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# Extending Species-Area Relationships Into the Realm of Ecoacoustics: The Soundscape-Area Relationship

Thomas Luypaert<sup>1</sup>  | Anderson S. Bueno<sup>2</sup>  | Torbjørn Haugaasen<sup>1</sup>  | Carlos A. Peres<sup>3,4</sup> 

<sup>1</sup>Faculty of Environmental Sciences and Natural Resource Management (MINA), Norwegian University of Life Sciences, Ås, Norway | <sup>2</sup>Instituto Federal de Educação, Ciência e Tecnologia Farroupilha, Júlio de Castilhos, RS, Brazil | <sup>3</sup>School of Environmental Sciences, University of East Anglia, Norwich, UK | <sup>4</sup>Instituto Juruá, Manaus, AM, Brazil

**Correspondence:** Thomas Luypaert ([thomas.luypaert@nmbu.no](mailto:thomas.luypaert@nmbu.no); [thomas.luypaert@outlook.com](mailto:thomas.luypaert@outlook.com))

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## ABSTRACT

The rise in species richness with area is one of the few ironclad ecological relationships. Yet, little is known about the spatial scaling of alternative dimensions of diversity. Here, we provide empirical evidence for a relationship between the richness of acoustic traits emanating from a landscape, or soundscape richness, and island area, which we term the SoundScape-Area Relationship (SSAR). We show a positive relationship between the gamma soundscape richness and island area. This relationship breaks down at the smallest spatial scales, indicating a small-island effect. Moreover, we demonstrate a positive spatial scaling of the plot-scale alpha soundscape richness, but not the beta soundscape turnover, suggesting a direct effect of species on acoustic trait diversity. We conclude that the general scaling of biodiversity can be extended into the realm of ecoacoustics, implying soundscape metrics are sensitive to fundamental ecological patterns and useful in disentangling their complex mechanistic drivers.

## 1 | Introduction

For many species, conveying information to others of their kind through acoustic signals is of vital importance for survival (Darwin 1872; Seyfarth and Cheney 2003). Consequently, acoustic sensory systems experience selective pressures to optimise signal transmission in local environments (Sensory Drive Hypothesis; Endler 1992). The physical environment, characteristics of acoustic signals (timing, frequency, and amplitude), and sonic context of sympatric species can affect the success of signal transmission by sound-producing species (Morton 1975; Slabbekoorn, Ellers, and Smith 2002).

Two main mechanisms are commonly believed to drive acoustic community assembly in space and exert selective pressures on the diversity of acoustic signals (Pijanowski, Villanueva-Rivera et al. 2011). Firstly, the acoustic signals of sympatric species propagate through a shared environment, which can cause interference and masking among signals with similar time-frequency features, potentially leading to ineffective communication (Siegert, Römer, and Hartbauer 2013). The Acoustic Niche Hypothesis (ANH) states acoustic niche space is a critical ecological resource for which sympatric species compete (Hödl 1977; Krause 1987; Pijanowski, Slabbekoorn et al. 2011). Acoustic competition can lead to the partitioning

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of acoustic frequency bandwidths (Villanueva-Rivera 2014), calling times (Hart et al. 2021), or the use of physical space (Sueur 2002). This interspecific competition for acoustic niche space was observed in various animal taxa (Chek, Bogart, and Lougheed 2003; Planque and Slabbekoorn 2008; Schmidt, Römer, and Riede 2013), and results in the diversification of acoustic traits with increasing species diversity. Secondly, the physical environment can act as a filter, selecting species with specific acoustic traits that optimise sound transmission and minimise signal attenuation (Chapuis 1971; Morton 1975; Mullet, Farina, and Gage 2017), which can occur through evolutionary processes (Acoustic Adaptation Hypothesis) or habitat selection (Acoustic Habitat Hypothesis). This selection process homogenises acoustic signal diversity locally but diversifies it across heterogeneous spaces. Although the relative importance of these contrasting processes remains debated (Villanueva-Rivera 2014; Hart et al. 2021; Mikula et al. 2021), both are tenable from an ecological and evolutionary perspective (Eldridge et al. 2018).

Beyond selection for optimal signal transmission, the diversity of acoustic traits in a landscape is influenced by a range of additional factors, including a species' evolutionary legacy, variations in species' relative abundance, the social context, variable vocal repertoires, and the presence on non-biological sounds in the environment (Pijanowski, Villanueva-Rivera et al. 2011; Hart et al. 2021; Alcocer et al. 2022). For instance, following the Morphological Constraints Hypothesis (MCH), a species' acoustic repertoire is limited by its physical characteristics (Ryan and Brenowitz 1985; Pearse et al. 2018). In birds, the size of the sound-producing organ correlates with body mass, with larger organs producing lower frequencies (Tietze et al. 2015). Similarly, the Phylogenetic Constraint Hypothesis (PCH) suggests that a species' evolutionary lineage restricts its range of sound frequencies (Pearse et al. 2018; Mikula et al. 2021). Deviations from the typical body size-vocalisation frequency relationship can occur due to evolutionary changes in the morphology of the sound-producing organ. Additionally, if acoustic features signal an individual's size, dominance, fighting ability, or health, these sounds may be subject to sexual selection (Sexual Selection Hypothesis; see Irwin 2000 and references therein). Consequently, selective pressures that affect morphological or phylogenetic diversity, or alter fitness, can also impact the diversity of acoustic signals in a landscape. These various mechanisms likely operate simultaneously, varying across space and time, resulting in a complex mosaic of soundscapes within and between habitats.

The soundscape (alternatively termed '*sonoscape*'—Farina and Li 2022), or collection of sounds emanating from the landscape (Pijanowski, Villanueva-Rivera et al. 2011), clearly contains useful information on the ecological and evolutionary mechanisms structuring acoustic assemblages (Stowell and Sueur 2020). Building on the aforementioned mechanisms of acoustic species assembly, the field of ecoacoustics uses the diversity of sounds in a landscape to study ecological and evolutionary processes (Farina and Gage 2017; Campos-Cerqueira and Aide 2017; Bradfer-Lawrence et al. 2020). Instead of identifying species by their calls, ecoacoustic analyses often rely on acoustic indices—quantitative metrics summarising the

