Integrating the concept of acoustic diversity into the functional ecology framework

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Abstract

The ecological relevance of sounds in ecosystems has gained increasing attention in the recent decade. While ecoacoustics seeks to study these roles, a majority of studies to date have focused on using Passive Acoustic Monitoring (PAM) for species monitoring or calculating integrative ecoacoustic indices as rapid proxies for biological diversity. This paper proposes an ecological perspective on acoustic diversity that distinguishes three core interconnected dimensions: (i) compositional acoustic diversity, reflecting the acoustic assemblage present; (ii) structural acoustic diversity, describing the spatial and temporal organisation of acoustic activity; and (iii) functional acoustic diversity, relating to variation in acoustic traits involved in information exchange. We aim to provide a clearer conceptualisation of what different approaches to acoustic diversity represent ecologically and how they can be related to biodiversity and ecosystem functioning. We present a conceptual framework for acoustic diversity, building on existing research and linking it to Noss's (1990) hierarchical classification of biodiversity. We define and distinguish compositional, structural, and functional acoustic diversity across spatial scales ranging from the individual to the soundscape, and consider variation in alpha, beta, and gamma diversity within these dimensions. We propose methods for quantifying these different aspects of acoustic diversity and provide application examples and exemplary hypotheses to illustrate how the framework could be operationalised.

Keywords: acoustic diversity, biodiversity, compositional diversity, ecoacoustics, functional diversity, structural diversity.

1. Introduction

The rapid development of Passive Acoustic Monitoring (PAM) and automated soundscape analysis has led to a growing accumulation of acoustic data across ecosystems and biomes. This expansion has been accompanied by important conceptual developments in ecoacoustics, which have provided foundations for understanding sound as an ecologically meaningful phenomenon and for linking acoustic patterns to biodiversity, ecological communities, and ecosystem processes (Farina, 2018; Grinfeder, Lorenzi, et al., 2022; Pijanowski et al., 2011; Ross et al., 2023; Sueur et al., 2021; Sueur & Farina, 2015). Although concepts such as soundscape and acoustic diversity have become central to ecoacoustics, their ecological meaning and relationship to biodiversity remain open to interpretation. In order to further develop the conceptual foundations of this emerging field, we revisit the concept of acoustic diversity from an ecological perspective. This allows us to distinguish three complementary facets of acoustic diversity in soundscapes: the **composition** of constituent sounds; the spatial and temporal **structure** of acoustic activity; and the **functional** processes associated with the acoustic habitat.

A soundscape not only represents an aggregate of sounds but carries signals from both biotic and abiotic sources across multiple biological and ecological scales (Sueur & Farina, 2015). Acoustic signals, whether considered individually or collectively, encode critical biological and ecological information. In terms of animal behaviour, they convey individual and species-specific signatures, group dialects, and labile motivational or emotional cues, all embedded within social or environmental contexts (Mathevon & Aubin, 2020). At the ecosystem scale, soundscapes reflect a network of interactions shaped by landscape configuration, acoustic community composition, and acoustic habitat quality. As a semiotic component of an ecosystem, sound also carries information among organisms and across ecological processes (Farina, 2018; McGregor, 2005; Sueur & Farina, 2015). Biotic sounds, referred to as biophony, arise from living organisms. Abiotic sounds include geophony, which originates from natural physical processes such as wind or rain, and technophony, which arises from human-made sources (Pijanowski et al., 2011; Farina et al., 2021a). The diversity and composition of biophony are directly influenced by the taxonomic composition of the acoustic assemblage and the nature of its intraspecific and interspecific interactions and lifecycle stages. At the same time, the soundscape as a whole influences the signalling behaviour of animals, including their communication strategies, as well as how they encode and decode information. It can also influence the composition of communities as organisms adapt their acoustic activity in response to the biological and non-biological conditions of their habitat (Farina, Mullet, et al., 2021; Francis et al., 2023; Mullet et al., 2017).

Acoustic diversity is therefore a multifaceted concept that spans several levels of biological organisation and spatio-temporal scales. It includes variation in call types within species, acoustic trait

differences among species, and the diversity of acoustic communities within and among habitats (alpha, beta and gamma diversity), and is closely linked to the structure and connectivity of acoustic niches.

