Received: 17 February 2021 | Accepted: 27 April 2022

DOI: 10.1111/2041-210X.13924

Methods in Ecology and Evolution BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

A framework for quantifying soundscape diversity using Hill numbers

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Funding information
Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 200463/2014-4 and 309473/2019-5; Natural Environment Research Council, Grant/Award Number: NE/J01401X/1; Norges Miljø- og Biovitenskapelige Universitet; Reserva Biológica do Uatumã; Rufford Foundation, Grant/Award Number: 17715-1; University of East Anglia

Handling Editor: Sarab Sethi

Abstract

1. Soundscape studies are increasingly used to capture landscape-scale ecological patterns. Yet, several aspects of soundscape diversity remain unexplored. Although some processes influencing acoustic niche usage may operate in the 24-hr temporal domain, most acoustic indices only capture the diversity of sounds co-occurring in sound files at a specific time of day. Moreover, many indices do not consider the relationship between the spectral and temporal traits of sounds simultaneously. To provide novel insights into landscape-scale patterns of acoustic niche usage at broader temporal scales, we present a workflow to quantify soundscape diversity through the lens of trait-based ecology.
2. Our workflow quantifies the diversity of sound in the 24-hr acoustic trait space. We introduce the Operational Sound Unit (OSU), a unit of diversity measurement that groups sounds by their shared acoustic properties. Using OSUs and building on the framework of Hill numbers, we propose three metrics that capture different aspects of acoustic trait space usage: (i) soundscape richness, (ii) soundscape diversity and (iii) soundscape evenness. We demonstrate the use of these metrics by (a) simulating soundscapes to assess whether the indices possess a set of desirable behaviours and (b) quantifying soundscape richness and evenness along a gradient in species richness.
3. We demonstrate that (a) the indices outlined herein have desirable behaviours and (b) the soundscape richness and evenness are positively correlated with the richness of sound-producing species. This suggests that more acoustic niche space is occupied when the species richness is higher. Additionally, species-poor acoustic communities have a higher proportion of rare sounds and use the acoustic space less evenly.

4. Our workflow generates novel insights into acoustic niche usage at a landscape scale and provides a useful tool for biodiversity monitoring. Moreover, Hill numbers can also be used to measure the taxonomic, functional and phylogenetic diversity. Using a common framework for diversity measurement gives metrics a common behaviour, interpretation and standardised unit, thus ensuring comparisons between soundscape diversity and other metrics represent real-world ecological patterns rather than mathematical artefacts stemming from different formulae.

KEYWORDS
acoustic indices, acoustic niche usage, ecoacoustics, Hill numbers, Operational Sound Units (OSUs), passive acoustic monitoring (PAM), soundscape diversity, trait-based ecology

1 | INTRODUCTION

Passive acoustic monitoring (PAM) offers promising opportunities for ecological monitoring. Automated acoustic sensors can record environmental sound at broad spatiotemporal scales with reduced cost and human effort compared to equivalent active acoustic sampling by an in-situ observer (Gibb et al., 2019). Using acoustic data, the taxonomic diversity of a biological community can be derived by isolating and identifying species' calls, thus providing an objective and permanent record of the resident soniferous (sound producing) biological community (Gibb et al., 2019; Sugai et al., 2019). Yet, obtaining species-level information for broad spatiotemporal scales or taxonomic breadth presents numerous analytical difficulties, such as the time-consuming and knowledge-demanding nature of aural annotation, and the paucity of reliable automated species identifiers and reference databases for most taxa and regions (Gibb et al., 2019; Kahl et al., 2021; Sugai et al., 2019; Toledo et al., 2015).

In addition to taxonomic information, species' sounds carry functional significance. Acoustic signals are crucial for a broad range of social interactions including courting behaviour, territorial defence, predator avoidance and food sharing (Darwin, 1872; Seyfarth & Cheney, 2003). As such, species' sounds are subject to selective pressures at multiple scales (Zsebők et al., 2021), resulting in a wide variety of acoustic traits that are expressed in the timing, frequency and amplitude features of acoustic signals. The field of soundscape ecology exploits this variation in acoustic traits, attempting to infer ecological information from the soundscape—that is, the collection of biological (biophony), geophysical (geophony) and human-produced (anthrophony) sounds emanating from a landscape—without the need for species identification (Krause, 1987; Pijanowski, Farina, et al., 2011; Pijanowski, Villanueva-Rivera, et al., 2011). This approach assumes that the diversity of acoustic traits in the landscape can be used to understand ecological processes across spatial and temporal scales (Pijanowski, Villanueva-Rivera, et al., 2011). Consequently, more than 60 acoustic indices have been developed (Buxton et al., 2018), each of which reflects some aspect of the diversity of acoustic traits in a sound file.

The diversity of acoustic signals in trait space can illuminate underlying ecological and evolutionary mechanisms (Gasc et al., 2013). For instance, one of the cornerstone theories of soundscape ecology is the Acoustic Niche Hypothesis, which views acoustic space as a core ecological resource for which soniferous sympatric species compete, leading to partitioning of the soundscape in the time–frequency domain to avoid spectro-temporal overlap in sound production (Krause, 1993). Therefore, a more speciose community should lead to increased competition and partitioning of acoustic niche space, which is reflected in the diversity of acoustic traits. Indeed, acoustic indices have been successfully applied as proxies for the diversity of species (Depraetere et al., 2012; Towsey et al., 2014) or sound types (Pijanowski, Villanueva-Rivera, et al., 2011).

Despite recent advances, several aspects of soundscape diversity quantification remain unexplored. For instance, most indices capture acoustic patterns using either time-averaged spectrograms (collapsed in the temporal domain) or measures of variation in amplitude over time (collapsed in the frequency domain). Hence, indices are fundamentally limited in their ability to detect diversity patterns across both the spectral and temporal dimensions simultaneously (Eldridge et al., 2016). Since spectro-temporal partitioning might be one of the mechanisms dictating acoustic community assembly, considering both the spectral and temporal dimensions of the acoustic trait space simultaneously may be key to evaluating how acoustic niches are structured. Moreover, most existing acoustic indices are calculated over relatively short-duration time-scales (e.g. 1-min sound files). We suggest that assembly processes structuring the presence and distribution of sound in acoustic trait space should also be considered at broader temporal scales. As many species' sound emissions follow circadian patterns (Agostino et al., 2020), some of the temporal partitioning of acoustic niches likely occurs in the 24-hr time domain. Yet, to date, explicit quantification of the relationship among sounds in the 24-hr acoustic trait space at a landscape scale has been scarce (but see Aide et al., 2017). To do so, we require a robust framework that produces informative metrics that capture within- and between-soundscape differences in spectro-temporal trait space usage.