distribution of acoustic energy (amplitude) in the time and/or frequency domain of a sound file (Sueur et al. 2014; Farina and Gage 2017; Eldridge et al. 2018). These indices have been widely applied to connect acoustic diversity in sound files and various factors, including landscape configuration (Tucker et al. 2014), ecosystem health (Fuller et al. 2015), diel patterns (Farina et al. 2015), seasonal changes (Farina, Pieretti, and Piccioli 2011), and habitat identity (Depraetere et al. 2012). Furthermore, using the proposed link between species- and acoustic diversity (e.g., Acoustic Niche Hypothesis), acoustic indices have been used as biodiversity proxies, sometimes showcasing strong correlations between both variables (e.g., Sueur et al. 2008; Farina, Pieretti, and Morganti 2013; Burivalova et al. 2019; Luypaert et al. 2022). However, recently, the need for caution when using these indices as biological proxies was highlighted (Alcocer et al. 2022). The performance of acoustic indices as biodiversity proxies can vary greatly within and between communities (Bradfer-Lawrence et al. 2019; Metcalf et al. 2021; Alcocer et al. 2022), sometimes producing conflicting results even with the same index (e.g., Mammides et al. 2017 vs. Bradfer-Lawrence et al. 2020). Here, we posit that the unpredictable behaviour of acoustic indices as biodiversity proxies might, in part, be attributed to poor understanding of the mechanisms that generate the observed soundscape-species diversity correlations.

Hydroelectric reservoirs are an excellent system for studying the mechanisms driving soundscape diversity in space. Following island biogeography theory, the species richness on an island depends on its size and isolation, with larger and less isolated islands holding more species than smaller and more isolated islands (MacArthur and Wilson 1967). The null hypothesis is that species-area relationships result from sampling effects, whereby larger islands are perceived to have more species due to ecological sampling processes or unequal sampling efforts (Schoereder et al. 2004; Chase et al. 2019). Conversely, the disproportionate effects hypothesis proposes that island size impacts biological processes that regulate species richness, whereby smaller islands support smaller populations, causing higher extinction rates and reduced species richness at local (alpha) and island-wide (gamma) scales (Schoereder et al. 2004). Finally, the heterogeneity effects hypothesis suggests larger islands contain a greater habitat diversity, each with its own set of species, thereby increasing compositional heterogeneity (beta) and island-wide (gamma) species richness (Williams 1964). Hence, the species richness gradient, modulated by island size and isolation in insularized landscapes, allows us to examine the relationship between acoustic indices and true species richness levels of sound-producing species. Moreover, the combination of high species richness and potential greater habitat diversity on larger islands provides an opportunity to investigate the relative role of species-based (e.g., *acoustic niche hypothesis*) versus habitat-based (*acoustic habitat/adaptation hypothesis*) mechanisms in shaping spatial soundscape diversity patterns and soundscape-species correlations.

In Luypaert et al. (2022), we tested the ability of the '*soundscape richness*' acoustic index to capture patterns in the richness of sound-producing species at an island-wide (gamma) scale using the species richness gradient at the Balbina Hydroelectric Reservoir in Brazilian Amazonia,

demonstrating a strong positive soundscape-species richness correlation. Yet, a positive soundscape-species richness correlation does not imply a causal relationship, which is necessary for reliably using acoustic indices as biodiversity proxies. This study aims to explore the mechanisms structuring spatial variation in acoustic trait diversity in fragmented landscapes and how they contribute to a previously observed positive gamma soundscape-species richness correlation at Balbina. We investigate soundscape richness at multiple spatial scales (alpha, beta and gamma) in relation to island size and isolation, and interpret observed relationships with expected patterns under different mechanistic pathways.

More specifically, we asked the following questions:

1. Does gamma soundscape richness follow island biogeography theory, increasing with island size and decreasing with isolation?
2. What mechanisms most likely drive spatial variation in soundscape richness in a fragmented landscape, and contribute to the previously observed positive gamma soundscape-species richness correlation in Luypaert et al. (2022)?
  - a. **Sampling artefacts:** Spatial scaling of soundscape richness results from inflated acoustic trait discovery on larger islands due to proportional sampling.
    - Expected patterns: Positive gamma soundscape-area relationship should vanish when accounting for sampling effort (rarefied gamma soundscape richness). No expected relationship between gamma soundscape richness and isolation (Figure 1A).
  - b. **Direct species effects:** Spatial scaling and positive soundscape-species correlations result from species richness influencing soundscape richness directly, through species-specific and spectro-temporally distinct vocalisations (e.g., Acoustic Niche Hypothesis). Previously observed soundscape-species correlations stem from a direct effect of sound-producing species on the soundscape richness.
    - Expected soundscape-area patterns: If disproportionate effects increase local (alpha) species richness on larger islands, alpha soundscape richness should also increase with island size (Figure 1B-1). If heterogeneity effects increase compositional heterogeneity (beta species richness) on larger islands, beta soundscape turnover should also increase with island size (Figure 1B-2). If both effects are present, both alpha soundscape richness and beta soundscape turnover should increase with island size (Figure 1B-3).
    - Expected soundscape-isolation patterns: Negative relationship between island isolation and gamma soundscape richness (Figure 1B).
  - c. **Indirect habitat effects:** Spatial scaling results from a greater habitat diversity on larger islands and the selection for acoustic traits that optimise signal transmission in local habitats (acoustic adaptation/habitat hypothesis). Positive soundscape-species correlations stem from an independent increase in species richness (disproportionate effects and/or heterogeneity effect) and soundscape richness (habitat diversity + environmental filtering) with island size.

- Expected soundscape-area patterns: Larger islands with greater habitat diversity have a greater beta soundscape turnover and gamma soundscape richness, but no increase in alpha soundscape richness.
- Expected soundscape-isolation patterns: No relationship between gamma soundscape richness and isolation (Figure 1C).

Importantly, all three mechanisms can result in the observed positive correlation between the island-wide (gamma) soundscape richness and species richness (Luypaert et al. 2022), but only the second scenario (2b) would provide the direct link between species richness and acoustic trait diversity required for the reliable use of acoustic indices as biodiversity proxies.

## 2 | Methods


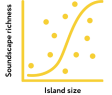
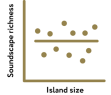
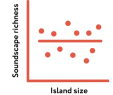




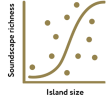
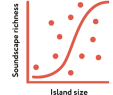
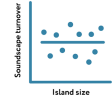

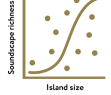
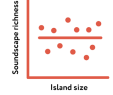
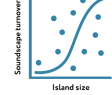



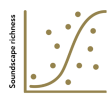
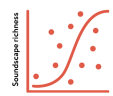
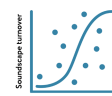
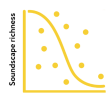



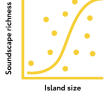
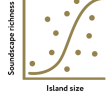
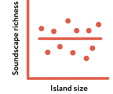
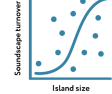

### 2.1 | Data Collection

Acoustic data were collected at the Balbina Hydroelectric Reservoir in Brazilian Amazonia (Figure 2). The Balbina reservoir was formed when the Uatumã River, a tributary of the Amazon, was dammed in 1987 (Fearnside 2016). This flooding event turned the hilltops of the former primary forest into over 3500 islands covering an area of approximately 300,000 ha, with island sizes ranging from 0.2 to 4878 ha (Fearnside 2016).

