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Methods in Ecology and Evolution

PERSPECTIVE

Using acoustic indices in ecology: Guidance on study design, analyses and interpretation

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Abstract

1. The rise of passive acoustic monitoring and the rapid growth in large audio datasets is driving the development of analysis methods that allow ecological inferences to be drawn from acoustic data.
2. Acoustic indices are currently one of the most widely applied tools in ecoacoustics. These numerical summaries of the sound energy contained in digital audio recordings are relatively straightforward and fast to calculate but can be challenging to interpret. Misapplication and misinterpretation have produced conflicting results and led some to question their value.
3. To encourage better use of acoustic indices, we provide nine points of guidance to support good study design, analysis and interpretation. We offer practical recommendations for the use of acoustic indices in the study of both whole soundscapes and individual taxa and species, and point to emerging trends in ecoacoustic analysis. In particular, we highlight the critical importance of understanding the links between soundscape patterns and acoustic indices.
4. Acoustic indices can offer insights into the state of organisms, populations, and ecosystems, complementing other ecological research techniques. Judicious selection, appropriate application and thorough interpretation of existing indices is vital to bolster robust developments in ecoacoustics for biodiversity monitoring, conservation and future research.

KEYWORDS
acoustics, biodiversity indices, ecoacoustics, index, monitoring, passive acoustic monitoring, soundscape

1 | INTRODUCTION TO SOUNDSCAPES & ACOUSTIC INDICES

Ecoacoustics is a growing ecological discipline that investigates the ecological role of sound across levels from individual organisms to communities and landscapes (Sueur & Farina, 2015). Recent technological advances have increased the availability of low-cost, robust, passive acoustic recorders (e.g. Hill et al., 2018), facilitating the collection of vast audio data sets (Roe et al., 2021). While audio recordings can be readily collected, the analysis methods needed to garner robust ecological insights from acoustic data are still in development (Deichmann et al., 2018; Scarpelli et al., 2021; Vella et al., 2022; Wimmer et al., 2013).

Large acoustic datasets necessitate automated processing and analysis. One approach to ecoacoustic analysis considers the acoustic environment—the **soundscape**—as a whole (Sueur & Farina, 2015), with soundscape components commonly categorised according to their source: **anthropophony**, **biophony** or **geophony** (Pijanowski et al., 2011) (bold terms defined in Table 1). There are circumstances where a target-signal approach of detecting and identifying individual sounds is the best approach. However, there are numerous situations when it may be necessary or preferable to consider broader soundscape patterns rather than identifying individual target signals. These include: (i) when species identification is difficult because vocalisations occur in dense, multi-species choruses; (ii) when studying systems where sound sources are unknown; or (iii) where questions extend beyond the species-level, focussing on issues such as community integrity, ecosystem functioning, habitat quality or the prioritisation of ecological complexity over species in restoration ecology (Bullock et al., 2022).

Soundscape analyses commonly use **acoustic indices**; numerical descriptors of the patterns and distribution of acoustic energy in an audio recording. Acoustic indices range from simple summaries such as the mean amplitude of a recording, to more complex calculations reflecting spectral and/or temporal changes within a soundscape (see Table S1 for an overview of widely used indices). No single index can provide a comprehensive description of the original recording and dozens of acoustic indices have been proposed reflecting different aspects of the soundscape (Buxton et al., 2018).

Acoustic indices characterise the soundscape or facets of the **acoustic community** and have successfully provided ecological insights without requiring species-specific identifications. For example, using acoustic indices it is possible to discriminate among habitat types (Bradfer-Lawrence et al., 2019; Do Nascimento et al., 2020; Eldridge et al., 2018; Metcalf et al., 2021), monitor the impacts of habitat disturbance (Burivalova et al., 2021, 2022; Duarte,

TABLE 1 A glossary of key terms used in ecoacoustics.