Here, we describe a workflow to decompose the diversity of sound in acoustic trait space, hereafter referred to as soundscape diversity. This workflow is grounded in the principles of acoustic niche theory and leans heavily on trait-based ecological research. However, rather than focussing on fine-scale temporal patterns (i.e. bioacoustics studies) or

assessing the soundscape diversity of an acoustic assemblage at a particular time of day (i.e. many soundscape studies), we propose a framework to investigate the relationship among all sounds produced in a broader 24-hr acoustic trait space at a given geographical location. We develop a novel unit of diversity measurement, the Operational Sound Unit (OSU), which groups sounds by their shared properties in acoustic trait space (i.e. sounds occupy the same temporal and frequency space). Using OSUs and building on the framework of Hill numbers (a mathematically unified family of diversity indices), we introduce three metrics that capture different aspects of the acoustic trait diversity of the soundscape: (i) soundscape richness, (ii) soundscape diversity and (iii) soundscape evenness.

Our workflow offers unique insights that complement existing soundscape diversity metrics. Dissecting the soundscape diversity into its facets can provide insights into various aspects of 24-hr acoustic trait space usage, including patterns of acoustic niche saturation, evenness, dominance or rarity. Moreover, using Hill numbers, we can quantify soundscape diversity at various scales, decomposing the regional metacommunity diversity (γ-diversity) into its local diversities (α-diversity) and a community turnover component (β-diversity) using a simple multiplicative relationship. Additionally, Hill numbers can also be used to quantify taxonomic, functional and phylogenetic diversity, which ensures that observed relationships between soundscape diversity and other facets of biodiversity represent real-world ecological patterns. If the Acoustic Niche Hypothesis holds, this means these various soundscape diversity components could shed light on the species richness or diversity of soniferous communities using a common framework of reference.

To illustrate our approach, we show that the proposed soundscape diversity metrics follow a set of fundamental criteria for trait-based diversity metrics and act in an ecologically intuitive way. Moreover, in our case study, we use an acoustic dataset from Brazilian Amazonia to investigate how the soundscape diversity metrics behave along a gradient of species richness. We find positive correlations for both soundscape richness and evenness with the richness of soniferous species.

2 | METHODS

The implementation of this workflow is facilitated by the SOUNDSCAPER package, written in the R-programming language (R Core Team, 2020) and found on GitHub (https://github.com/ThomasLuypaert/soundscapeR).

2.1 | Defining acoustic trait space

The timing, frequency and amplitude of sounds are important acoustic traits that are subject to evolutionary processes and influence community assembly. As such, we use the timing and frequency of sounds as the variables that delineate a two-dimensional acoustic trait space and employ an amplitude-based threshold value to quantify the detection/non-detection of sounds within this acoustic space.

Although soniferous species produce sounds ranging from infrasound to ultrasound, we recommend constraining the upper-frequency limit to 22,050 Hz, which is approximately the maximal frequency audible to humans (Farina, 2013). Most wildlife sounds can be found in this frequency range (Farina & James, 2016), so the evolutionary mechanisms structuring acoustic assemblages are likely strongest in this range. Moreover, in downstream analyses, we use a spectral acoustic index to capture soundscape structure, and the effects of ultrasonic frequencies on such indices are not well studied. In the temporal domain, we follow Aide et al. (2017) and consider acoustic trait space over 24 hr. The reasoning here is twofold. First, we are interested in investigating the presence of all sounds produced at a given site for a particular time of year, not just sounds at a particular time of day. Second, almost all living organisms have 24-hr circadian rhythms in sound emission (Agostino et al., 2020; Cui et al., 2011; da Silva et al., 2014; Wang et al., 2012), making 24 hr an ecologically relevant sample duration.

2.2 | Defining a unit of soundscape diversity measurement

In trait-based ecology, diversity metrics are usually based on the traits of taxonomic species and their abundance (Shaner et al., 2021). Yet, taxonomic information is not always available. In some fields of research where the taxonomic identity of individuals is unknown, Operational Taxonomic Units (OTUs)—or groups of related individuals which share a set of observed properties (Sokal & Sneath, 1963)—are used to infer system diversity. Here, we attempt to measure and compare the acoustic properties of entities (sounds) in a system (acoustic trait space) without a taxonomic link to the source organisms. Hence, to quantify the soundscape diversity, we require a unit of measurement that groups sounds by their shared acoustic properties without the need for taxonomic information.

In analogy to OTUs, we propose a novel unit of diversity measurement, Operational Sound Units (OSUs), which group sounds by their shared spectro-temporal properties. OSUs are obtained by subdividing acoustic trait space into many discrete spectro-temporal bins which are the soundscape equivalent of the time–frequency bins in a spectrogram. Despite being conceptually analogous to the time–frequency bins used to calculate the 'Acoustic Space Use' (ASU) metric in Aide et al. (2017), the OSU differs in the amplitude features that are used to capture the presence and abundance of sound in acoustic trait space, and in the resolution along the temporal axis (see below).

2.2.1 | Assessing the presence of sound in acoustic trait space

Methodological choices made during acoustic data collection, such as the temporal sampling regime and sampling rate, will affect

subsequent analyses. We provide recommendations regarding these choices in the context of our workflow in S1 and S6.1. Here, we use a sampling regime of 1 min of recording every 5 min (henceforth 1 min/5 min) and a sampling rate of 44,100 Hz.

We are interested in all biological sounds produced at a given site, regardless of which source they emanate from. Therefore, we focus on the presence of sounds exceeding a 3-dB amplitude threshold for a certain duration of time in each 1-min recording. We pool sound files from the acoustic survey at a specific site into 24-hr samples of the acoustic trait space, each sample containing all 1-min sound files obtained in a single day (00:00–23:59 hr; Figure 1a). To determine where (frequency domain) and when (time domain) sound is present in the acoustic trait space, we use the Acoustic Cover (CVR) spectral acoustic index. For each 1-min sound file, the CVR index produces a vector of values, one value for each frequency bin of the spectrogram. Each value reflects the proportion of cells in a noise-reduced frequency bin that exceeds a 3-dB threshold and ranges between 0 and 1 (see Towsey, 2017 for a detailed breakdown of index computation). We calculate the CVR index for all 1-min sound files in each 24-hr sample. Acoustic recordings are processed following Towsey (2017), computing indices using the QUT Ecoacoustics Analysis Programs software (Towsey et al., 2018; Figure 1b).

The CVR index vectors for all 1-min files in a sample are concatenated chronologically, creating a data frame with the time of recording as columns, the frequency bins as rows, and the value of the CVR index for each time–frequency bin as cells. This reveals the presence and distribution of sound in each sample of the 24-hr acoustic trait space (Figure 1c).

2.2.2 | The Operational Sound Unit (OSU)

By assessing the presence of sound in acoustic trait space as described in Section 2.2.1., we have divided the trait space into discrete time–frequency bins, grouping sounds by their acoustic properties (shared time and frequency values in trait space), thus capturing our concept of Operational Sound Units (Figure 2).