We used a standardised spatial sampling design, scaling the number of plots per island with island size (Schoederer et al. 2004). Long-duration acoustic surveys were conducted at Balbina between July and December 2015, sampling 74 forest islands (Bueno et al. 2020). The number of sampling plots per island ranged from 1 to 7 and increased with island size (see Supporting Information S1). At each plot, a passive acoustic sensor was deployed on a tree trunk at 1.5 m height with the microphone pointing downward. Each sensor consisted of an LG smartphone in a waterproof case linked to an omnidirectional microphone, set to record 1 in every 5 min at a sampling rate of 44.1 kHz for 4–10 days using the ARBIMON Touch application ([arbimon.rfcx.org](http://arbimon.rfcx.org)). Due to poor recording quality, low sampling effort, and to retain proportional sampling, some sites were excluded from the study (see Supporting Information S1), retaining 69 sampling plots (1–4 plots per island) on 49 islands (0.45–668.03 ha; Figure S1; Table S1).

### 2.2 | Calculating Predictor Variables: Island Size and Isolation

As islands at Balbina may contain non-forest patches, we focused on soundscapes produced by forest-dwelling species. Thus, island size was calculated as the total forest area per island, omitting areas of non-forest vegetation or bare soil. We downloaded a classified image from MapBiomas (30 m resolution; Souza et al. 2020) and calculated the amount of ‘dense forest’ per island (pixel value 3), as other pixel values contained either heavily degraded or non-forest cover types (Bueno et al. 2020).

MECHANISMS GOVERNING SOUNDSCAPE RICHNESS	MECHANISMS GOVERNING SPECIES RICHNESS	EXPECTED SPATIAL SOUNDSCAPE RICHNESS PATTERNS					CAUSAL SOUNDSCAPE-SPECIES LINK?
		ISLAND SIZE				ISOLATION	
<b>A.</b>  SAMPLING ARTEFACTS	<b>ANY</b>	GAMMA (UNRAREFIED) 	GAMMA (RAREFIED) 	ALPHA (RAREFIED) 	BETA (RAREFIED) 	GAMMA (UNRAREFIED) 	
<b>B.</b>  DIRECT SPECIES EFFECTS	<b>1. DISPROPORTIONATE EFFECTS ONLY</b> 	GAMMA (UNRAREFIED) 	GAMMA (RAREFIED) 	ALPHA (RAREFIED) 	BETA (RAREFIED) 	GAMMA (UNRAREFIED) 	
	<b>2. HETEROGENEITY EFFECTS ONLY</b> 	GAMMA (UNRAREFIED) 	GAMMA (RAREFIED) 	ALPHA (RAREFIED) 	BETA (RAREFIED) 	GAMMA (UNRAREFIED) 	
	<b>3. DISPROPORTIONATE AND HETEROGENEITY EFFECTS</b> 	GAMMA (UNRAREFIED) 	GAMMA (RAREFIED) 	ALPHA (RAREFIED) 	BETA (RAREFIED) 	GAMMA (UNRAREFIED) 	
<b>C.</b>  INDIRECT HABITAT EFFECTS	<b>DISPROPORTIONATE / HETEROGENEITY EFFECTS</b> 	GAMMA (UNRAREFIED) 	GAMMA (RAREFIED) 	ALPHA (RAREFIED) 	BETA (RAREFIED) 	GAMMA (UNRAREFIED) 	

**FIGURE 1** | A conceptual model outlining the expected patterns in the soundscape richness in response to different island biogeographic variables and mechanistic processes structuring the soundscape diversity across space. (A) Neither species nor habitat effects influence the landscape-scale soundscape richness, and observed trends are likely the result of sampling effects or other unknown processes. (B) Gamma species richness increases with island size due to increased local (alpha) species richness (disproportionate effects) and/or compositional heterogeneity (beta species richness; heterogeneity effect) on larger islands, and species influence soundscape diversity directly (e.g., Acoustic Niche Hypothesis), resulting in positive alpha- and/or beta- and gamma soundscape-area relationships and a negative soundscape-isolation relationship. (C) Larger islands have a greater species richness (disproportionate effects and/or heterogeneity effects) and habitat diversity. Acoustic signals are acoustically adapted/selected to each unique habitat (e.g., Acoustic Adaptation/Habitat Hypothesis), resulting in an increased gamma soundscape richness and beta soundscape turnover with island size, but spatial scaling of alpha soundscape richness. Species richness and soundscape richness increase with island size through independent mechanisms. Gamma soundscape richness has no relationship with island isolation.