Despite its widespread use, the term "acoustic diversity" lacks a consistent definition in the literature (see the glossary in the supporting information for further details). It is often associated with temporal and spectral variability and with overall soundscape complexity. Ecoacoustic indices, frequently referred to as acoustic diversity indices, quantify these patterns. A wide range of acoustic indices have been developed over the last decade that quantify soundscape properties in different ways (Sueur et al., 2014; Ulloa et al., 2021). They have been applied to discriminate between habitats differing in vegetation structure, habitat type, land use, wilderness gradients and landscape configuration (Barbaro et al., 2022; Carruthers-Jones et al., 2019; Fuller et al., 2015; Müller et al., 2022; Shaw et al., 2024). They have also been used as proxies for taxonomic richness, particularly bird species richness (Alcocer et al., 2022). However, acoustic indices are based on the distribution of acoustic energy in time and frequency, irrespective of sound source identity and the encoded acoustic information. As a result, they primarily describe the spectral and temporal structure of soundscapes. Although these aspects - taxonomic richness of soniferous species and acoustic structural diversity - may be correlated, these relationships are likely to be context dependent. This is often the case when one dimension of biodiversity is used as a proxy for another, as in the use of surrogate species or canopy cover to indicate broader biodiversity patterns. This lack of distinction creates ambiguity about what different metrics actually capture (Alcocer et al., 2022; Llusia, 2024), and can result in misunderstandings that threaten to undermine the field before it has matured (Sugai et al., 2026). In particular, while acoustic diversity has primarily been used to characterise acoustic communities and their diversity, its potential to provide information about ecosystem functioning has received comparatively little conceptual and empirical attention despite growing empirical evidence (Folliot et al., 2022; Gasc et al., 2013; Schillé et al., 2024). Addressing this gap requires distinguishing the dimensions of acoustic diversity and identifying metrics that can be linked to specific ecological processes and functions.

Thus, in this paper, we distinguish **compositional, structural, and functional acoustic diversity** to clarify their relationships with biodiversity and ecosystem functioning (Figure 1). Compositional and structural diversity are already implicit in the literature but have rarely been formalised as distinct dimensions. We further propose functional acoustic diversity as a dimension linked to communication as an ecosystem *process*. Acoustic communication is central to many animal species and is shaped by the acoustic habitat, where facilitative and competitive interactions occur (Rossetto & Laiolo, 2024). Distinguishing these dimensions enables us to test their relationships rather than *assuming* that

variation in one reflects variation in another. Building on foundational work in ecoacoustics (Farina, 2018; Farina & James, 2016; Grinfeder, Lorenzi, et al., 2022; Mullet et al., 2017; Sueur et al., 2021), we seek to advance a more integrated ecological perspective. We define the ecological information captured by soundscapes across the three dimensions and propose illustrative hypotheses to connect them to broader ecological questions (Ross et al., 2023). Importantly, acoustic observations reflect a chain of sound production, propagation, and detection. Thus, measures derived from passive acoustic monitoring (PAM) reflect not only the acoustic assemblage and its activity but also the conditions under which sounds are transmitted and detected.

2. Definition and conceptualization of compositional, functional and structural acoustic diversity.

Ecosystems can be characterised by their composition, structure, and function (Franklin et al., 1981 in Noss, 1990) a framework that Noss (1990) subsequently extended to biodiversity. To link acoustic observations with ecological processes, in the context of ecoacoustics, it is necessary to consider how these three dimensions are expressed through the acoustic environment. We therefore define compositional, structural, and functional acoustic diversity across scales ranging from individuals to landscapes (see Figure 1).

Compositional acoustic diversity describes *what sounds are present and which species produce them*. It encompasses the richness, identity, and relative abundance of acoustically active species, as well as the diversity of sound types and song elements. Only species producing sound during the observation period contribute to acoustic species richness; acoustically inactive species present in the environment are excluded.

Structural acoustic diversity describes *how sounds are organized* across spatial, temporal, and spectral dimensions. It encompasses the arrangement and overlap of acoustic events and the structure of the acoustic communication network that shapes spectro-temporal structures of the resulting soundscape in space and time.

Functional acoustic diversity describes *how sounds function* within the soundscape. It encompasses the acoustic traits that determine sound production, propagation, and perception, and how these influence communication through processes such as information transfer, masking, and encounter rates.