Acoustic community	An aggregation of soniferous species at a specific location and time (Farina & James, 2016)
Acoustic Adaptation Hypothesis (AAH)	The assumption that animals' soniferous signals have evolved to take account of sound propagation in their preferred habitats and that animals emit signals that optimise propagation (Marten & Marler, 1977; Morton, 1975). Support for this hypothesis is mixed (Boncoraglio & Saino, 2007)
Acoustic Niche Hypothesis (ANH)	The assumption that as acoustic space is a limited resource, animals will spatiotemporally partition their calls to avoid interference from other sounds (Krause, 1993). There is mixed support for this hypothesis (e.g. Gomes et al., 2021; Hart et al., 2021; Tobias et al., 2014)
Acoustic index	Numerical summary of the patterns and distribution of acoustic energy in digital soundscape recordings. Summaries can reflect temporal features, frequency features, or both. Sometimes called 'soundscape metrics', 'features', 'descriptors' or 'representations' (Sueur et al., 2014)
Anthropophony/ Technophony	Sound of an anthropogenic origin. Anthropophony is the older term and includes both engine noise and human speech (Pijanowski et al., 2011). Some have proposed that the latter ought to be included in biophony and so technophony has sometimes been used for anthropogenic sounds of mechanical origin
Biophony	Sound of a biological origin such as insect stridulations or bird song, but generally excluding human vocalisations (Pijanowski et al., 2011)
False-colour spectrogram (FCS)	Similar to a spectrogram (see below), but instead of a colour gradient representing amplitude, three acoustic indices are mapped to red, green and blue channels. As index values can be calculated for large datasets, FCS enables rapid visualisation of soundscapes across a range of temporal scales (Towsey, Wimmer, et al., 2014)
Geophony	Sound from natural processes such as running water, rainfall or wind as it interacts with vegetation or other landscape features (Pijanowski et al., 2011)
Sound truth	Listening to recordings to ascertain the different soundscape features therein (Holgate et al., 2021). This has also been described as 'aural survey' or 'aural inventory' of recordings. Sound truth is distinct from ground truthing, where researchers visit recording sites to identify soundscape features through in situ aural surveys for example
Soundscape	The acoustic environment of a landscape, composed of biophony, geophony and anthropophony, which create patterns of sound varying over spatial and temporal scales (Pijanowski et al., 2011). This has also been termed the 'objective soundscape' and is the focus of the current paper. This contrasts with the 'subjective soundscape', which refers to the acoustic environment as perceived by individual organisms within it, see Farina et al. (2021) and Grinfeder et al. (2022)
Spectrogram	A visual representation of the matrix derived by converting a raw audio recording using a Fast Fourier Transform, with time on the x-axis, frequency on the y-axis and amplitude values in each cell reflected with a colour or intensity gradient (Sueur, 2018)

Sousa-Lima, et al., 2021; Gasc et al., 2018; Gottesman et al., 2021; Rappaport et al., 2022), track habitat recovery following restoration (Borker et al., 2020; Lamont et al., 2022; Müller et al., 2022) and assess the suitability of that habitat for particular species in the future (Znidersic & Watson, 2022).

While there is abundant guidance on acoustic monitoring (Browning et al., 2017; Metcalf et al., 2023; Sugai et al., 2020) and methodological developments related to acoustic indices (Abrahams et al., 2021; Bradfer-Lawrence et al., 2019; Harris et al., 2016; Metcalf et al., 2021; Villanueva-Rivera et al., 2011), there remain fundamental questions regarding the appropriate use of acoustic indices. Ecoacoustics is a young field and will develop substantially. However, robust scientific advances will only be achieved if research using current acoustic indices is based on solid understanding of basic acoustics, digital signal processing, strong methodological design and clear, critical interpretation of results.

Here, we provide nine points of guidance across three phases of the research cycle to support best practice in using acoustic indices (Figure 1). We outline potential pitfalls in study design, analysis and interpretation, and provide recommendations on how best to practically address these when planning passive acoustic monitoring studies. These points have emerged from our own experiences carrying out soundscape research over the last decade and were consolidated through discussion with researchers and practitioners from the international ecoacoustic community at two workshops in 2022.

2 | IDENTIFYING YOUR PARADIGM

It is important to consider the purpose of using acoustic indices, as this will determine both the methodology and how effective they are likely to be in answering a given ecological question. To date, applications of acoustic indices can be divided into two main analytical frameworks: (i) those describing soundscape patterns and dynamics, and (ii) those using indices as proxies for biodiversity metrics such as species richness or functional diversity (Alcocer et al., 2022). These approaches require different analyses and interpretation, but the academic literature rarely draws a clear distinction between the two paradigms.

Acoustic indices can be excellent soundscape descriptors. Acoustic indices compress highly complex acoustic data into a