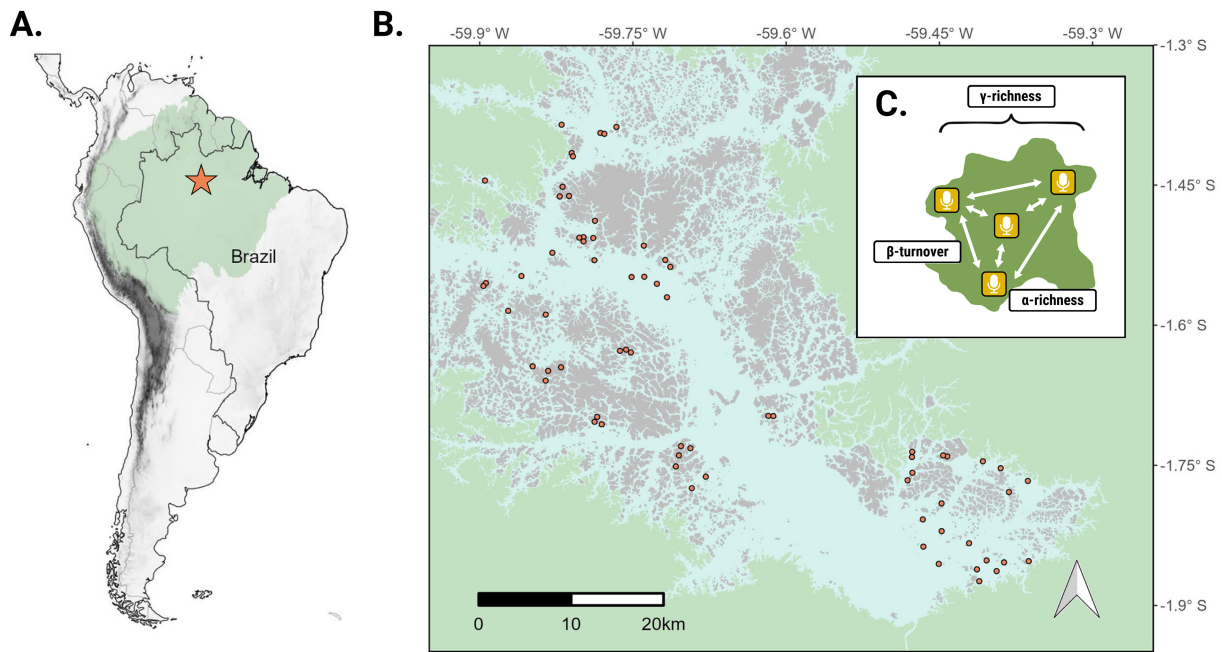
Many different definitions for island isolation exist, and the most appropriate metric likely varies between ecosystems, island type (i.e., oceanic vs. land-bridge), taxonomic groups, and more (Itescu et al. 2020). To assess whether different metrics influence the perceived impact of isolation on the soundscape richness, we calculated three metrics: (i) distance to nearest mainland (DNM; island-to-reservoir-edge); (ii) distance to the nearest island (DNI; island-to-island-edge); and (iii) proportion of water (PW) within a buffer around the island perimeter (see Supporting Information S3). The optimal scale-of-effect for the ‘proportion of water in surrounding buffer’ isolation variable (see Jackson and Fahrig 2015) was determined by trialling 40 different buffer sizes (50–2000m at 50m intervals), choosing the

spatial scale at which isolation attained the strongest relationship with soundscape richness (see Supporting Information S3.2).

## 2.3 | Calculating Response Variables: Soundscape Richness

### 2.3.1 | Data Preparation

To quantify the diversity of acoustic traits emanating from the landscape, we followed the analytical pipeline outlined in Luypaert et al. (2022) to calculate the *soundscape richness* index. To capture ecological patterns without identifying species, the



**FIGURE 2** | (A) Location of the Balbina Hydroelectric Reservoir (BHR; orange star) in central Amazonia (green), Brazil. (B) A detailed overview of the BHR (blue) showing over 3500 hilltop islands (grey), surrounded by continuous forest (green). For this study, 69 sites (orange) were sampled on 49 islands. (C) An overview of the spatial sampling design employed in this study. The green area represents an island, with multiple acoustic sampling plots in yellow. This sub-island scale sampling design allows us to quantify not only the island-wide gamma ( $\gamma$ ) soundscape richness but also the local-scale alpha ( $\alpha$ ) soundscape richness and beta ( $\beta$ ) turnover components.

pipeline quantifies the richness of Operational Sound Units (OSUs), a unit of measurement that groups sounds by their shared spectro-temporal coordinates in the 24-h acoustic space in which species produce sound (see Supporting Information S2).

To ensure consistency in temporal sampling efforts, we designated a 5-day period for sampling across all study plots (see Supporting Information S2). Using a sampling rate of 44,100 Hz and a window length of 256 frames, we calculated the Acoustic Cover (CVR) spectral index for each 1-min sound file at each plot (Towsey 2017). The CVR index produces a series of values, each corresponding to a specific frequency bin within a 1-min noise-reduced spectrogram. Each bin's CVR value represents the proportion of cells surpassing a 3-dB threshold, ranging from 0 to 1 (Figure 1 in Luypaert et al. 2022). We merged these CVR-index files for each sampling plot chronologically, resulting in a frequency-by-time dataframe that contains the CVR-index values. By employing the 'IsoData' binarization algorithm, we converted raw CVR-index values into a binary variable. Doing so, we determined whether OSUs were detected within each 24-h sample of the soundscape (Figure 2 in Luypaert et al. 2022). Subsequently, an incidence matrix was constructed for each plot, providing information on the detection or non-detection of OSUs in each 24-h soundscape sample throughout the 5-day acoustic survey. These incidence matrices serve as the foundation for all subsequent computations related to soundscape richness.

### 2.3.2 | Partitioning Soundscape Richness Into Gamma, Alpha and Beta Components

We quantified the soundscape richness using an adapted version of the multi-scale and multi-metric framework (see Figure 1) outlined in Chase et al. (2019). We analysed the spatial scaling in

soundscape richness using four metrics at various scales: (i) unrarefied island-wide gamma soundscape richness; (ii) rarefied island-wide gamma soundscape richness; (iii) local plot-scale alpha soundscape richness and (iv) between-plot beta soundscape turnover.

To calculate the unrarefied island-wide (gamma) soundscape richness, we combined OSU-by-sample incidence matrices from all plots per island by merging the columns and counting the distinct OSUs detected across all soundscape samples. Next, we rectified the uneven sampling effort across islands using a rarefaction procedure. Chao et al. (2023) provide a framework that uses coverage-based rarefaction to decompose rarefied gamma diversity into alpha and beta diversities using a multiplicative relationship (calculated as  $\gamma = \alpha \times \beta$  following the framework of Hill numbers; see Jost 2007) and accommodates incidence-based data such as our own. Following Chao et al. (2023), we used the 'iNEXT.beta3D' function in the identically titled R package (Chao et al. 2023; Chao and Hu 2023) to obtain standardised gamma, alpha, and beta soundscape richness ( $q=0$ ), rarefying or extrapolating sample coverage between islands to two coverage values: (i)  $C_{\min}$  = minimum observed sample coverage for study islands; (ii)  $C_{\max}$  = minimum sample coverage at minimum sample size  $\times 2$ . This was done using the 'incidence\_raw' data type and performing 2000 bootstraps for estimation of 95% confidence intervals (see Supporting Information S2).