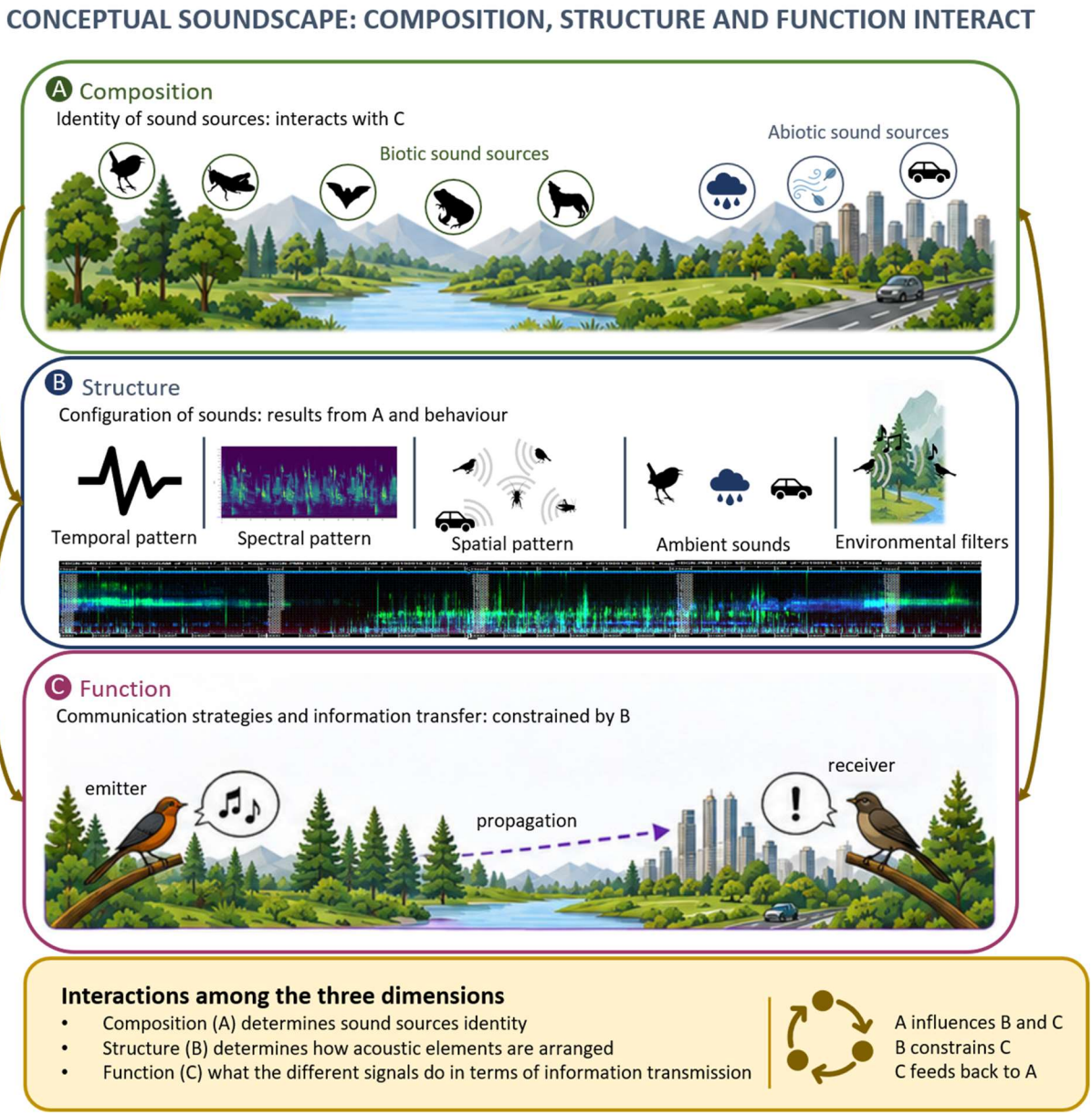


Figure 1: Conceptualisation of compositional, structural and functional acoustic diversity.

2.1 Compositional acoustic diversity

Compositional acoustic diversity can be classified at four levels: individuals, populations, communities, and soundscape. At the species and population level compositional acoustic diversity would refer to the richness of acoustic elements and their relative abundance (Tabelle 1). At the community level, compositional acoustic diversity reflects the identity and acoustic activity of species or acoustic groups such as birds, anurans, and crickets. Importantly, because PAM detects soniferous activity rather than

species presence per se, the resulting acoustic composition reflects both which taxa are present and which are acoustically active under prevailing environmental conditions. The resulting acoustic composition is therefore shaped by processes operating at different temporal scales:

1. Long-term shifts in acoustic assemblage composition across space and time, reflecting species turnover and broader ecological dynamics (Morrison et al., 2021).
2. Short-term behavioural responses of soniferous taxa to environmental conditions, including atmospheric conditions, conspecific and heterospecific cues, habitat structure, and anthropogenic noise.