As with time–frequency bins in spectrograms, the resolution of OSUs in acoustic trait space, and thus the total number of OSUs, is variable. The temporal width of OSUs is dictated by the sound file length and the total number of OSUs in the temporal domain by the recording schedule. The 1-min duration employed for index calculation retains enough detail in the acoustic features for long-duration soundscape analysis, facilitates rapid computation, and has been used as the de facto standard in most soundscape studies (Truskinger & Towsey, 2019).

In the frequency domain, OSU resolution is determined by the width of the frequency bins of the CVR index vector. This is dictated by the sampling rate and window length, which are specified in the Fast Fourier Transformation (FFT). Choosing the appropriate window length depends on the soniferous community of interest. In S.2, we provide guidance on window length choice and recommend using a 256-sample window length. With our recording settings (44,100 Hz sampling rate, 1 min/5 min sampling regime and a window length of 256), the frequency domain consists of 128 frequency bins (number of bins = window length/2) of 172 Hz width (bin width = [sampling rate/2]/number of bins). The temporal domain consists of 288 bins (24 hr = 1440 min with 1 min/5 min recorded = 288 bins). As such, the total number of detectable OSUs in the trait space using these settings is 36,864 (128 frequency bins * 288 temporal bins).

2.3 | Assessing the prevalence of OSUs in acoustic trait space

Next, we need to attribute an importance value to each OSU. Instead of using the raw CVR values obtained in Section 2.2.1, we use an incidence-based approach to derive an importance value for each OSU.

For every 24-hr sample of each site, we use a site-specific threshold to convert the OSU's raw CVR values to a binary variable. This binary variable captures the detection (CVR value ≥ threshold = 1) or non-detection (CVR value < threshold = 0) of sound for the section of the acoustic trait space delineated by each OSU (Figure 3a). The choice of the threshold depends on the study system and is influenced by the sound transmission characteristics of the habitat and the amount of ambient noise in the surrounding environment (Darras et al., 2016). For a comparison of thresholding methods, consult S.3.

To ensure site-specific binarisation thresholds are objective, we use the 'IsoData' binarisation algorithm, available in the AUTOTHRESHOLDR R-package (Landini et al., 2017). The IsoData algorithm is borrowed from image segmentation analysis and is designed to separate pixels in the foreground from those in the background (Ridler & Calvard, 1978). In the context of our workflow, the algorithm determines an initial threshold value based on the mean CVR index value of the site's soundscape. Based on this threshold, it divides the OSUs into two classes (foreground and background), calculates their mean CVR index values and updates the threshold to be the mean of these two mean values. This process is repeated iteratively until threshold convergence is achieved.

Finally, we compute the mean relative OSU abundance by averaging each OSU's binary values across all 24-hr samples of the acoustic trait space for a site (Figures 3b,c). To avoid confusion between sound frequency (Hz) and incidence frequency (relative number of OSU occurrences), we henceforth refer to the OSU importance value as the relative abundance.

2.4 | Quantifying soundscape diversity using Hill numbers

When quantifying the diversity of a system, diversity is typically broken down into two components: richness and evenness (Hill, 1973). Here, we add a third component, soundscape diversity, which incorporates aspects of the former two. Although a large number of indices have been proposed to measure diversity,

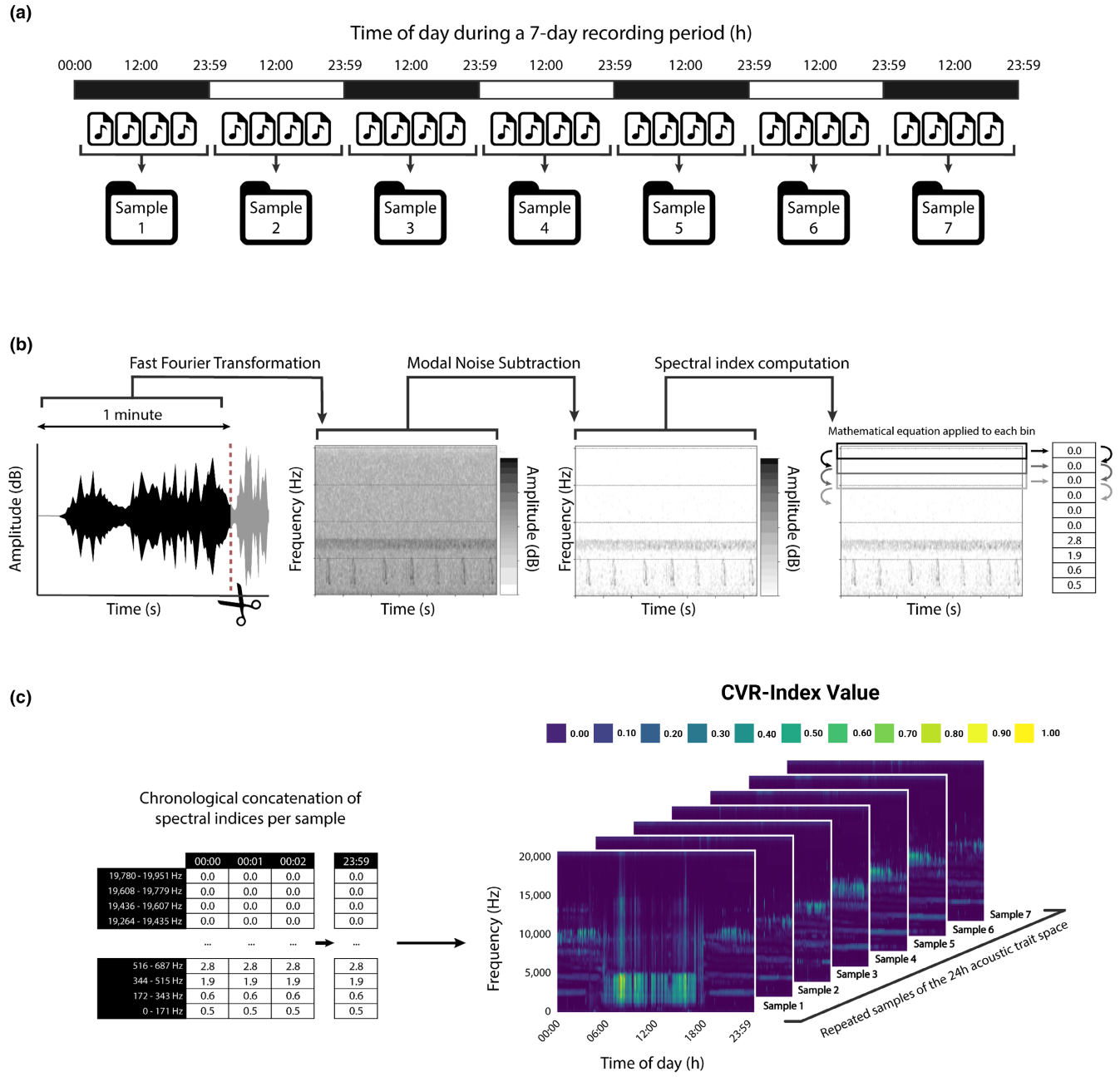

FIGURE 1 A visual representation of the workflow steps used to assess the presence of sound in acoustic trait space. (a) Sounds in the recording period (7 days) are pooled into 24-hr samples of the acoustic trait space. (b) For each sample, all sound files are cut into 1-min segments. Each 1-min segment is subjected to a Fast Fourier Transformation (FFT), followed by modal noise subtraction and spectral index computation, resulting in a spectral index vector (CVR index) for each 1-min file. (c) For all sound files per 24-hr sample, the CVR index vectors are concatenated chronologically, resulting in a data frame with time-of-day as columns, frequency bins as rows and the CVR values as cells. Finally, we obtain repeated samples of the 24-hr acoustic trait space, each of which shows the presence of sound in the time–frequency domain.