### 2.4 | Assessing the Effect of Island Size and Isolation on Soundscape Richness

As the effect of island size on species richness often breaks down at small scales (*small island effect*; Lomolino 2000), we

checked for the presence of a small-island effect on soundscape richness values. Although debated (Tjørve 2003, 2012; Triantis, Guilhaumon, and Whittaker 2012), the effect of island size on species richness is most often approximated using the power law function (Arrhenius 1921), defined as  $S = cA^z$ , where  $S$  is the number of species units,  $A$  is habitat patch area, and  $c$  and  $z$  represent the intercept and slope of the equation in log–log space respectively. To test for small island effects, we used model selection to compare four small island models. Piecewise regression paired with power-law models was used on unrefined gamma soundscape richness using the ‘*sar\_threshold*’ function from the ‘*sars*’ R-package (Matthews et al. 2019; see Supporting Information S4). If a small-island effect was detected, subsequent modelling was performed on three datasets (i) all study islands; (ii) islands > small-island threshold and (iii) islands < small-island threshold.

To examine the relative importance of island size and isolation, for each dataset, we used partial regression plots to explore each variable’s influence on unrefined soundscape richness while considering the variability accounted for by the other variables (Supporting Information S5.3). Moreover, we tested for potential interactions between island size and isolation using conditioning scatterplots (Supporting Information S5.4). Finally, we fitted 11 linear models, using an information theoretic approach for model selection (Supporting Information S5.5; Table 1).

We tested the best-fitting models ( $\Delta AICc < 2$ ) for multicollinearity by calculating Variance Inflation Factors (VIFs) using the ‘*vif*’ function from the ‘*car*’ R-package (Fox and Weisberg 2019). A VIF < 5 represented an acceptable value to retain both predictors in the model (James et al. 2013). As interaction terms in models often lead to high VIFs, we did not consider models containing interaction terms when assessing VIFs. All models without interaction terms had acceptable VIFs (Table S7). For

the best-fitting model of each dataset, we tested model assumptions (see Supporting Information S5.6).

## 2.5 | Decomposing the Mechanisms Driving Soundscape Richness in Space

To gain insights into the mechanisms driving the spatial variation in the soundscape richness, and potentially underlying soundscape-species correlations at Balbina, we built power-law models in a log–log space using the ‘*lin\_pow*’ function from the ‘*sars*’ R-package (Matthews et al. 2019).

As we used a proportional sampling scheme, larger islands were sampled more intensely. Therefore, the observed soundscape richness values are influenced not only by ecological processes, but also by sampling effort (number of plots per island) and completeness (representation of true diversity in samples). Hence, to see if sampling artefacts were at play, we assessed the soundscape-area relationship for the unrefined and rarefied gamma soundscape richness by fitting power-law models to both variables and comparing model parameter values (Figure 1A). Moreover, to discern whether soundscape-area relationships did not just result from passive sampling, and to elucidate whether soundscape richness was driven by species- or habitat-effects (Figure 1B,C), we investigated soundscape richness at both local plot scales (rarefied alpha soundscape richness) and between-plot turnover (rarefied beta soundscape richness). As the beta-turnover cannot be computed for islands containing a single plot, 1-plot islands were removed (remaining islands = 13). Finally, to assess whether the width of 95% confidence intervals around rarefaction estimates had an influence on power-law model parameter estimates, we performed a sensitivity analysis using a bootstrapping approach (Supporting Information S6).

**TABLE 1** | Structure of the 11 linear models used to estimate the relative influence of the island size and isolation variables on the unrefined gamma soundscape richness.

Model	Model description
1	$\log_{10}(\text{gamma soundscape richness}) \sim \log_{10}(\text{island size}) + \text{PW} + \log_{10}(\text{island size}) \times \text{PW}$
2	$\log_{10}(\text{gamma soundscape richness}) \sim \log_{10}(\text{island size}) + \log_{10}(\text{DNI} + 1) + \log_{10}(\text{island size}) \times \log_{10}(\text{DNI} + 1)$
3	$\log_{10}(\text{gamma soundscape richness}) \sim \log_{10}(\text{island size}) + \log_{10}(\text{DNM}) + \log_{10}(\text{island size}) \times \log_{10}(\text{DNM})$
4	$\log_{10}(\text{gamma soundscape richness}) \sim \log_{10}(\text{island size})$
5	$\log_{10}(\text{gamma soundscape richness}) \sim \log_{10}(\text{island size}) + \text{PW}$
6	$\log_{10}(\text{gamma soundscape richness}) \sim \log_{10}(\text{island size}) + \log_{10}(\text{DNI} + 1)$
7	$\log_{10}(\text{gamma soundscape richness}) \sim \log_{10}(\text{island size}) + \log_{10}(\text{DNM})$
8	$\log_{10}(\text{gamma soundscape richness}) \sim \text{PW}$
9	$\log_{10}(\text{gamma soundscape richness}) \sim \log_{10}(\text{DNI} + 1)$
10	$\log_{10}(\text{gamma soundscape richness}) \sim \log_{10}(\text{DNM})$
11	$\log_{10}(\text{gamma soundscape richness}) \sim 1$

Abbreviations: DNI, distance to the nearest island; DNM, distance to nearest mainland; PW, proportion of water within buffer.

### 3 | Results

#### 3.1 | The Effect of Island Size and Isolation on Soundscape Richness

In the scale-of-effect analysis, the correlation between soundscape richness and the 'proportion of water within buffer' isolation variable (PW) peaked at 650 m (Supporting Information S3; Figure S3). Piecewise regression analyses revealed a small island effect, supporting a continuous one-threshold and left-horizontal one-threshold model with threshold values of 9.40 and 12.68 ha, respectively (Supporting Information S4; Table S2; Figure S4). The lower threshold (9.40 ha) was chosen to create three subsets for modelling: (i) all islands; (ii) islands > 9.4 ha and (iii) islands < 9.4 ha.

The proportion of water in a 650 m buffer around each island (PW) provided the best descriptor of island isolation for the 'all islands' dataset. We focus on this variable, and analyses with island isolation measured as the 'distance to nearest island' (DNI) or 'distance to nearest mainland' (DNM) are mostly found in Supporting Information S5. Controlling for isolation effects, partial regression plots demonstrated a significant positive relationship between island size ( $\log_{10}$ ) and soundscape richness ( $\log_{10}$ ) in the 'all-islands' dataset (Figure 3A) and 'islands > 9.4 ha' dataset (Figure 3B), but not the 'islands < 9.4 ha' dataset (Figure 3C). Notably, for islands smaller than 9.4 ha, isolation had a slight positive effect on soundscape richness when accounting for island size (Figure 3C). This observation was confirmed by conditioning plots: an interaction effect between island size and isolation was evident for the 'all-islands' dataset (Figure S14A) but disappeared when excluding islands below the threshold (Figure S14B). The modelling output confirmed these findings partially (Table 2; Table S6). For the 'all-islands' dataset, the most parsimonious model included island size, isolation, and the area  $\times$  isolation interaction (Table S3). Excluding islands above the threshold resulted in a model describing a positive relationship between the soundscape richness and island isolation (Table S5). Finally, when excluding islands below the small-island threshold, we found comparable support for two models: (i) a positive effect of island size and a negative effect of DNM (distance to nearest mainland) on the soundscape richness (Table S4; Figure S13B) and (ii) a positive effect of island size on the soundscape richness (Table S4).