Thus, although these processes may themselves involve functional or ecological mechanisms, they jointly determine the acoustic composition observed in a given place and at a given time.

2.1.1 Measuring compositional acoustic diversity

Quantifying compositional acoustic diversity requires identifying the acoustic sources contributing to a soundscape and measuring their occurrence and relative activity across time and space. This parallels compositional biodiversity assessment in community and conservation ecology, but focuses on acoustic detection and acoustic behaviour, increasingly through automated passive acoustic monitoring (PAM). Depending on the level of analysis, these entities may be acoustic elements, soniferous individuals or populations, acoustic communities, or soundscape components.

The measures described below primarily characterize **acoustic α-diversity** at different hierarchical levels, from individual organisms to species and acoustic assemblages and, ultimately, soundscapes. At each level, analogous approaches can be used to quantify **β-diversity** as compositional turnover or dissimilarity among units, and **γ-diversity** as the total acoustic richness or diversity across a broader spatial or temporal extent. Thus, the same compositional framework can be applied across hierarchical scales, while the acoustic entities considered—e.g., song elements, call types, species, or soundscape components—change with the level of analysis diversity (Arend et al., unpublished; Scanferla et al., 2026).

Individual and population level

Composition and richness of acoustic elements: At the individual level, compositional acoustic diversity can be quantified by measuring the richness and relative abundance of distinct acoustic elements, such as song or call types. These measures characterize the variety of acoustic elements produced by an individual and can be used to investigate vocal repertoires and acoustic variation (Bessert-Nettelbeck et al., 2014). At the population level, differences in acoustic element composition can reveal geographic differentiation, dialects, and cultural transmission (Lachlan et al., 2018; Wang et al., 2022). Acoustic traits have also been used to characterize acoustic morphospecies, including crickets and freshwater organisms (Desjonquères et al., 2018; Riede, 1998).

Metrics for acoustic abundance: For bird communities the number of acoustic detections per unit time is referred to as vocal activity rate (**VAR,** Pérez-Granados et al., 2019), whereas the **detected vocal activity rate (DVAR)** gives the number of detections per unit time **and** unit area (Pérez-Granados & Traba, 2021). **Detection Rate (DR)** counts the proportion of recordings in which a species' vocalizations was detected (Hutschenreiter et al., 2024). These measures characterize aspects of acoustic activity and detection and can be used to assess acoustic abundance. This variation is species specific and driven by a range of endogenous and exogenous factors. Consequently, it serves as a direct indicator of species behaviour and communication processes in response to environmental factors.

Assemblage level

Bioacoustic Richness and Diversity: The richness and diversity of acoustically active species within a given time period, as assessed either overall or within taxonomic groups (e.g. birds or anurans). Compositional measures can also quantify the relative contribution of different acoustic community groups (e.g., birds, anurans, and crickets) without resolving individual species. At the species level, measures rely on species-resolved acoustic detections and may combine species identity with relative acoustic activity (e.g., detection rates) using metrics such as Shannon diversity or Hill numbers (Arend et al., unpublished; Scanferla et al., 2026). Species richness and identity describe compositional attributes, whereas the relative distribution of species-specific acoustic activity may also reflect structural attributes. Similarly, song and call types can have compositional or functional relevance, depending on whether they are considered as distinct sound categories or in relation to their ecological and communicative roles. This context dependence reflects the hierarchical nature of ecological organization and analysis (Allen and Starr, 1982).

Soundscape level

At the landscape scale, soundscape composition encompasses the relative contributions of biophonic, geophonic, and anthropophonic sources. AI-based models can classify these components and quantify their contributions to the overall soundscape (Arend et al., 2025; Grinfeder, Haupert, et al., 2022; Quinn et al., 2022). This enables a holistic assessment of soundscape composition, including interactions among soundscape components and their environmental drivers.

2.1.2 Hypotheses: compositional acoustic diversity and community assembly

The study of compositional acoustic diversity is closely linked to animal behaviour and community ecology. Analysing the identity, richness, and relative contributions of soniferous species allows researchers to investigate how acoustic assemblages are shaped by evolutionary processes, behavioural interactions, and environmental, behavioural or morphological constraints. The following hypotheses illustrate how compositional measures can be used to investigate these processes across ecological scales.