there is a growing consensus that Hill numbers are the most appropriate framework to separate system diversity into its various components (Chao et al., 2014; Hill, 1973; Jost, 2006). Unlike entropy indices, Hill numbers scale proportionally with underlying diversity—when system diversity doubles, so does the index value (the replication principle—see S.5.4 for demonstration). Moreover, Hill numbers can be used to measure not only soundscape diversity, but also taxonomic, functional and phylogenetic diversity, giving metrics a common behaviour, interpretation and standardised unit (Chao et al., 2014). This ensures comparisons between soundscape diversity and other diversity types represent real-world ecological patterns, rather than mathematical artefacts stemming from different formulae. Finally, this framework also allows decomposing the regional metacommunity diversity (γ-diversity) into its local diversity (α-diversity) and community turnover (β-diversity) components.

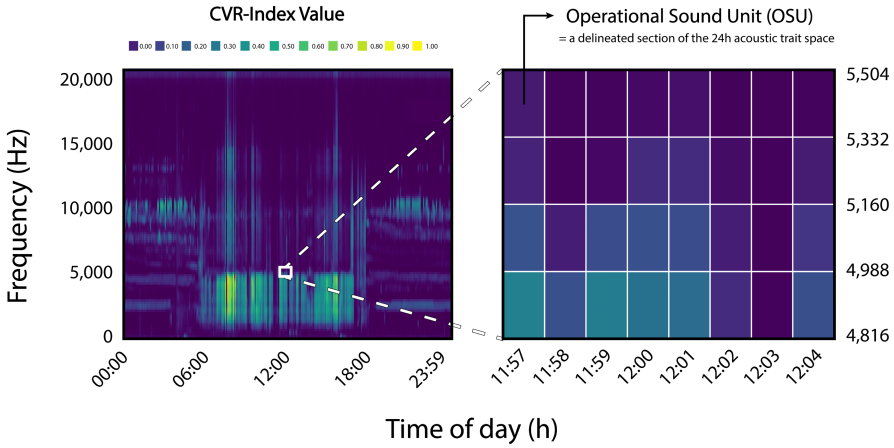

FIGURE 2 A conceptual visualisation of Operational Sound Units (OSUs) in the 24-hr acoustic trait space. Each 24-hr sample of the acoustic trait space can be divided into sections which we define as OSUs. These OSUs are delineated by the frequency-bin width of the spectral index vector (frequency domain) and the recording interval of the sampling regime (temporal domain), and group sounds by their shared functional properties in acoustic space.

Hill numbers are computed as follows:

$$ {}^{q}D = \left(\sum_{i=1}^{S} p_i^q \right)^{\frac{1}{(1-q)}} \quad (1) $$

With S being the number of OSUs, *pi* the relative abundance of OSU *i*, and *q* the order of diversity. This equation expresses the diversity of the system as the 'effective number of entities' (OSUs)—the number of equally abundant OSUs that would yield the same value of diversity.

Here, we briefly describe the soundscape richness, diversity and evenness components and introduce the indices used for their measurement in the acoustic trait space.

2.4.1 | Soundscape richness and diversity

Sensitivity to the relative abundance of OSUs is modulated using the order of diversity (*q*) without changing the interpretation of ${}^{q}D$. When $q = 0$, relative abundance is disregarded and Equation (1) yields ${}^{0}D$=S, that is, the richness of OSUs in acoustic trait space—or soundscape richness. In our workflow, soundscape richness measures the amount of acoustic trait space occupied by OSUs throughout the acoustic survey at a site without considering their relative abundance. Conceptually, our soundscape richness metric is analogous to the soundscape saturation metric in Burivalova et al. (2018); however, they measure the saturation of acoustic trait space at a 1-min scale. Similarly, our metric is related to the acoustic space use (ASU) metric described in Aide et al. (2017), which quantifies the saturation of acoustic trait space on a 24-hr scale, but uses a different methodology to detect sounds and aggregates those sounds at broader 1-hr intervals.

The higher the order of diversity *q*, the greater the weight given to highly abundant OSUs. For instance, when $q = 1$, soundscape diversity ${}^{1}D$ equals the exponential of the Shannon entropy or the number of common OSUs in the soundscape. When $q = 2$, the soundscape diversity ${}^{2}D$ equals the inverse of the Simpson index, or the number of dominant or highly abundant OSUs in the soundscape. These three Hill numbers represent simple transformations of the traditional and well-established diversity indices and calculate mean species rarity using the arithmetic ($q = 0$), geometric ($q = 1$) and harmonic means ($q = 2$; Hill, 1973). Although the soundscape richness and diversity metrics are usually expressed in the total number of OSUs, soundscape metrics can still be compared between soundscapes with differing dimensions (a different number of detectable OSUs due to window length/sampling regime differences) by dividing the soundscape richness or diversity by the total number of detectable OSUs in the soundscape.

2.4.2 | Soundscape evenness

Evenness describes the equitability of abundances (Hill, 1973). Various measures of evenness can be calculated by taking the ratio between Hill numbers ${}^{q}D$ with $q = 1, 2, \ldots$, and the richness ${}^{0}D$ (Jost, 2010). Here, the choice of *q*-value determines the importance of OSU abundance on the evenness metric. For instance, since ${}^{1}D$ roughly represents the number of common OSUs in the acoustic trait space, the evenness ratio ${}^{1}D/{}^{0}D$ represents the proportion of common OSUs in the community. Similarly, as ${}^{2}D$ represents the number of dominant OSUs, the evenness ratio represents the proportion of dominant OSUs. Different *q*-values differ in the sharpness of the cut-off between rarity, commonness or dominance.

These patterns in evenness are best represented by constructing diversity profiles, a type of visualisation showing a series of Hill numbers derived using a continuous function of the order of diversity *q* (Chao et al., 2012; Jost, 2007; see Figure S11). Diversity profiles provide the most complete representation of the soundscape evenness, giving the relative abundance distribution of OSUs in the soundscape, and highlighting changes in diversity with changing importance of rarity. As soundscape diversity and evenness can both be calculated for an infinite number of *q*-values, for the remainder of this work we will follow Jost (2006) and define diversity as ${}^{2}D$ and evenness as ${}^{2}D/{}^{0}D$. We make this choice because $q = 2$ corresponds to a common biodiversity metric used in literature (the Simpson index) and the *q*-value is large enough to incorporate patterns of rarity and dominance in the acoustic community.