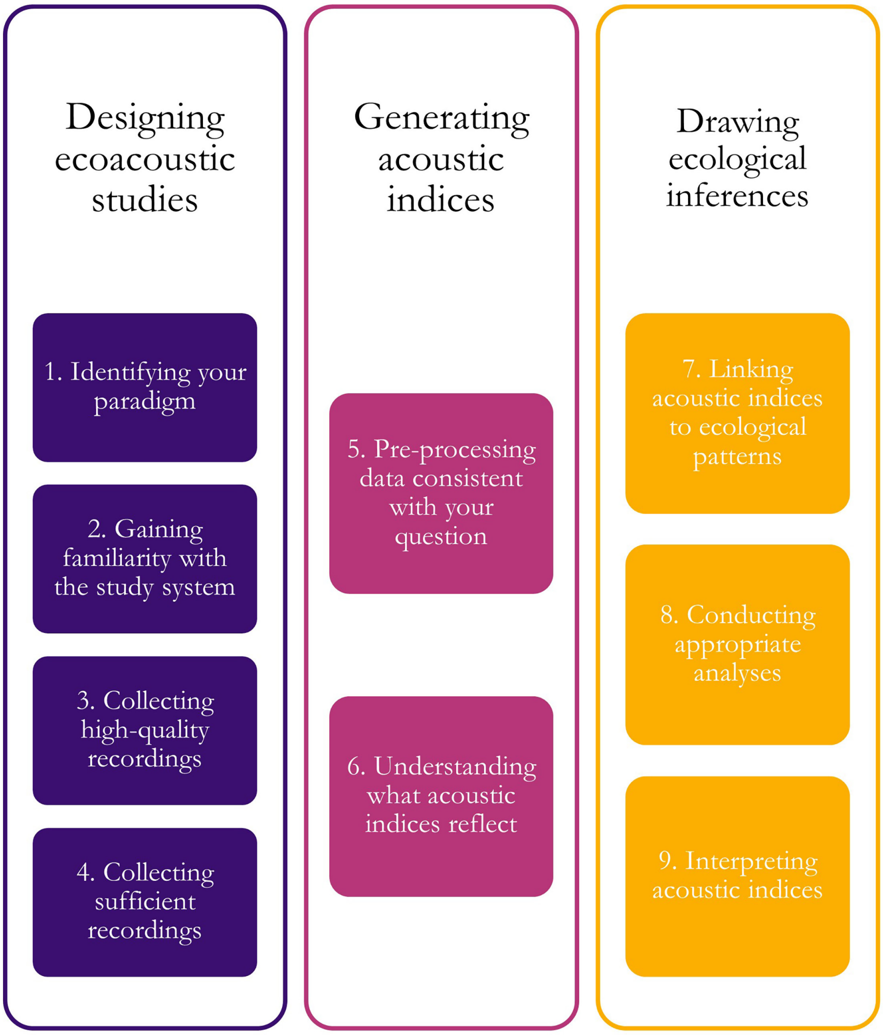

FIGURE 1 This Perspective provides guidance for decision making on nine key points at three principal stages of the ecoacoustic research process.

single value or vector of values, providing concise descriptions of soundscape patterns and thus facilitating comparisons within and among recordings. Indices can reflect biotic vocalisations, habitats and landscape features such as rivers and non-biological sounds like weather events. Analyses in this paradigm are particularly useful for:

(i) Supporting data-cleaning workflows by quickly identifying recordings for exclusion prior to other analyses, perhaps because of microphone degradation (Phillips et al., 2018), distortion (Eldridge et al., 2018) or excessive geophony (Metcalf et al., 2020; Sánchez-Giraldo et al., 2021). See Section 6.
(ii) Rapidly visualising large data sets to facilitate qualitative interpretation. For example, **false-colour spectrograms** can condense years of data into a single plot, which permits identification of dominant soundscape patterns and seasonal changes (Brodie et al., 2022; Phillips et al., 2018; Towsey et al., 2018; Towsey, Zhang, et al., 2014).
(iii) Detecting strong temporal and spatial trends, aiding identification of large-scale soundscape patterns and areas of acoustic interest (e.g. Phillips et al., 2018; Ross et al., 2018; Scarpelli et al., 2021). This applies across ecological domains—dawn or dusk choruses are readily detectable in habitats as diverse as temperate grassland, tropical rainforest and coral reefs (Barbaro et al., 2022; Burivalova et al., 2021; Lamont et al., 2022).

Acoustic indices can be used as biodiversity proxies. Much of the early ecoacoustic literature investigated the potential for acoustic indices to act as direct proxies for some facet of biodiversity, particularly species richness (Sueur et al., 2008). This approach leans heavily on the **Acoustic Adaptation Hypothesis** and the **Acoustic Niche Hypothesis**. The latter posits that taxa evolve to fill available temporal and frequency niches to improve communication; many indices were designed to characterise acoustic diversity on the assumption that acoustic diversity predicts biodiversity.

Wider testing has demonstrated that associating acoustic indices with biodiversity metrics, such as species richness, diversity or abundance, is not straightforward. There has been some success in linking acoustic indices to the presence of individual species (Brodie et al., 2022; Papin et al., 2019; Towsey et al., 2018; Znidersic et al., 2020), or to broader taxon richness (Allen-Ankins et al., 2023; Bradfer-Lawrence et al., 2020; Dröge et al., 2021; Roca & Van Opzeeland, 2020). However, there are contradictory patterns reported in the literature. There do not appear to be any acoustic indices that hold a consistent relationship with species richness or density across regions or taxonomic communities, limiting their potential as biodiversity proxies (Alcocer et al., 2022; Sethi et al., 2023). Some contradictory findings may arise from issues in research design (see considerations below), but other inconsistencies reflect soundscape differences among species, acoustic communities, biomes and ecosystems (Barbaro et al., 2022; Buxton et al., 2018; Eldridge et al., 2018).

There are at least four reasons to be cautious when using acoustic indices as a direct proxy for aspects of biodiversity such as species richness:

(i) Biodiversity metrics are themselves already simplified indices of a complex ecological environment.
(ii) Acoustic index values derived from a shifting soundscape will not consistently reflect a static biodiversity metric. There is substantial rapid variation as individual animals move relative to the recorders, and this intersects with differences in microhabitat-driven sound attenuation (Alcocer et al., 2022; Bradfer-Lawrence et al., 2020; Darras et al., 2016; Lellouch et al., 2014). Therefore, acoustic index values can change over short timescales, while species richness, for example, remains the same.
(iii) Relationships between biodiversity metrics and acoustic indices are not linear. Doubling the number of vocalising species or individuals in a recording will not double the value of an acoustic index.
(iv) Not all species are represented equally in the soundscape—species with loud, varied or frequent vocalisations will have greater prominence, disproportionately impacting some acoustic indices. For example, Eurasian Skylark *Alauda arvensis* is an excellent mimic with varied song and could generate higher acoustic diversity than an entire species-rich woodland bird assemblage.