C1 – Acoustic niche partitioning shapes community composition - the acoustic niche hypothesis. Co-occurring soniferous species are expected to exhibit non-random patterns of acoustic co-occurrence and temporal activity, consistent with acoustic niche partitioning and biotic interactions (Azar & Bell, 2016; Krause, 1987; Luther, 2009; Rossetto & Laiolo, 2024). Playback experiments and observational studies can test these predictions. Testing this hypothesis would help distinguish the contributions of biotic interactions and behavioural trade-offs to acoustic community assembly.

C2 – Environmental conditions shape acoustic community composition - the acoustic adaptation hypothesis and acoustic habitat hypothesis. Signal structure evolves in response to habitat-specific sound transmission properties. Thus, habitat characteristics, climatic gradients, and sound transmission conditions are expected to predict variation in the identity, richness, and relative activity of soniferous species (Grant & Samways, 2016; Morton, 1975; Mullet et al., 2017; van der Mescht et al., 2021). Testing this hypothesis would clarify how environmental filtering shapes acoustic assemblages across spatial scales.

C3 – Anthropogenic change alters acoustic composition and increases community homogenization. Noise pollution, land-use change, and habitat fragmentation are expected to alter the identity and relative representation of acoustically active species, potentially increasing compositional similarity

among sites (Derryberry et al., 2020; Francis et al., 2017). Testing this hypothesis would establish the value of compositional acoustic measures for monitoring ecological change.

Table 1. Metrics for diversity across hierarchical levels. For illustrative purposes, we list a few application examples. This is by no means a complete list. Some have been widely studied and others rarely or not at all. To the best of our knowledge, we indicate this with footnotes: 1: "implemented in research", and 2: "potential implementation, but not yet".

Level	Example Metrics	Ecological Information	Application examples
Compositional acoustic diversity			
Individual/ population[1]	Call/song type richness, acoustic activity (VAR, DVAR, DR)	Dialects, geographic differentiation, isolation, cultural transmission, environmental filtering	Intra-individual differences in song composition in relation to geographic distance (Bessert-Nettelbeck et al., 2014); geographic differentiation, dialects (Wang et al., 2022)
Assemblage (Alpha)[1]	Acoustic richness, Shannon diversity, Hill numbers	Assemblage composition, richness and evenness of soniferous species contributions	Differences in vocal activity within a bird community (Müller et al., 2025)
Assemblage (Beta)[1]	Jaccard, Sørensen, Bray–Curtis, Hill numbers	Spatial/temporal assemblage differentiation	Land use effects on turnover in orthopteran composition (Arend et al. unpublished)
Assemblage (Gamma)[2]	Hill numbers, total regional acoustic richness	Landscape-scale acoustic richness and diversity	-
Soundscape[1]	Biophony, geophony, anthropophony	Composition and interaction among different soundscape components	Landscape scale temporal patterns of soundscape composition (Grinfeder, Haupert, et al., 2022; Mullet et al., 2016)
Structural acoustic diversity			
Individual/ population[1]	Configuration of acoustic elements	Behavioural variability and plasticity, adaptation, social interactions, evolution	Variation in song structure along an elevation gradient, indicating vocal adaptation (Branch & Pravosudov, 2020)

Level	Example Metrics	Ecological Information	Application examples
Assemblage[1/2] (Alpha)	Ecoacoustic α-indices filtered or aggregated at assemblage level, species rank– acoustic activity curves, soniferous species–area relationships	Acoustic niche partitioning (ANH), acoustic interactions (AAH), diel and seasonal dynamics, response to environmental gradients.	Acoustic resource partitioning (Riede, 1997); effects of habitat characteristics on acoustic structure of a community (García-Navas et al., 2023)
Assemblage (Beta)[1]	Ecoacoustic β-indices filtered or aggregated at assemblage level, sonotype heterogeneity, dissimilarity in species rank– acoustic activity curves, and soniferous species–area relationships	Link between environmental heterogeneity and turnover in acoustic structure.	Tracking temporal and spatial turnover in acoustic community structure using acoustic dissimilarity indices (Rodriguez et al., 2014), or Bray-Curtis distance of acoustic index composition (Müller et al., 2022)
Assemblage (Gamma)[1/2]	Structural diversity of regional acoustic assemblage adopting Hill numbers	Macroecological patterns in acoustic habitat structure and effects on ecosystem functioning and evolution	Soil acoustic richness (alpha and gamma in Metcalf et al., 2024); Luypaert et al., 2022, 2024) conceptualize the use of Hill numbers based on acoustic indices
Soundscape[1]	Ecoacoustic indices; classification of bio-geo-, and anthropophony; sonotypes	Acoustic habitat heterogeneity and dissimilarity, quantification of acoustic niche space, topology and structure of communication networks	Studies of ecoacoustic index patterns in relation to habitat characteristics, (Dröge et al., 2024; Fuller et al., 2015; Müller et al., 2024)
Functional acoustic diversity			
Individual/ population[1]	Communication traits (e.g. frequency, pulse length timing, duration, amplitude) involved in i.a. mate choice, alarm, territorial defence	Social interaction, dominance, facilitation, cooperation.	Song performances can inform decisions to compete or form coalitions (Goodwin & Podos, 2014), relation between habitat structure