In S.4, we outline the theoretical framework for decomposing the soundscape diversity into its alpha, beta and gamma components.

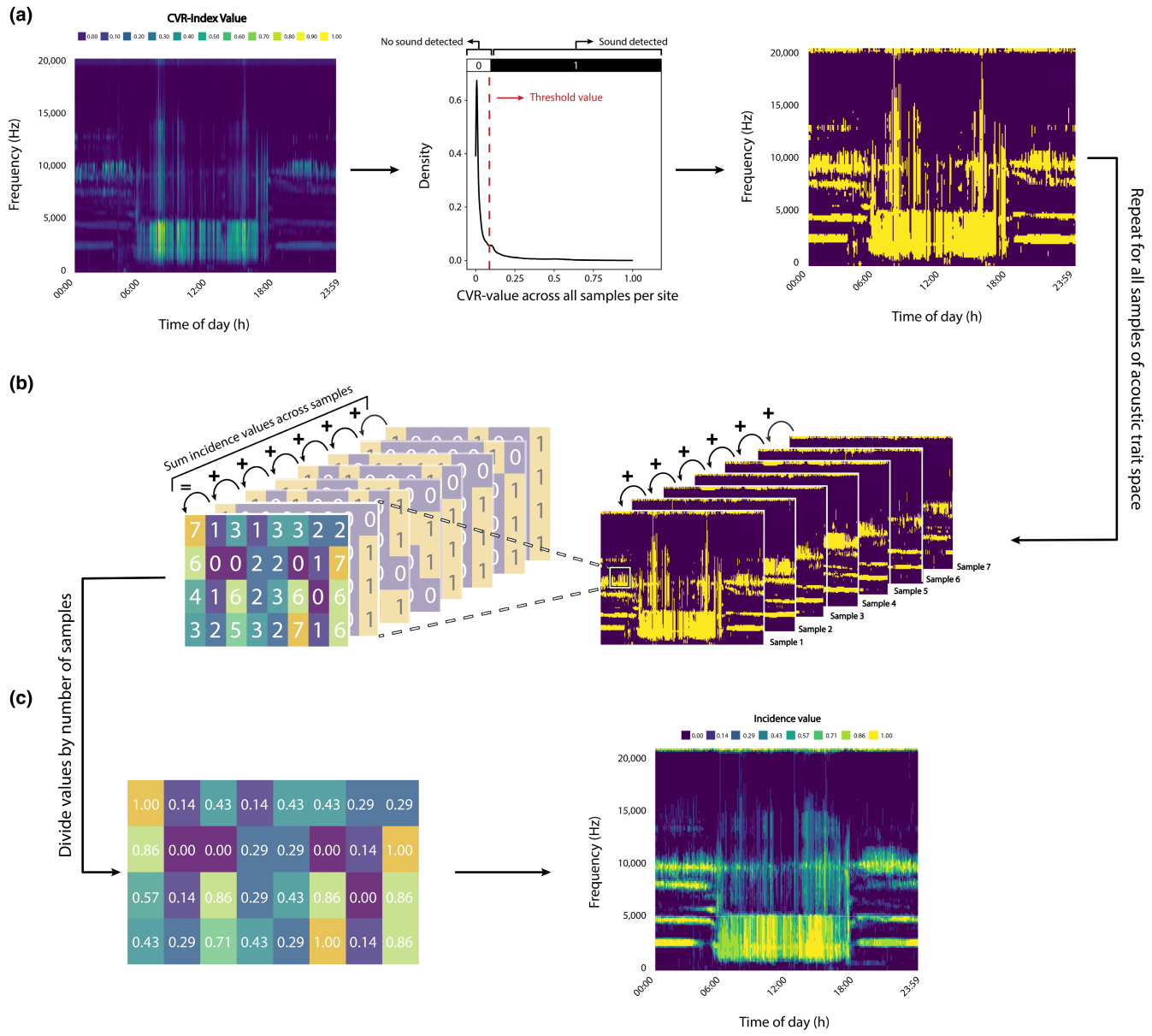

FIGURE 3 A conceptual representation of the methodology used to attribute an importance value to OSUs in acoustic trait space. (a) Per site, a binarisation algorithm is applied to each sample of acoustic trait space, resulting in a binary variable representing the detection/non-detection of OSUs across samples; (b). For each OSU, the detection (1) or non-detection (0) values are summed across all 24-hr samples of acoustic trait space for that site and divided by the number of samples to obtain the OSU's relative abundance (incidence frequency); (c) The presence, relative abundance and distribution of OSUs in acoustic trait space.

In S.5, we illustrate the behaviour and intuitive properties of the proposed soundscape diversity metrics by simulating artificial soundscapes. The simulated datasets serve to demonstrate the behaviour of the metrics with respect to some fundamental criteria for trait-based diversity metrics, as outlined in Ricotta (2005), Villéger et al. (2008), and Mouchet et al. (2010).

3 | CASE STUDY

To explore the behaviour of our metrics of soundscape diversity in a real-life ecological setting, we characterised the soundscape richness and evenness along a gradient in soniferous species richness using an empirical dataset from Brazilian Amazonia (1°40′S, 59°40′W). Acoustic data were collected at 35 sites for 4–10 days in the Balbina Hydroelectric Reservoir (BHR) in Brazilian Amazonia (see Supporting Information S6.2 and Bueno et al., 2020 for further details). This work was conducted under the SISBIO 49068 research permit.

Under the Acoustic Niche Hypothesis, we expected soundscape richness to be positively related to soniferous species richness (Krause, 1993). For soundscape evenness, we did not expect a relationship with species richness unless changing species richness was associated with a shift in the relative abundance distribution of the acoustic community (Wilsey et al., 2005).

3.1 | Compound species richness of soniferous taxa

To assess the relationship between the soundscape diversity metrics and soniferous species richness, we generated a compound species richness index of three major tropical forest soniferous taxa: (i) anurans (Bueno et al., 2020), (ii) birds (this study) and (iii) primates (Benchimol & Peres, 2015). Species richness data for these three groups came from a manual and automated extraction from audio recordings and data from the literature (see Supporting Information S6.3). A total of 34 anuran species, 71 bird species and 7 primate species were detected across the 35 sites. We summed the richness values for these three taxa to obtain the compound richness index. Due to the absence of available taxonomic richness data, this compound richness did not include insects, a dominant acoustic group in tropical forests (Aide et al., 2017). However, we deem the combined acoustic activity of these three taxonomic groups to be sufficiently strong to influence the rainforest soundscape, and therefore be detectable with our soundscape diversity metrics.