#### 3.2 | Mechanisms Driving Soundscape Richness in Space

Here, we were primarily interested in the spatial scaling of soundscape richness with island size and its underlying mechanisms, so we excluded all islands smaller than 9.40 ha from subsequent analyses (44 plots on 24 islands retained). Doing so, the power-law model showed a substantially improved positive relationship between island size and gamma soundscape richness in log-log space compared to the full dataset (Figure 4A). Although slightly weaker, this relationship persisted when accounting for unequal sampling effort using coverage-based rarefaction to  $C_{\min}$  (Figure 4A) or  $C_{\max}$  (Figure S21).

At the plot scale, power-law models also showed a positive log-log relationship between island size and the rarefied alpha soundscape richness (Figure 4B). Conversely, the variation in the rarefied beta soundscape turnover was poorly explained by island size (Figure 4C). The sensitivity analysis revealed these results were robust to the width of rarefaction confidence intervals (Supporting Information S6; Figures S22 and S23).

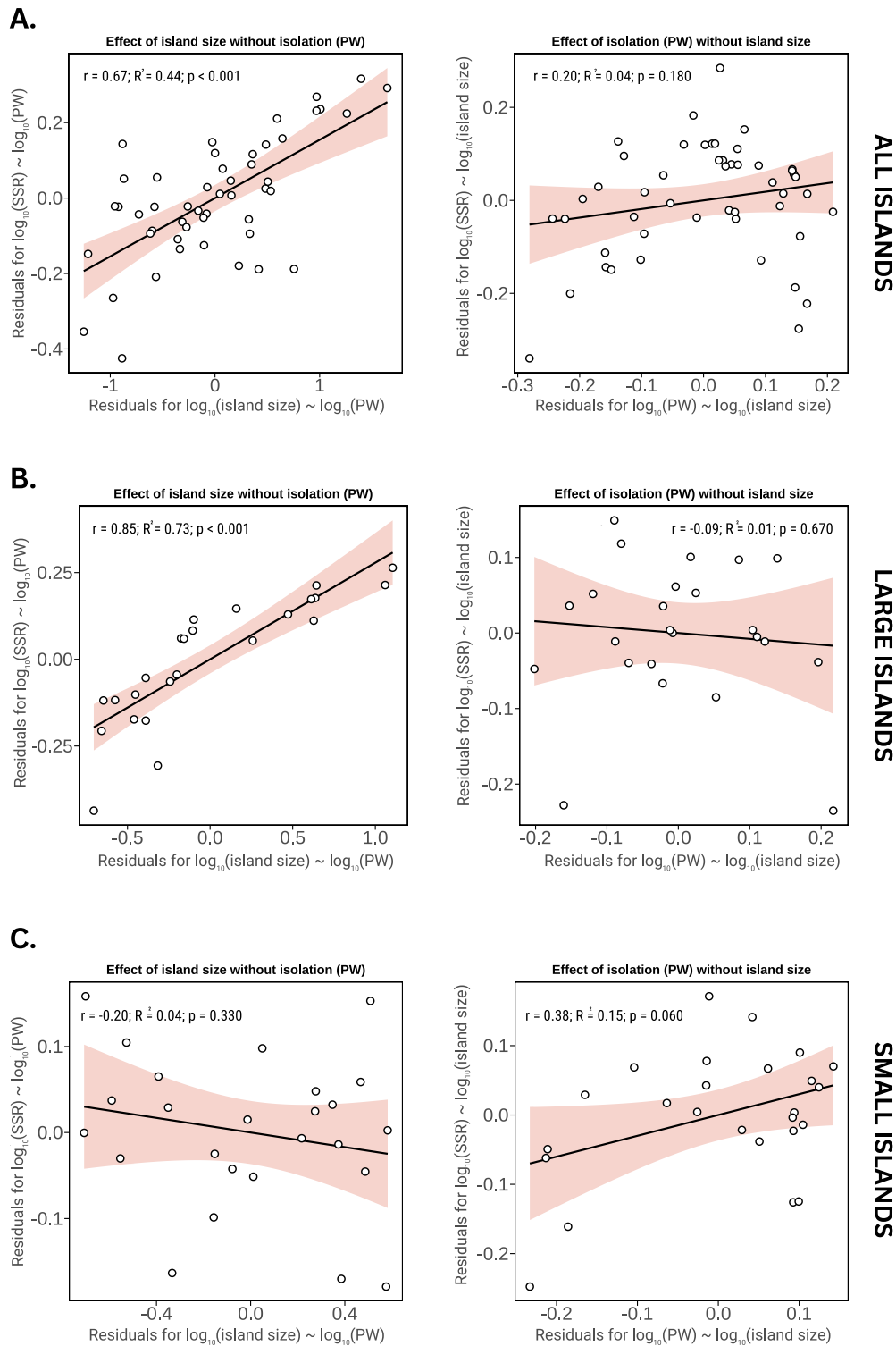
### 4 | Discussion

In insular systems, species richness is governed by island size and isolation, a key tenet of island biogeography theory. We extended this principle to ecoacoustics, examining the importance of island size and isolation on the spectrotemporal richness of acoustic traits, or soundscape richness. Additionally, we disaggregated soundscape richness at sub-island scales to understand which ecological mechanisms drive spatial variation in soundscape richness and underlie previously observed soundscape-species richness relationships at Balbina (see Luypaert et al. 2022).

#### 4.1 | The Effect of Island Size and Isolation on Soundscape Richness

When considering all islands, island size positively affected soundscape richness, yet this effect decreased as isolation (PW) increased (Figure S14; Table 2). This negative interaction effect challenges island biogeography theory (Kadmon and Allouche 2007; MacArthur and Wilson 1967), which predicts a stronger species-area relationship with increasing isolation due to decreasing immigration rates.