Level	Example Metrics	Ecological Information	Application examples
			and vocal behaviour (Netoskie et al., 2023)
Assemblage (Alpha) [1]	Community weighted means on acoustic response and effect traits	Information flow, community cohesion, resilience to noise, species loss, disturbance	Synchronisation in signalling pathways (clustering of traits) among closely related species could indicate interspecific communication networks (Tobias et al., 2014)
Assemblage (Beta) [1/2]	β-Indices e.g. Hill numbers for acoustic traits.	Functional dissimilarity in communication strategies, reflecting assemblage composition or adaptation to the acoustic environment	Spatial distribution of acoustic traits in bird assemblages along regional bioclimatic gradients (Busana et al., 2026)
Assemblage (Gamma)[2]	γ-Indices e.g. Hill numbers for acoustic traits.	Landscape-scale diversity of communication strategies and acoustic niches	-
Soundscape[2]	Acoustic connectivity: quantification and mapping of propagation channels	Acoustic barriers, effects of acoustic connectivity or disconnectivity on other ecosystem processes and functions	Acoustic connectivity, conceptualized in Croci et al., unpublished.

2.2 Structural acoustic diversity

Structure refers to the physical organization or pattern of a system (Noss, 1990). By analogy with vegetation structural diversity, defined as “the degree of heterogeneity in biomass distribution in three-dimensional space” (Ehbrecht et al., 2021), acoustic structural diversity can be conceptualized as heterogeneity in the distribution of sound energy across time, frequency, and space. Operationally, structural acoustic diversity describes the distribution and configuration of acoustic energy and signals across time, frequency, and space, including their arrangement within the multidimensional signal space of the communication network. This conceptualization underlies many ecoacoustic indices, that quantify spectro-temporal patterns of acoustic energy and are often used to describe soundscape

structure (Bouché et al., 2025; Guerrero et al., 2025; Retamosa Izaguirre & Barrantes Madrigal, 2023). These metrics can be integrated into ecological models, and comparative studies suggest that structural acoustic diversity can indicate habitat quality, degradation, disturbance, or resilience (Dröge et al., 2024; Eldridge et al., 2018; Gitau et al., 2025; Müller et al., 2024).

Structural acoustic diversity can be described across nested spatial scales, analogous to α-, β-, and γ-diversity in ecology, e.g. by adopting Hill-number approaches for ecoacoustic indices (Luypaert et al., 2022, 2024):

- α structural acoustic diversity refers to the heterogeneity and configuration of acoustic energy or signals within a single site or recording.
- β structural acoustic diversity describes differences in acoustic structure between sites, habitats, or time periods (e.g. turnover in signal space or changes in temporal partitioning).
- γ structural acoustic diversity captures the overall structural diversity across a region or landscape, integrating multiple communities and soundscapes.

Recordings can be filtered or aggregated using manual annotations or AI-based models to analyse song structure, acoustic assemblage structure, and their responses to environmental gradients and acoustic habitat conditions (Arend et al., 2025; Bradfer-Lawrence et al., 2023; Rossetto et al., 2026; Shaw et al., 2024). As in forest ecosystems, where structural features are shaped by dominant tree species, acoustic structure is often driven by dominant sound sources (Müller et al., 2025). Temporal structure remains less well understood than spatial structure, although acoustic activity varies across multiple cyclical scales, from circadian to circannual (Hillebrand et al., 2018; Ross et al., 2023; White & Hastings, 2020).