3.2 | Soundscape diversity data

We calculated the soundscape richness and evenness for all sites using the workflow described above (see S.6.4). A priori knowledge of acoustic space usage can be used to subset the acoustic trait space to those time-frequency coordinates used by the soniferous groups of interest (Metcalf et al., 2020). This can reduce signal masking, and increase the sensitivity of soundscape metrics to species richness. We restricted the frequency domain below 11,025 Hz, where most anuran, bird and primate sounds are found, and excluded the part of the frequency spectrum dominated by insects. As the sampling duration was unequal between plots in the study, and we wished to retain the maximal amount of information, we used sample size-based rarefaction to equalise sampling effort among plots (see S.1). At most, we extrapolated to double the minimal sample size (Chao & Jost, 2012). We used the R-package *'iNEXT'* (Hsieh et al., 2016) to calculate soundscape richness (${}^0D$) and evenness (${}^2D/{}^0D$) at a sampling effort of 8 days (twice the minimal sampling duration). Finally, we used a simple linear regression model to investigate the relationship between soundscape richness and evenness, and compound soniferous species richness. We provide additional analyses on the effect of sampling regime and window length on the relationship between soundscape richness and species richness in S.1.2.2 and S.2.

4 | RESULTS

4.1 | Properties of soundscape diversity metrics

Soundscape richness, evenness and diversity had strictly positive values constrained between 0 and 1, and are theoretically independent of the species richness (S.5.1). The monotonicity criterion held true for the soundscape richness and diversity metrics, but not for soundscape evenness (S.5.2). Soundscape richness and evenness were independent of one another and described unique aspects of the soundscape diversity (S.5.3). Conversely, soundscape diversity at $q = 2$ displayed a positive relationship with both soundscape richness and evenness, and thus did not conform to the independence criterion. Unlike some commonly used biodiversity indices (i.e. Shannon–Wiener and Simpson biodiversity index), our metrics scaled linearly with the underlying diversity of the system—a theorem known as the replication principle (S.5.4). Finally, the same analytical workflow can be used to quantify the soundscape diversity at multiple scales or hierarchical levels, decomposing the regional metacommunity diversity (γ-diversity) into its local diversity (α-diversity) and community turnover (β-diversity) components using a simple multiplicative relationship (S.4; S.5.6).

4.2 | Relationship between soundscape metrics and species richness

The correlation between soundscape richness and soniferous species richness in our case study was strongly positive ($r = 0.85$; $R^2 = 0.72$; $p < 0.001$; Figure 4a-1; Table S4). This positive correlation was consistent, even for lower intensity sampling regimes (S.1.2.2), with r values staying high (>0.8) at all tested sampling intensities. We found that window length had a negligible impact on the correlation between both metrics ($r > 0.83$ for all window lengths; see S.2). Based on the visual inspection of acoustic trait space, sites containing a lower richness of soniferous species (Figure 4a-2) appeared to have more empty and less complex trait spaces than species-rich sites (Figure 4a-3). The trait space of low-richness sites had impoverished daytime soundscapes and lacked many of the sounds exceeding 5000 Hz that were present at taxonomically rich sites. For soundscape evenness, the correlation with soniferous species richness was weakly positive ($r = 0.40$; $R^2 = 0.16$; $p < 0.05$: Figure 4b-1). For low-evenness sites, low abundance sounds were more common compared to sites with a high soundscape evenness (Figure 4b-2 and 3).

5 | DISCUSSION

5.1 | Advantages of the workflow

Our soundscape metrics abided by a set of fundamental criteria for trait-based diversity indices (Mouchet et al., 2010; Ricotta, 2005; Villéger et al., 2008) and behaved in an ecologically intuitive manner. Furthermore, separating soundscape diversity into richness, evenness and diversity, and assessing how these behaved along a gradient of species richness, shed light on patterns of acoustic niche usage. Among the various theories that explain acoustic community assembly and niche usage, two hypotheses prevail in the soundscape literature: the Acoustic Adaptation Hypothesis and the Acoustic Niche Hypothesis (Pijanowski, Farina, et al., 2011; Pijanowski,