2.1 | Recommendation: Decide which paradigm the acoustic indices study falls into

This is critical as it will impact on all eight of the key points discussed below. Soundscape analyses using acoustic indices as descriptors are likely to be simpler to undertake and make fewer assumptions than studies using acoustic indices as proxies for biodiversity. If using acoustic indices as a proxy for biodiversity, it is imperative to undertake calibration and validation for the region and taxonomic group (see Section 8). Although current acoustic indices do not consistently predict simple biodiversity metrics, it does not undermine the approach in principle. Rather it reinforces the need for systematic research and careful inference to generate insight and guide the design and application of next generation of soundscape descriptors for ecological research and monitoring.

3 | GAINING FAMILIARITY WITH THE STUDY SYSTEM

It is important to utilise existing ecological knowledge of the study system to formulate hypotheses and design meaningful studies. Researchers would not undertake a bird survey without familiarity with the avian community of a region. Similarly, effective soundscape analysis relies on familiarity with acoustic patterns in the study system. This is not to imply that researchers need to know every species or vocalisation in a system, but rather to understand broad acoustic trends, such as when anuran choruses occur or the influence of a rainstorm on the soundscape. Nor does this negate the enormous potential for exploratory ecoacoustic research in understudied ecosystems where soundscape knowledge is currently limited, such as in soil or freshwater aquatic environments. However, the complexity and breadth of studies in lesser-known environments will likely be restricted to relatively simple descriptive studies until the knowledge base has grown.

3.1 | Recommendation: Listen to the study system

Researchers should undertake pilot recordings when designing their study. By design and necessity, indices discard a vast amount of information; familiarity with the study soundscapes provides essential foundations for designing data collection and interpreting analyses (see Section 10).

3.2 | Recommendation: Consider how sound travels in the study environment

Most acoustic indices were developed for audible frequencies in terrestrial systems (Alcocer et al., 2022), and may not reflect patterns in aquatic soundscapes for example, as sound transmission is so different in water (Duarte, Chapuis, et al., 2021). Applications of acoustic indices to aquatic or subterranean systems (Abrahams et al., 2021; Linke et al., 2018) and to frequencies beyond the audible spectrum (de Aguiar Silva et al., 2022) are to be welcomed as exciting developments in the discipline, but researchers should not expect indices patterns to match those from audible, terrestrial soundscapes (see Section 7).

4 | COLLECTING HIGH QUALITY RECORDINGS

Collecting usable data requires equipment appropriate to the study context, and awareness of technical features which may affect recording quality. We highlight some key sources of variation below but cannot provide a thorough treatment of these topics here. Researchers should consult literature offering technical guidance on these elements (e.g. Browning et al., 2017; Metcalf et al., 2023; Sueur, 2018; Sugai et al., 2020) and conduct trials to gain familiarity in practice.

4.1 | Recommendation: Get to know your recording equipment

Some key equipment features and sources of variation that will affect audio recordings, derived acoustic indices values or both are outlined here:

(i) Sound anomalies generated by recorders. Some recorders, including Swift and SoundTrap 300, generate a sound at the start of each recording. These sounds are unrelated to the soundscape but have the potential to influence acoustic indices values. Remove a short section from the beginning of each recording prior to calculating acoustic indices. See Marcot (2022) for further details.

(ii) Recorder malfunction causing a DC offset. Errors in an electronic component can cause a fixed voltage offset, meaning amplitude values are shifted above or below zero. This results in a low frequency artefact that can distort spectral indices, and a non-zero mean amplitude that can affect temporal indices. For spectral indices this can be resolved with a high pass filter that removes the low frequency artefacts (Bradfer-Lawrence et al., 2019; Hyland et al., 2023).

(iii) Recorder self-noise. This is very low frequency sound that is always present in recordings, generated by current running through the recorder's internal circuitry. This can be removed with a high pass filter that restricts sounds below a specified frequency (Bradfer-Lawrence et al., 2019; Hyland et al., 2023).

(iv) Microphone sensitivity. Features such as signal-to-noise ratio and detection ranges will influence what is recorded; an extensive test can be found in Darras et al. (2020). If recorders can accept external microphones, investigate technical documentation to ensure equipment meets the demands of the study.

(v) Microphone degradation. Long-term exposure to the elements can cause microphones to lose sensitivity. Check microphones before and after deployment. Calibrate microphones if technically possible. See Metcalf et al. (2023) for further discussion.

5 | COLLECTING SUFFICIENT RECORDINGS

It is relatively easy to collect huge acoustic datasets and therefore assume that sufficient data has been collected. However, there is increasing awareness in other big data methodologies such as citizen science that smaller, targeted datasets can give more precise results than huge unfocussed datasets (Boyd et al., 2023; Johnston et al., 2021). Inadequate or biased sample sizes will not provide meaningful ecological insights, and researchers need to consider this when collecting acoustic data, just as they would for traditional biodiversity surveys (Buckland & Johnston, 2017).