Island size and isolation are negatively correlated at Balbina (Figure S10), meaning less isolated small islands and more isolated large islands were mostly absent from our study. The smallest, most isolated islands showed a breakdown of the soundscape-area relationship (threshold = 9.4 ha; Figure S4; Table S2). Hence, this negative interaction may stem from stochastic small-island effects (Lomolino 2000). Previous species-based studies at Balbina showed similar breakdowns of species-area relationships below 10 ha (Benchimol and Peres 2015; Bueno and Peres 2019). Alternatively, the small-island effect could stem from the positive effect of isolation on soundscape richness in highly isolated islands (islands < 9.4 ha; Figure 3C; Table 2). The effect of isolation on island soundscapes has not been well studied. Han et al. (2022) found increased soundscape evenness on more isolated land-bridge islands but limited evidence for isolation effects on soundscape diversity. Robert, Melo, et al. (2021) reported reduced syllable calling rates but increased syllable diversity in oceanic island birds due to acoustic character release (Robert, Lengagne, et al. 2021). The low species richness on small, highly isolated islands at Balbina could theoretically lead to competitive release and increased signal diversity in response to isolation, thus increasing soundscape richness. However, the young age of the Balbina island system, along with reductions in soundscape richness in response to reduced species richness (Luypaert et al. 2022) and island size (this study), makes this hypothesis unlikely.



**FIGURE 3** | Partial regression plots showing the relationship between island size (ha) or isolation (measured as the proportion of water within a buffer) and the unrarefied soundscape richness (SSR), considering the variation accounted for by the other variable for: (i) all islands (A); (ii) large islands > 9.4 ha (B); and (iii) small islands < 9.4 ha (C).

Removing small islands eliminated the negative interaction effect (Figure S14), resulting in two equally supported models: (i) a positive effect of island size with a slight negative effect of isolation (DNM) or (ii) a positive effect of island size alone (Table 2). While the positive scaling of biodiversity with island size is well-documented

for species richness (Connor and McCoy 1979; MacArthur and Wilson 1967; Matthews et al. 2016), the spatial scaling of acoustic diversity with island size is a relatively novel concept that has received limited attention (but see Han et al. 2022). We refer to this pattern as the ‘SoundScape-Area Relationship’ (SSAR).



TABLE 2 | Output of the best-fit models for: (i) all islands; (ii) large islands; (iii) small islands.

Model	Intercept	$\log_{10}(A)$	PW	$\log_{10}(A) \times PW$	$\log_{10}(DNI+1)$	$\log_{10}(A) \times \log_{10}(DNI+1)$	$\log_{10}(DNM)$	$\log_{10}(A) \times \log_{10}(DNM)$	df	$R^2_{adj}$	AICc	$\Delta AICc$
All islands												
1	0.56 <sup>****</sup>	0.71 <sup>****</sup>	0.85 <sup>****</sup>	-0.73 <sup>****</sup>					45	0.64	-79.06	0.00
Large islands (> 9.4 ha)												
7	1.17 <sup>****</sup>	0.28 <sup>****</sup>				-0.05			21	0.73	-39.35	0.00
4	1.05 <sup>****</sup>	0.20 <sup>****</sup>							22	0.71	-39.16	0.19
Small islands (< 9.4 ha)												
8	1.06 <sup>****</sup>		0.32 <sup>**</sup>						23	0.12	-44.05	0.00

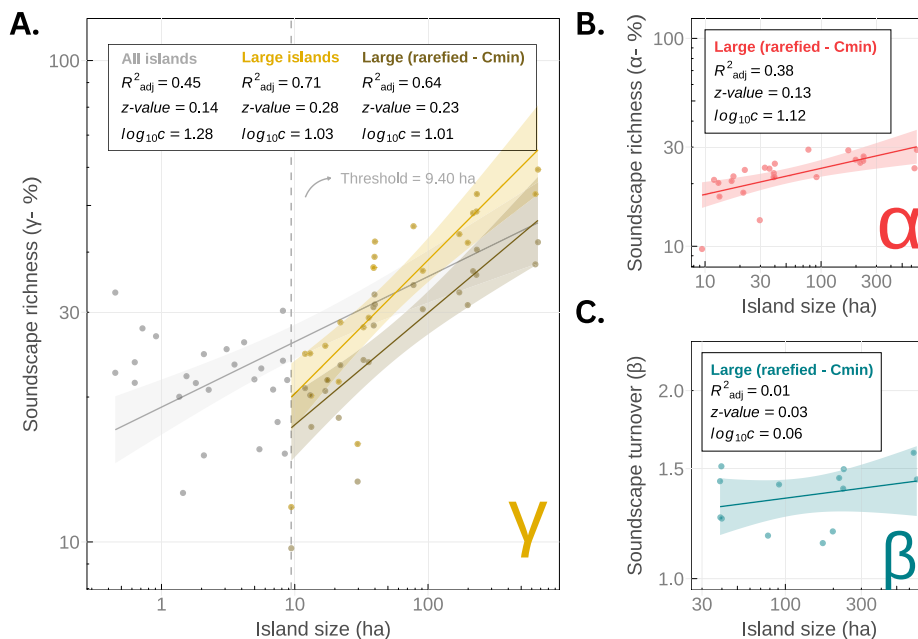
Note: Island isolation values are indicated as PW (proportion of water in buffer), DNI (distance to nearest island) and DNM (distance to nearest mainland). Models were compared using an information-theoretic approach, selecting models with the lowest  $\Delta AICc$  and/or  $\Delta BIC$  values. Parameter significance codes: "\*\*\*\*" =  $p < 0.001$ ; "\*\*\*\*" =  $p < 0.01$ ; "\*\*\*\*" =  $p < 0.05$ ; "\*" =  $p < 0.1$ ; " " =  $p > 0.1$ .

## 4.2 | The Mechanisms Driving Soundscape Richness in Space

Positive gamma SSARs can arise through various mechanisms, including sampling artefacts (Figure 1A), a direct effect of soniferous species on soundscape richness (Figure 1B), or increased habitat diversity on larger islands coupled with environmental filtering or adaptation of acoustic traits in local environments (Figure 1C). Identifying the mechanisms driving the spatial scaling of soundscape richness in fragmented landscapes is crucial for interpreting previously observed soundscape-species richness correlations (Luypaert et al. 2022) and using soundscape richness as a biodiversity proxy.