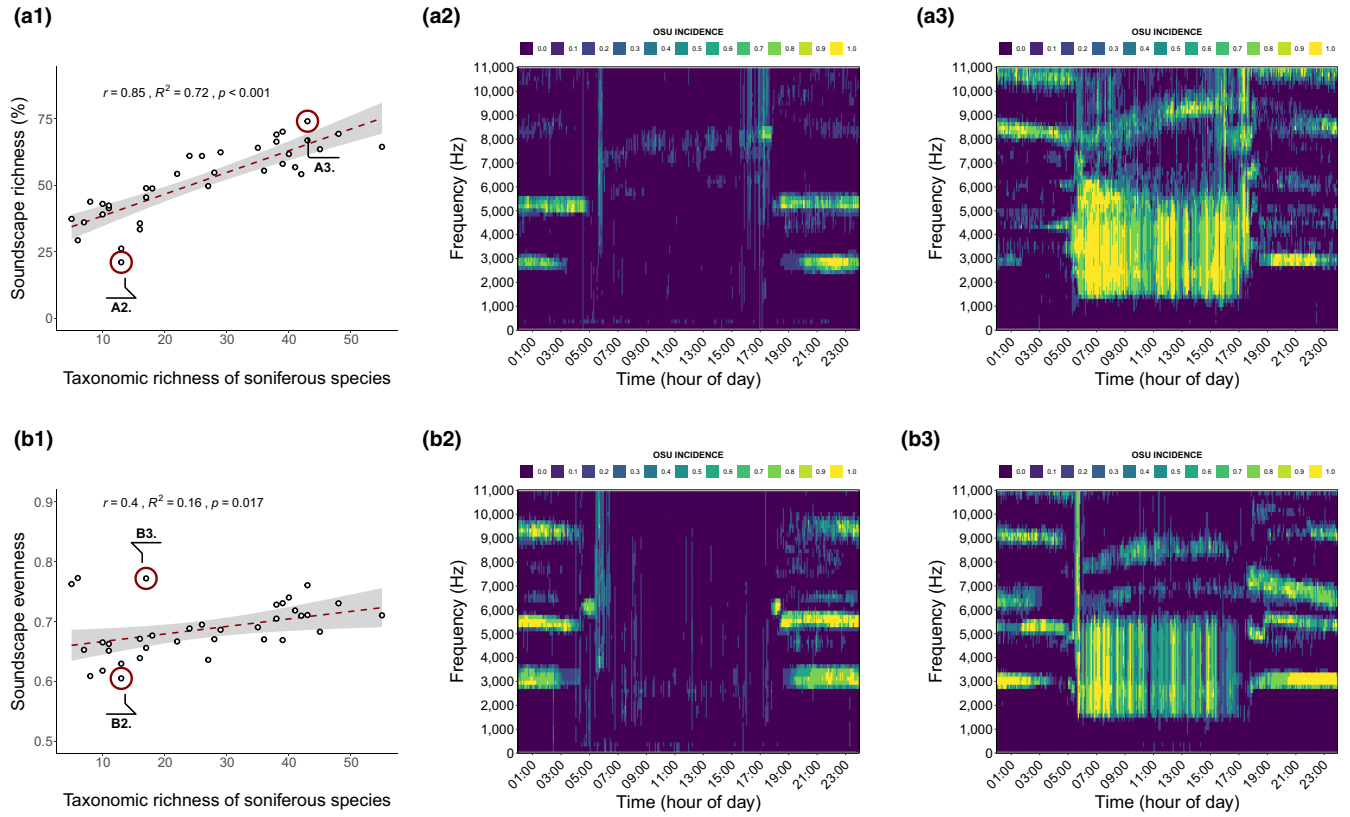

FIGURE 4 (a) The relationship between the soundscape richness and the richness of soniferous species (a1) with a visual representation of the 24-hr acoustic trait space for low-richness (a2) and high-richness (a3) soundscapes. The Pearson correlation coefficient and associated R^2- and *p*-values indicate a strong positive relationship ($r = 0.85$) between the soundscape richness and species richness of sound-producing vertebrates. (b) The relationship between the soundscape evenness and the richness of soniferous species (b1) with a visual representation of low-evenness (b2) and high-evenness (b3) soundscapes. The Pearson correlation coefficient and associated R^2- and *p*-values indicate a weak positive correlation ($r = 0.40$) between the soundscape evenness and species richness.

Villanueva-Rivera, et al., 2011). The former posits that species' acoustic traits (e.g. signal frequency, amplitude, timing and duration) are more similar than expected by chance as the environment filters for traits that maximise effective sound propagation and minimise attenuation (Mullet et al., 2017). The latter states that acoustic trait space is a core ecological resource and sonically sympatric species partition their acoustic niche so as to avoid spectro-temporal overlap in their vocalisations, which would lead to inefficient communication (Garcia-Rutledge & Narins, 2001; Krause, 1993). The Acoustic Niche Hypothesis implies that evolutionarily archaic and undisturbed ecosystems have acquired an evolutionary balance between all sounds in the landscape, resulting in soundscapes with high spectro-temporal complexity and signal diversity, and minimal overlap (Eldridge et al., 2016; Krause, 1993; Pijanowski, Farina, et al., 2011; Pijanowski, Villanueva-Rivera, et al., 2011). Conversely, disturbed systems in which '*acoustically optimised*' species have been lost from the habitat are then characterised by an unbalanced equilibrium, showing readily detectable gaps in the soundscape.

Our soundscape richness metric quantifies the amount of acoustic niche space occupied by OSUs independent of how frequently OSUs were occupied over multiple days (the relative abundance). In our case study, we found a strong positive correlation ($r = 0.85$; $R^2 = 0.72$; $p < 0.001$) between soundscape richness and soniferous species richness. Soundscape richness is theoretically independent of species richness, so the observed relationship likely arose through processes of species assembly. Following the Acoustic Adaptation Hypothesis, we expected the richness of OSUs, driven by the richness of acoustic trait values, to be mostly insensitive to the richness of soniferous species. Given the strong positive relationship between soundscape richness and soniferous species richness, it is likely the acoustic community in the case study was structured by competition for acoustic niche space. As the species richness gradient in our study area originated from a disturbance event, it is plausible that the observed correlations between soundscape richness and species richness stemmed from the loss of species occupying unique acoustic niches in the acoustic trait space, resulting in a lower niche saturation at lower species richness.

The soundscape evenness metric captures the degree to which the relative abundances of OSUs are distributed in niche space. Hence, it quantifies how evenly the available acoustic resources are used at a landscape scale and sheds light on patterns of dominance and rarity. In the case study, soundscape evenness displayed a weak positive correlation ($r = 0.40$; $R^2 = 0.16$: $p < 0.05$)

with soniferous species richness. Changes in soniferous species richness were associated with changes in the distribution of the relative abundance of sounds in acoustic trait space. We posit that the correlation between soundscape evenness and soniferous species richness could reflect an unbalanced equilibrium, in which the acoustic community consists of a few acoustically dominant and many rare sound-producing species (Krause, 1993). As such, it appears that disturbed species-poor acoustic communities used acoustic niche resources less effectively (Mason et al., 2005). Indeed, the combination of both richness and evenness metrics provides unique insights into acoustic niche usage. Yet, many existing soundscape diversity metrics focus solely on the presence of sound in a short duration recording without accounting for the prevalence of sound in those same areas of acoustic trait space over the course of multiple days, thus overlooking the evenness component of soundscape diversity.

Our workflow potentially offers a robust and cost-effective method to track biodiversity changes at large spatial and temporal scales, or in systems where the knowledge of the resident biological community is incomplete. The strong positive correlation between soundscape richness and an independent estimate of soniferous species richness suggests this metric can be used as a proxy to infer taxonomic diversity patterns. Hence, it could be used as an early warning system, alerting researchers when declines in soundscape diversity exceed natural fluctuations (Krause & Farina, 2016; Pijanowski, Farina, et al., 2011; Pijanowski, Villanueva-Rivera, et al., 2011). The soundscape richness metric performed well as a biodiversity proxy compared to analogous metrics in the literature. For instance, in Burivalova et al. (2019), soundscape saturation (saturation of acoustic niche space for 1-min sound files), achieved a correlation of $r = 0.56$ and $R^2 = 0.31$ with the number of unique vertebrate calls (sonotypes) identified in the same sound file. The Acoustic Space Use metric in Aide et al. (2017) has a similarly strong relationship to our metric (Spearman's $\rho = 0.85$), but had a relatively small sample size (8 plots). Moreover, both studies investigated the correlation with the number of unique calls, whereas our study investigated the correlation with species richness. The former can be expected to attain higher correlations, as different calls tend to take up different parts of acoustic trait space and thus influence the soundscape saturation or acoustic space use more directly. Still, our workflow achieved high correlations, corroborating the robustness of the method.

Furthermore, even when a correlation is absent, our method allows us to measure where and when in acoustic trait space the occurrence and relative abundance of sound changes across space, time or hierarchical levels (e.g. local, regional or global) without requiring a link to the taxonomic identity of OSUs. In our case study, a visual comparison of acoustic trait space use between two extremes of the soundscape richness gradient showed that low-richness sites had an impoverished daytime soundscape and lacked sounds over 5000 Hz. Moreover, the low-evenness soundscape had a higher proportion of rare OSUs, suggesting the acoustic niche resource was used less effectively.