One common practice when collecting audio recordings is the use of temporal subsampling, which lowers power and memory requirements during deployments (thus extending recorder time in the field), and reduces data processing time (Sugai et al., 2020). The pattern of temporal subsampling can be an important consideration. For studies concerned with assessing facets of biodiversity, simulation studies show that a greater number of smaller samples will generally produce a more precise estimate of an unknown value than fewer larger samples (Schweiger et al., 2016). This holds true with acoustics; splitting up a recording period into evenly distributed, smaller sections will capture the focal acoustic community more comprehensively than a single, long sample (Metcalf et al., 2022) and reduce error in representation (Francomano et al., 2020). However, repeated temporal sampling can lead to pseudoreplication which must be accounted for when designing the analysis (see Section 9).

5.1 | Recommendation: Decide if temporal subsampling is appropriate

This will depend on whether acoustic surveys are comparing soundscapes or used as biodiversity proxies (see Section 2):

(i) Studies using deployments of many months may be able to capture broad soundscape patterns without continuous recordings (Francomano et al., 2020), making efficient use of limited battery life and memory capacity. If using short deployments (i.e. <2 weeks), then temporal subsampling will reduce survey comprehensiveness (Bradfer-Lawrence et al., 2019). Alternatively, focussing on specific periods in the diel cycle and/or narrower frequency limits can reduce variability among recordings, potentially permitting smaller sample sizes than if comparisons are across entire temporal and frequency ranges (Metcalf et al., 2021).

(ii) If acoustic indices are being used as biodiversity proxies, then it is appropriate to narrow the recording window to the periods of the diel and annual cycles when the focal taxon is most prominent in recordings (Bradfer-Lawrence et al., 2020; Metcalf et al., 2021; Sugai et al., 2020; see Section 6).

5.2 | Recommendation: Both daily and seasonal temporal subsampling protocols should be designed with the focal soundscape in mind

For example, if studying avian assemblages, sampling only the dawn chorus will likely give low detections of nocturnal species. A pilot study using continuous recording will help researchers to design an appropriate temporal schedule for a given focal soundscape (Sugai et al., 2020; see Section 3). For long-term projects, it is important to consider the impact of changing phenology, as this could confound inferences from very short sampling periods within the annual cycle.

6 | PRE-PROCESSING DATA CONSISTENT WITH YOUR QUESTION

Not all audio data will be informative or useful. More robust ecological conclusions can be achieved by pre-processing, which might include either exclusion or treatment of recordings.

6.1 | Recommendation: Acoustic indices can be a good way to identify outliers

When recordings are not representative of the soundscape they should be removed before analysis. Examples include noise created during deployment and collection of devices, recorder malfunction (see Section 4) or distortion due to wind, rain or interference from curious organisms. After calculating a suite of acoustic indices across the entire dataset, outlier recordings can be identified using standard multivariate statistical or dimensionality reduction methods (Sethi et al., 2020).

6.2 | Recommendation: Cleaning data does not necessarily mean excluding recordings entirely

Where recordings include anomalies because of recorder features, or when signals are obscured by non-target sound, these can potentially be cleaned by excluding portions of the spectrogram (see Section 4; Juodakis & Marsland, 2022).

What counts as signal or noise will be dependent on the study objectives:

(i) When characterising soundscapes, biophony, anthropophony and geophony all contribute to the unique acoustic signature of that location (Pijanowski et al., 2011) and so can be useful to identify differences.

(ii) Conversely, studies using acoustic indices as a proxy for biodiversity metrics should remove irrelevant geophony, anthropophony and even non-target biophony. For instance, in a study relating index values to avian species richness, cicada chorusing is irrelevant noise that potentially masks valuable signals (Hart et al., 2015; Metcalf et al., 2021; Ross et al., 2021).

7 | UNDERSTANDING WHAT ACOUSTIC INDICES REFLECT

Understanding the link between soundscape patterns and acoustic indices requires researchers know exactly what each index aims to measure, the mathematics underpinning them, and their underlying assumptions. Formulating meaningful hypotheses necessitates a clear understanding of how indices will reflect soundscape patterns. For instance, if anticipated soundscape changes are primarily in the frequency domain, an index that measures amplitude variability among frequencies is a better choice than one that measures amplitude variability over time.

The names of acoustic indices can be misleading (Table S1). For example, the Acoustic Complexity Index does not measure complexity in any formal sense (e.g. Parrott, 2010); it was originally designed to distinguish bird song from anthropophony and is the sum of the changes in amplitude in discrete frequency bands through time. The Acoustic Diversity Index is derived by calculating the Shannon entropy of the distribution of acoustic energy among frequency bands (Villanueva-Rivera et al., 2011). Higher values therefore indicate a more even energy distribution among bands. Conversely, the Acoustic Evenness Index is calculated using the Gini coefficient on that same distribution (Villanueva-Rivera et al., 2011). In this case, higher values indicate that acoustic energy is *less* evenly distributed among frequency bands. These details are not intuitive given the index names, complicating interpretations for those unfamiliar with the underlying calculations.