The positive relationship between island size and gamma soundscape richness persisted after accounting for differences in sampling effort by rarefying to  $C_{min}$  (Figure 4A) and  $C_{max}$  (Figure S21). This consistent spatial scaling of gamma soundscape richness rules out sampling artefacts as the only mechanism (Figure 1A), suggesting the observed SSAR is likely driven by other ecological or evolutionary processes. If gamma SSARs were primarily driven by increased soundscape heterogeneity on larger islands—due to greater habitat diversity leading to higher species heterogeneity (heterogeneity effects; Williams 1964) combined with a direct species effect on soundscape richness (e.g. Acoustic Niche Hypothesis; Krause 1987)—we would expect beta soundscape turnover to scale positively with island size (Figure 1B–2, B–3). Similarly, if the relationship was driven by increasing habitat diversity with island size, coupled with environmental filtering (Acoustic Habitat Hypothesis; Mullet, Farina, and Gage 2017) or adaptation of acoustic traits (Acoustic Adaptation Hypothesis; Chapuis 1971; Morton 1975) to enhance signal transmission in each distinct habitat, we would expect a positive beta soundscape-area relationship (Figure 1C). Yet, beta soundscape turnover only showed a weak spatial scaling with island size (Figure 4C), suggesting these mechanisms are unlikely to be the primary drivers of spatial variation in soundscape richness at Balbina. Instead, rarefied alpha soundscape richness showed a strong positive relationship with island size (Figure 4B), aligning with expectations from disproportionate effects elevating local species richness levels on larger islands (Schoereder et al. 2004) and a direct effect of soniferous species on soundscape richness (Figure 1B–1). Similarly, the slight negative effect of isolation on gamma soundscape richness after removing small islands (Table 2) points towards a direct species effect (Figure 1B–1).

This direct species effect could indicate the existence of species-specific and spectrotemporally unique vocalisations, establishing a direct link between the richness of sound-producing species and soundscape richness. This can be explained by the Acoustic Niche Hypothesis (Hödl 1977; Krause 1987; Pijanowski, Slabbekoorn et al. 2011), where sympatric species show evolutionary divergence in acoustic traits through competition for acoustic niche space. Since islands at Balbina were formed by fragmentation of primary forest following flooding, it is plausible that smaller islands experienced localised extinctions of soniferous species occupying unique acoustic niches, leading to a reduction in



**FIGURE 4** | (A) Relationship between island size ( $\log_{10}$ ) and the unrarefied (light grey and yellow) and rarefied (brown) gamma soundscape richness (SSR;  $\log_{10}$ ) for all islands ( $n=49$ ; light grey) and for islands larger than the 9.4-ha small-island threshold ( $n=24$ ; yellow; brown). (B) Relationship between island size ( $\log_{10}$ ) and rarefied alpha soundscape richness ( $\log_{10}$ ), using coverage-based rarefaction to  $C_{min}$ . (C) Relationship between island size ( $\log_{10}$ ) and the rarefied beta soundscape turnover ( $\log_{10}$ ), using coverage-based rarefaction to  $C_{min}$ .

soundscape richness. Although there is evidence supporting evolutionary divergence in acoustic traits due to interspecific competition in sympatry (e.g. Höbel and Gerhardt 2003; Jang and Gerhardt 2006; Kirschel, Blumstein, and Smith 2009), the same pattern can arise through evolutionary mechanisms beyond acoustic niche partitioning. For instance, acoustic signal divergence can also occur as a byproduct of morphological divergence in sound-producing structures, such as beak size (Podos 2001). Furthermore, for some songbirds, the evolution of spectrotemporally distinct vocalisations appears to be largely driven by geographic isolation in allopatry (Drury et al. 2018). Although rarely assessed, fragmentation-induced changes in the relative abundance, ecological context and social environment may also contribute to the observed positive alpha soundscape-area relationship. Smaller islands often support smaller groups of vocal species like primates and trumpeters (Benchimol and Peres 2021), and both calling rates (Payne, Thompson, and Kramer 2003; Fernandez, Vignal, and Soula 2017; Radford and Ridley 2008) and vocal repertoire complexity (Teixeira, Maron, and Rensburg 2019) correlate with group size. In summary, defaunation on smaller islands may result in the extinction of species with spectrotemporally unique calls, and acoustic communities with simpler vocal repertoires (Laiolo and Tella 2007) and lower calling rates, thus lowering observed soundscape richness.

### 4.3 | Soundscape Richness as an Ecological Proxy

Our findings suggest a direct link between soniferous species and soundscape richness. The gamma SSAR slope observed in this study ( $z=0.28$ ) closely matches those from species-based meta-analyses for inland islands ( $z=0.28$ ) and vertebrates

( $z=0.29$ ; Triantis, Guilhaumon, and Whittaker 2012), as well as slope values for sound-producing taxa at Balbina (Table S9). Additionally, the similarity between our identified small island thresholds and those in species-based studies at Balbina (Benchimol and Peres 2015; Bueno and Peres 2019) further strengthens evidence of a positive relationship between soniferous species richness and soundscape richness, as previously observed in Luypaert et al. (2022). These findings highlight the potential utility of soundscape richness as a proxy to capture patterns in soniferous species richness and explore the processes that drive them.

## 5 | Conclusion

In this study, we extended the principles of island biogeography to the field of ecoacoustics. We examined the relative importance of island size and isolation in predicting the spectrotemporal richness of acoustic traits in the landscape, also known as soundscape richness. We provide evidence for a positive relationship between the soundscape richness and island size, which we term the SoundScape Area Relationship (SSAR). We further show that this relationship breaks down at the smallest spatial scales, a phenomenon known as the small-island effect. By partitioning the soundscape richness into components of alpha, beta, and gamma diversity, and linking observed trends with expected patterns under various ecological mechanisms, we offer support for a direct effect of soniferous species on the acoustic trait diversity across the landscape. These findings point towards the potential use of soundscape richness as a biodiversity proxy and highlight the use of acoustic indices as non-invasive and efficient tools to study biogeography and spatial biodiversity dynamics in biologically complex ecosystems like

rainforests. Finally, the results of this study have broader implications for understanding the effects of habitat loss and fragmentation/insularization on biodiversity, demonstrating that such effects extend beyond species loss to a general reduction in the complexity of ecological communities, including the impoverishment of natural soundscapes.

### Author Contributions

T.L. performed the data analysis and drafted the manuscript. A.S.B. and C.A.P. were responsible for the sampling design and data collection. T.L., A.S.B., C.A.P., and T.H. all contributed substantially to the study conception and manuscript revisions.

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### Data Availability Statement

The data and code that support the findings of this study are openly available on Data Dryad at <http://doi.org/10.5061/dryad.p2ngf1vzw>.

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### Supporting Information

Additional supporting information can be found online in the Supporting Information section.