Finally, our workflow is robust, identifying an ecological gradient in an acoustically complex tropical rainforest setting. We used an amplitude threshold to remove transient and non-biological sounds. Although this step did not remove persistent non-focal high amplitude sounds, such as rain showers, thunder or wind, from the data, we still found strong positive correlations with species richness. Moreover, both the window length and sampling intensity had a minimal effect on the soundscape richness–soniferous species richness correlation. Additionally, the soundscape variability was captured with fewer hours of recording (a minimum of 24 hr) than previously suggested (i.e. 120 hr in Bradfer-Lawrence et al., 2019), although the minimum acoustic survey length needed to be the same (5 days). Yet, as ecosystems can differ in their sound turnover rate and therefore require different sampling efforts, we recommend sampling the soundscape for longer durations and/or higher sampling intensity if possible.

5.2 | Avenues of future research

The soundscape diversity metrics outlined herein treated all OSUs as equally similar. In reality, OSUs are not independent elements, but rather correlated units in acoustic trait space. As such, future work on our soundscape diversity metrics should incorporate the difference in acoustic trait values (time–frequency coordinates) of a particular OSU from all other OSUs in the acoustic space (Scheiner et al., 2017). Incorporating the distinctiveness of OSUs in acoustic trait space (soundscape dispersion) would allow us to further quantify the degree to which acoustic trait space is partitioned, providing further insights into acoustic niche differentiation and resource competition (Mason et al., 2005). For instance, if acoustic communities are structured by competition for acoustic space, we might expect overdispersion in acoustic trait space compared to the same number of OSUs drawn randomly from the regional OSU pool. Conversely, when the dispersion of OSUs in acoustic space is lower than expected compared to the randomly drawn OSU pool, environmental filtering is likely to be an acting process (Scheiner et al., 2017).

In this paper, we opted for an incidence-based approach to attribute an importance value to OSUs. Yet, the use of threshold values to convert continuous variables to detection/non-detection data has been critiqued in the literature (Lawson et al., 2014), as it results in information loss and complicates comparisons between different sites/studies for which different optimal threshold values may apply. Still, we posit this approach can be appropriate for soundscape data. Although acoustic indices are known to capture animal activity, there is an ongoing debate about their ability to capture patterns of abundance (Boelman et al., 2007; Bradfer-Lawrence et al., 2020). Moreover, acoustic indices can be sensitive to confounding environmental factors (Gasc et al., 2015). For instance, CVR index values may respond to abiotic sounds, such as geophony and anthrophony, which are considered confounding factors if the aim is to capture biophonic sounds. Additionally, the index values

can also be susceptible to the relative amplitude of songs in recordings, which, in turn, are shaped by the properties of the surrounding vegetation, the distance of the sound-emitting animal to the sensor, inherent biological differences between species and meteorological conditions (Bradfer-Lawrence et al., 2020). We argue that converting raw CVR index values to binary detection/non-detection data will reduce potential differences among sites and eliminate the non-focal transient and low amplitude sounds from the data. Even so, the influence of incidence-based versus continuous importance values on the observed patterns warrants further investigation.

Nonetheless, choosing a threshold value that is valid in all ecological contexts and accurately removes non-target sounds while retaining enough information to capture patterns in niche usage represents a challenge. Deriving a unique threshold value for each study system by validating the ability of the soundscape diversity metrics to capture a species richness gradient is not a feasible approach, as taxonomic data will not always be available. We found that the approach in Burivalova et al. (2018), for which the chosen threshold yields the most normal distribution of the obtained soundscape metric, did not yield the strongest correlation with species richness. Although a constant threshold value worked well for our specific case study, this threshold value will likely be different for other ecosystems, seasons or levels of non-target sound. We recommend that future studies derive incidence data using context-aware binarisation algorithms (see S.3). These algorithms produce a unique binarisation threshold per site by considering the distribution of CVR values in the acoustic trait space, which, in turn, is influenced by the soniferous community and sound transmission characteristics of the habitat. We found that the 'IsoData' binarisation algorithm worked best for our data, but further research in a wider variety of habitats is needed to confirm that this algorithm is consistently most appropriate.

Finally, we only used the CVR index to capture the amplitude features of our soundscapes. We posit that other spectral indices, alone or in combination, may better reflect sounds from specific taxonomic groups. For instance, cicada choruses are characterised by loud and long-duration stridulations, usually restricted to narrow frequency bands and often leaving wide frequency band footprints due to harmonics. Previous work suggests these features can be captured by a set of spectral indices: low spectral entropy, high background noise and high spectral density (Brown et al., 2019; Ferroudj et al., 2014; Towsey et al., 2014). Thus, these three indices could be combined into a compound soundscape diversity index, which could then be used to decompose the diversity of cicada choruses in 24-hr acoustic trait space.

6 | CONCLUSION

In this study, we present a novel workflow for the quantification of soundscape diversity that builds on trait-based ecology and uses Hill numbers to generate a robust set of soundscape diversity metrics. By broadening the temporal scope of soundscape diversity quantification to cover 24 hr, and considering the spectral and temporal traits of sound simultaneously, these soundscape diversity metrics can yield novel insights into acoustic trait space usage at multiple spatiotemporal scales and act as a useful tool for biodiversity monitoring.

AUTHORS' CONTRIBUTIONS

T.L. designed the workflow, coded the accompanying package, analysed the case study and supplementary material data, and wrote the manuscript; A.S.B., T.H. and C.A.P. made significant contributions to the study conception, design and manuscript revision; A.S.B. and C.A.P. managed the design and collection of acoustic data; G.S.M. and I.L.K. performed identification of anuran species in sound files; M.C.-C. performed the aural identification of bird species in sound files. All authors contributed to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

For their assistance in data collection, we are very grateful to Evanir Damasceno, Tatiane Abreu and Carla Fonseca. We are thankful to the staff at Reserva Biológica do Uatumã for logistical support. Data collection was funded by the Rufford Foundation (grant 17715-1), Reserva Biológica do Uatumã (ICMBio), the University of East Anglia and a NERC/UK grant (NE/J01401X/1) awarded to C.A.P. A.S.B. was funded by a PhD studentship (grant 200463/2014-4) from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq)—Brazil, which also awarded a productivity grant to I.L.K. (309473/2019-5). T.L. is supported by a PhD studentship from the Norwegian University of Life Sciences. We thank two anonymous reviewers for their constructive comments which considerably improved the manuscript quality.

CONFLICT OF INTEREST

We declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The raw sound files used in the case study and supplementary materials are stored at https://arbimon.rfcx.org/project/balbina/dashboard. The processed data and code used in the case study and supplementary materials are available at https://doi.org/10.5061/dryad.1vhhmgqtq (Luypaert et al., 2022).

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SUPPORTING INFORMATION

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

How to cite this article: Luypaert, T., Bueno, A. S., Masseli, G. S., Kaefer, I. L., Campos-Cerqueira, M., Peres, C. A., & Haugaasen, T. (2022). A framework for quantifying soundscape diversity using Hill numbers. *Methods in Ecology and Evolution*, *13*, 2262–2274. https://doi.org/10.1111/2041-210X.13924