It is critical that researchers consider the assumptions underlying each index, any differences between the development context and their own study (Table S1), and whether they can adjust index parameters to their situation. For example, the Normalised Difference Soundscape Index (NDSI) is designed to represent the ratio of anthropophony to biophony, assuming these occur in the 1–2 kHz and 2–8 kHz range respectively (Kasten et al., 2012). However, these frequency ranges may not be appropriate in some contexts; biophony can often occur at low-frequencies, such as howler monkeys between 0.3–1 kHz (Whitehead, 1995), and anthropophony at high-frequencies, including engines and sirens reaching 12 kHz and above (Fairbrass et al., 2017). These patterns can be even more extreme when applying indices in different realms; many marine fish choruses are concentrated between 0.5 and 2.5 kHz (Siddagangaiah et al., 2019), so biophony patterns are very different to those in terrestrial recordings. Similar assumptions about the origins of sounds at different frequencies are made for the default settings for a range of other indices, including the commonly used Bioacoustic Index (Boelman et al., 2007; Table S1).

7.1 | Recommendation: Develop a full understanding of the underlying assumptions and calculations of the chosen acoustic indices

Acquiring such knowledge involves reading the canonical papers introducing the indices (Table S1), conducting substantial exploratory analysis comparing recordings, **spectrograms**, and indices values, and may also require examination of the underlying source code used to calculate index values.

7.2 | Recommendation: Ensure index parameters are appropriate

Confirm the study ecosystem and soundscape meet the assumptions of the index; if the index is not meaningful or appropriate then do not use it (see Section 8). If the index can be tuned then use custom settings appropriate to the study, such as altering the spectrogram frequency limits (Metcalf et al., 2021). Detailed advice on parameter tuning is beyond the scope of this Perspective, but can be found in Metcalf et al. (2021, 2023).

8 | LINKING ACOUSTIC INDICES TO ECOLOGICAL PATTERNS

The breadth of research highlighted in the Introduction shows that acoustic indices can accurately reflect ecological patterns. However, even simple analyses will be confounded if ecological change has a minimal impact on the soundscape, or if the index chosen is insensitive to the relevant soundscape changes. There are three key aspects to consider when deciding whether acoustic indices are likely to represent the acoustic features of interest:

(i) Are the soundscape recordings likely to reflect the study's focus? If the signal is not present, or is masked in some way, then the target will not be reflected in acoustic indices values. Likewise, if two entirely different ecological processes result in a similar spectrogram,

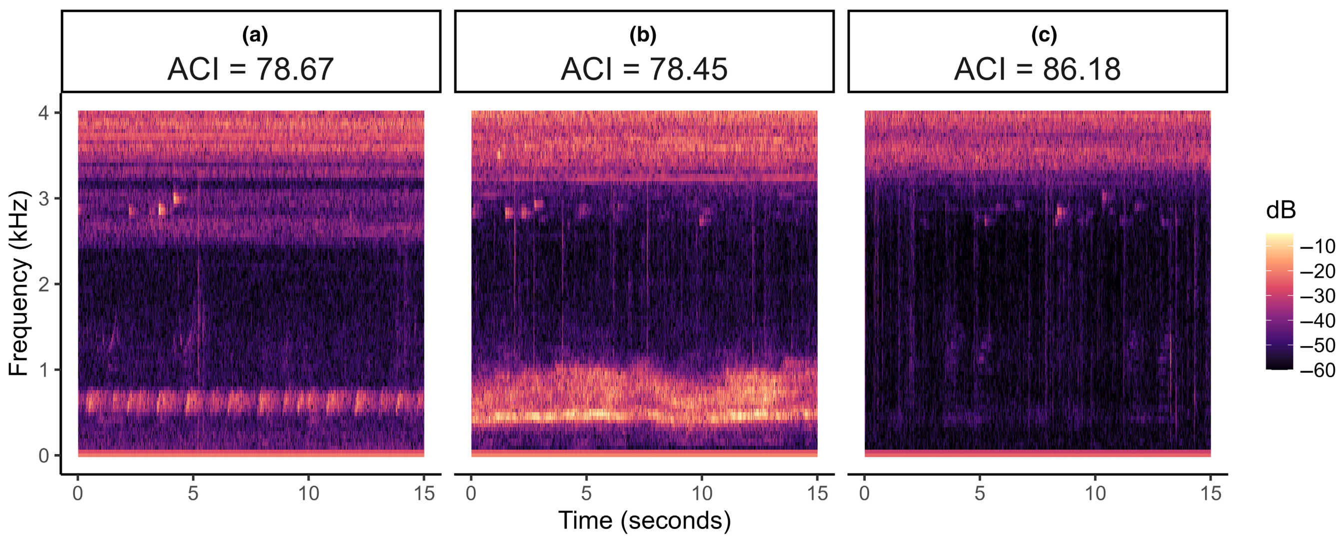

FIGURE 2 Sounds from very different ecological sources can produce similar spectral signatures and hence similar acoustic index values. This figure shows three 15 s spectrograms from Amazonia, with the Acoustic Complexity Index calculated between 0 and 4 kHz. (a) Anuran chorus 0.4–0.8 kHz, ACI value 78.67. (b) Spix's Red-handed Howler Monkey *Alouatta discolor* chorus 0.3–1.2 kHz, ACI value 78.45. (c) From the same location as (b) approximately 1 h later; less consistent activity in the lower frequencies leads to an increased ACI value of 86.18.

there may be no way to differentiate between them with acoustic indices despite the very different ecological causes (Figure 2).

