have vast living spaces, abundant resources and heterogeneous habitats (MacDonald et al., 2018; Ricklefs & Lovette, 1999; Whittaker & Fernández-Palacios, 2007).

Inter-island variation in habitat diversity was an important predictor for observed positive soundscape complexity–area relationships in our study islands (Table 1 and Figure 4). In general, the soundscape is a collection of biological and geophysical sounds. The rich habitat types thus provide a variety of ambient sounds on islands (e.g. tree salsa and wind; Pijanowski, 2011; Pijanowski & Farina, 2011; Pijanowski et al., 2011), which will increase the soundscape richness. Second, on large islands, diverse habitats make the acoustic spaces more redundant, and increased interspecific competition drives the differentiation of acoustic niches within bird assemblages (Kohn & Walsh, 1994; Ricklefs & Lovette, 1999; Robert et al., 2019). Therefore, the acoustic space accommodates sounds of different frequencies and intensities from bird species, resulting in higher acoustic complexities on larger islands. Third, island soundscapes may result from the mutual selection between bird assemblages and the environment. The sound characteristics of birds determine whether sound signals can be efficiently transmitted in habitats (Krause, 1987, 1993). For example, in our study, the recorded low-frequency audios often came from species on relatively large islands, such as Black Kite (*Milvus migrans*) and Black Bulbul (*Hypsipetes leucocephalus*). The more background noises on the continents than on small islands may also explain the differences of island soundscapes (Bradbury & Vehrencamp, 1998; Robert et al., 2019; Zhou et al., 2019). In contrast to soundscape complexity and amplitude, we found that soundscape evenness decreases with increasing island area. It indicates that the soundscape of larger islands has a more uneven distribution of sound energy across frequencies (Figures 3 and 4), which is consistent with the findings from previous studies (Bradfer-Lawrence et al., 2020; Eldridge et al., 2018). The habitat diversity (e.g. habitat types) affects the generation of background noises. For example, compared to islands, the background noise of tropical continents is more diverse, covering the frequency of bird vocalizations, so birds may communicate effectively through frequency modulation (Bradbury & Vehrencamp, 1998; Morton, 1975; Robert et al., 2019). Accordingly, we suspect that there may also be various background noises on large islands than smaller islands that reduces the evenness of the soundscape, which need further evidence to verify this finding.

In our system, except for the AEI, we did not observe a clear negative relationship between soundscape diversity and isolation (distance to the mainland) (Figures S2 and S6). This result suggests that the relatively short distance (the most isolated island is 3261 m from the mainland) between islands and the mainland may not limit the movement for the vast majority of birds (MacArthur & Wilson, 1967; Morand, 2000; Si et al., 2014). In our case, the soundscape exhibited an even signal on remote islands. In other words, the reduction in acoustic unevenness on remote islands may be associated with near-silent recordings with no acoustic activity (Bradfer-Lawrence et al., 2019; Villanueva-Rivera et al., 2011). Alternatively, although most bird species can disperse among islands in this system, it may be considered that birds tend to use more energy to move to remote islands or simply due to the fear of predators out of the forests, so birds may prefer to stay on islands close to the mainland (Hurlbert, 2004; Jonsson et al., 2011). As a result, isolation does not correlate with the avian soundscape diversity.

The synergistic development of biogeography with soundscape ecology will revolutionize our understanding of the spatiotemporal dynamics of biodiversity. Here we explored that the performance of acoustic diversity was similar to the patterns predicted by ETIB. However, the theoretical framework to explain the acoustic component of biodiversity in biogeography is still lacking in acoustic studies. Our research verified the possibility of using soundscape diversity as a proxy for species richness. While using sound instead of species surveys is still somewhat controversial, advances in soundscape analysis tools have made it more available and convenient to record and describe sounds objectively (Lomolino & Pijanowski, 2021; Morrison et al., 2021; Pijanowski et al., 2011). In particular, in contrast to traditional biodiversity assessment methods, acoustic monitoring can collect data across regions over a long period of time with lower costs and perhaps more importantly, can reduce the disturbance to local organisms (López-Bosch et al., 2021; Shamon et al., 2021; Sueur, Pavoine, et al., 2008). On the other hand, massive acoustic data require a relatively uniform standard in the statistical process, which will help integrate the observed acoustic recordings and explore the global pattern of acoustic assemblages (Lomolino & Pijanowski, 2021). Moreover, biogeography can also analyse and explain seemingly elusive acoustic phenomena in geographical space (i.e. spatial patterns of soundscape along major geographical gradients, such as area, isolation and elevation) (Lomolino & Pijanowski, 2021; Lomolino et al., 2015; Pijanowski et al., 2011). In addition to verifying consistent patterns with acoustic assemblages, acoustic data may also bring new insights into explaining biogeographical variation in population characteristics (Lomolino & Pijanowski, 2021; Lomolino et al., 2015; Robert et al., 2019), such as ‘geographical dialect’, the communication tool of a species within a certain geographical area (Goodfellow & Slater, 1986; Jenkins, 1978). Therefore, benefiting from the development of acoustic technology, exploring the geography of acoustic assemblages will advance our understanding of fundamental biogeographical processes and to enrich the theories of island biogeography.

In summary, we studied patterns of geographical variations in the acoustic properties of bird assemblages across island area and isolation in a land-bridge island system. We demonstrated that the variations in avian soundscape diversity were positively correlated with the island area. Bird assemblages on larger islands had higher richness and heterogeneity of soundscapes. By disentangling the direct and indirect effects of island area and isolation, our study highlights that higher species diversity and habitat diversity on islands favour the maintenance of higher soundscape diversity. Our results indicate that the loss of soundscape diversity due to species extinction may be unavoidable on small and remote islands. Further research examining the role of species and habitat diversity will help us better understand the mechanisms that shape biological soundscapes.

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CONFLICT OF INTEREST

The authors have declared that no competing interests exist.

DATA AVAILABILITY STATEMENT

Data for analysing relationships between soundscape diversity and island attributes are provided in the supplementary data.

ORCID

Yuhao Zhao https://orcid.org/0000-0002-8985-9633
Xingfeng Si https://orcid.org/0000-0003-4465-2759

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BIOSKETCH

Peng Han is a Ph.D. student at East China Normal University. His research focuses on changes in biodiversity and soundscape diversity after habitat fragmentation, functional traits and acoustic information in studies of island biogeography and urbanization.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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