(ii) Biota, and the emergent biophony, may not have common dynamics. In some cases, a community largely reacts in unison to stimuli—dawn and dusk choruses being a prominent example. This strong univariate response is likely to be reflected by almost any acoustic index applied at human-audible frequency bandwidths. However, in many situations we cannot expect common patterns, for instance responses to disturbance often diverge among taxa (Burivalova et al., 2021, 2022; Gottesman et al., 2021) and even within taxa there can be idiosyncratic responses across regions (Moura et al., 2015).

(iii) Ecological context will inform index choice and the temporal and frequency scales at which to apply it. Imagine a study investigating impacts of predatory mammal control on breeding birds. Following management intervention there were 100 fewer nocturnal mammal vocalisations between 0 and 1 kHz but a corresponding increase of 100 diurnal bird calls between 4 and 10 kHz. Despite the underlying soundscape change, a simple count of acoustic events calculated across all frequency bands over 24 h would show no difference between the two soundscapes.

8.1 | Recommendation: Develop a strong research plan

Researchers need a clear ecological question, a well-defined hypothesis of the likely impact of the ecological subject on the soundscape, and then a solid a priori understanding of the subsequent relationship between soundscape patterns and acoustic index values (see Section 7; Bradfer-Lawrence et al., 2020).

8.2 | Recommendation: Select acoustic indices sensitive to the predicted soundscape changes

For example, in a study looking at community turnover, a single Acoustic Complexity Index value is almost meaningless but a vector of values corresponding to the presence or absence of sound in different regions of a spectrogram has been used with great effect (Burivalova et al., 2021).

8.3 | Recommendation: Apply indices at appropriate temporal scales and frequency ranges

For instance, if a dawn chorus occurs between 1 and 5 kHz, those soundscape signals could be swamped if index scores were calculated across 0–192 kHz (Metcalf et al., 2021). Similarly, averaging indices values across long time periods of an hour or more will likely obscure brief soundscape patterns.

8.4 | Recommendation: Use a suite of indices where appropriate

Each index only reflects one aspect of the soundscape, so researchers can consider several indices in combination to reflect multiple facets at once (Bradfer-Lawrence et al., 2019; Eldridge et al., 2018; Scarpelli et al., 2021; Sueur et al., 2014; Towsey, Zhang, et al., 2014). Interpretation of multiple indices is complex and requires simultaneous consideration of different soundscape patterns but can lead to greater ecological insight. However, researchers should not calculate a large suite of indices simply because it is possible to do so; index inclusion should be based on a priori expectations of soundscape patterns.

9 | CONDUCTING APPROPRIATE ANALYSES

Analysis of acoustic indices should follow standard statistical best-practice. For example, acoustic indices have often been tested as proxies for biodiversity metrics using simple statistical comparisons such as correlation analysis and linear models (e.g. Bobryk et al., 2016; Jorge et al., 2018) yet most acoustic indices values are skewed and bounded, violating the assumptions of such approaches (Bolker, 2008). It is also commonplace for acoustic data to suffer from temporal autocorrelation and pseudoreplication (Alcocer et al., 2022; Scarpelli et al., 2021); audio samples taken from the same recorder deployment at the same location at regular time intervals are not truly independent. Failing to account for this can result in poorly-fitting or over-fitted models, potentially leading to spurious conclusions.

9.1 | Recommendation: Evaluate sample sizes and power to address ecological questions

Are the data sufficient to answer the ecological question? Researchers should consider whether they can create subsets of data or simulated datasets that will enable power analyses (Bradfer-Lawrence et al., 2019; Wood et al., 2021).

9.2 | Recommendation: Acknowledge and account for any non-independence

Use analytical methods, such as Generalised Estimating Equations or Mixed models, that can account for pseudoreplication arising from temporal autocorrelation among recordings or spatial correlation within sites. Numerous papers have used machine learning to identify soundscape patterns or recordings of interest (e.g. Do Nascimento et al., 2020; Scarpelli et al., 2021; Towsey et al., 2018; Znidersic et al., 2020) but temporal or spatial non-independence can also be problematic with these approaches (Colegrave & Ruxton, 2018; Forstmeier et al., 2017). It is important to select independent data for validation sets, so that any overfitting due to non-independence can be identified (Chatfield, 1995).

9.3 | Recommendation: Consider normalising and scaling data

Comparisons among indices are complicated as they are often on different scales. Normalising and scaling data will facilitate analyses and increase comparability (Bradfer-Lawrence et al., 2020; Fairbrass et al., 2017).

9.4 | Recommendation: Consult with expert analysts and the relevant literature

We cannot provide more detailed guidance as each study is unique. We encourage researchers who are less experienced with analysis to consult with statistical or machine learning experts and specialist statistical texts (e.g. Bolker, 2008; Matthiopoulos, 2011).

10 | INTERPRETING ACOUSTIC INDICES

Ultimately, researchers need to accurately interpret and clearly communicate what the acoustic indices reveal about soundscape patterns (Ross et al., 2021). As with all ecological data, exploratory analyses are necessary to sense-check apparent trends against the patterns that acoustic indices may reflect (Table S1 and the references therein). This is particularly important when associating indices with biodiversity metrics; our current understanding is that there is no widely generalisable relationship between acoustic diversity and biodiversity (Alcocer et al., 2022; Sethi et al., 2023). Moreover, 'biodiversity' includes a broad range of different metrics, which themselves should be carefully selected for each ecological question. Recommendations in Sections 2–9 above will provide the foundations for a considered and justifiable interpretation of the acoustic indices.

10.1 | Recommendation: Interpret acoustic indices clearly

Explain how soundscape patterns are reflected in acoustic indices values. Merely describing numerical or statistical trends without referring to the potential underlying soundscape drivers is insufficient. While it is tempting to focus on significant results, researchers should ensure that these results match their knowledge of the soundscape, and that they are consistent with any non-significant patterns in other indices.

10.2 | Recommendation: Link acoustic indices patterns to ground- or sound-truthed data

A part of clear interpretation requires researchers to tie indices values to soundscape patterns and, ideally, ecological features. The method and quantity of recordings assessed for this task is likely to vary depending on study objectives—with very small datasets this requirement may make the use of soundscape analysis redundant as all recordings can be manually assessed. However, in most cases, the amount of manual effort required is likely to be far less than that needed when directly sampling ecological trends.

10.3 | Recommendation: Clear explanations linking acoustic indices values and soundscape patterns are particularly important when describing ecoacoustic research to non-acousticians

Failure to meet this challenge is limiting effective comparison with existing research and advancement of the field. Indices are not as intuitive as some biodiversity metrics such as species richness. If we are to encourage uptake and development of acoustic indices in ecology and realise the potential of this approach for ecosystem monitoring, we need to increase accessibility to non-specialists by drawing clear links between indices values, soundscape patterns and ecological processes.

11 | EMERGING TRENDS IN ECOACOUSTIC ANALYSES

Ecoacoustics is a rapidly moving field, and we present these guidelines in the context of ongoing developments in soundscape analysis. We see emerging trends in three key areas: (i) novel applications of methods that characterise and quantify soundscape dynamics and complexity (Eldridge, 2021; Monacchi & Farina, 2019); (ii) methods to segment, cluster and classify samples borrowing from pattern recognition and unsupervised machine learning methods (Michaud et al., 2023; Ulloa et al., 2018); and (iii) new methods to generate numerical descriptors of audio samples using deep learning, as alternatives to acoustic indices.

Rather than *designing* acoustic indices heuristically, deep learning algorithms *learn* a numerical soundscape description from a given audio set. These can be with pre-trained models (Sethi et al., 2020) or use self-supervised methods (Rowe et al., 2021). Learned representations are high dimensional, data-driven descriptors and, unlike current acoustic indices, not based on human assumptions about links between soundscapes and ecology. These approaches are powerful, but there are some drawbacks. Firstly, existing methods are prone to over-fitting; it is not clear how well representations learned from one soundscape generalise to novel contexts (Sethi et al., 2023). Secondly, these methods are notoriously opaque, making interpretation difficult (Rudin, 2019); future research should take inspiration from the field of machine vision (e.g. Selvaraju et al., 2017) to increase interpretability and provide insight into the basis of model predictions. Finally, training these models is generally energy intensive; ecoacoustics will benefit from advances in low-energy, embedded AI methods (e.g. Seng et al., 2021).

Such advances promise new insights into the ecological role of sound and the relationships between soundscape, biodiversity and ecosystem complexity and functioning. However, the development and application of all ecoacoustic methods can only proceed via well-designed data collection, careful analysis and considered interpretation of results; many of the recommendations we offer for acoustic indices are just as relevant to these emerging methods.

12 | CONCLUSIONS

Acoustic surveys in general and acoustic indices in particular have considerable potential for ecology. Yet, as with any methodology, this potential is balanced against inherent limitations. In a young discipline, such limitations have often been overlooked or misunderstood, and inappropriate application of acoustic indices weakens their potential, and undermines scientific advancement in the field. Given the climate and biodiversity crises, and the urgent need to accurately monitor changing environments, current acoustic indices—and future methods—could make substantial contributions to ecological research, conservation, restoration, and land management. This context further reinforces the need for scientifically rigorous use of acoustic indices, in order to advance our understanding of the relationships between ecological communities and soundscapes, and to underpin the robust development of future methods for research and application.

AUTHOR CONTRIBUTIONS

Tom Bradfer-Lawrence, Camille Desjonqueres, Alice Eldridge, Alison Johnston and Oliver Metcalf conceived the ideas presented here and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

There were no data or code in this Perspective.

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SUPPORTING INFORMATION

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

Table S1: An overview of some of the most widely used acoustic indices.

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