Beyond ecoacoustic indices, structural acoustic diversity can also be understood as the organization of intra- and interspecific communication networks across **individuals, populations, and communities**. For example, Chhaya et al. (2021) define acoustic assemblage structure as the organization of species in signal space, including their spatial and temporal signalling patterns, composition, and activity. At the **landscape scale** Guerrero et al. (2025), propose graphical methods to characterize acoustic structure using *sonotypes*, defined as distinct acoustic signatures occupying specific time–frequency domains. While these approaches describe bioacoustic structure, they could be extended to include abiotic components. Geophony and anthropophony are integral to ecoacoustic structure, as biophonic patterns cannot be fully understood without the acoustic environment in which they are embedded. This is consistent with the acoustic adaptation and acoustic habitat hypotheses (Mullet et al., 2017).

2.2.1 Measuring structural acoustic diversity

Structural acoustic diversity can be quantified at different organizational and spatial scales using complementary approaches (Table 1).

Individual and population level

Structural acoustic diversity refers to the intra-individual variation in the configuration of signal elements in time and frequency. For example, humpback whales progressively change song structure across seasons and years while also exhibiting stochastic individual variation (Mercado, 2022). Similarly, song structure in birds can vary along environmental gradients (Branch & Pravosudov, 2020). These approaches primarily capture α-structural diversity within individuals or species.

Assemblage level

Ecoacoustic indices and acoustic features describe the distribution of signals in time–frequency space, as well as trait-based analyses of signal space occupation. In addition, acoustic activity distributions, such as rank–abundance curves, and species–area relationships derived from acoustic detections can be used to characterize assemblage structure. These approaches allow the quantification of α-diversity within communities and β-diversity across habitats or environmental gradients.

Soundscape level

Ecoacoustic indices quantify the heterogeneity and distribution of acoustic energy, while dissimilarity metrics between recordings capture spatial and temporal turnover in acoustic structure. Sonotype-based or cluster-based approaches provide alternative representations of acoustic structure (Castro-Ospina et al., 2024; Sethi et al., 2020), and recent AI-based methods enable the separation of soundscape components, allowing indices to be calculated specifically for biophony, geophony, or anthropophony (Arend et al., 2025; Bouché et al., 2025; Grinfeder, Haupert, et al., 2022; Quinn et al., 2022).

Temporal structure (cross-scale)

Across all levels, temporal structure can be quantified through metrics of temporal partitioning, as well as the variability and cyclicity of acoustic activity across diel, seasonal, or longer time scales. However, such approaches remain less developed and represent an important area for future research, particularly for linking temporal α- and β-diversity.

2.2.2 Hypotheses: structural acoustic diversity across ecological scales

Ecoacoustic approaches extend beyond traditional biodiversity monitoring by capturing not only species presence but also patterns of acoustic activity and organisation in signal space. Structural acoustic diversity may reflect variation in species richness, activity, and niche partitioning, providing a potential link between macroecological patterns and community assembly processes. Integrating PAM and ecoacoustic metrics into macroecology therefore offers a scalable framework for testing ecological hypotheses across spatial and temporal scales (Darras et al., 2024; Morrison et al., 2021; Ross et al., 2023). However, the extent to which acoustic measures reliably capture these ecological dimensions, and under which conditions they can serve as proxies for large-scale biodiversity patterns, remains an open empirical question. Biogeographical theory predicts consistent gradients in biodiversity across latitude, elevation, area, and environmental heterogeneity (see Turlington et al., 2024 for a review on tested relationships). Translating these patterns into the acoustic domain would allow the formulation of explicit, testable hypotheses.

Large-scale spatial gradients

S1 – Compositional diversity and acoustic structure are related but non-equivalent. Greater richness or activity of soniferous species may be associated with greater structural acoustic diversity, but the strength of this relationship depends on how acoustic activity is distributed across time, space, and frequency. Testing this hypothesis would establish when structural diversity reflects compositional variation and when it captures additional information about acoustic organization (Mitchell et al., 2020).

Environmental heterogeneity and β-diversity

S2 – Environmental heterogeneity increases structural β-diversity. More heterogeneous landscapes are expected to exhibit greater turnover in acoustic structure among sites due to variation in habitat conditions and acoustic community composition (Müller et al., 2022; Stein et al., 2014). Testing this hypothesis would clarify how environmental heterogeneity shapes spatial variation in soundscape organization.

S3 – Anthropogenic disturbance homogenizes acoustic structure. Noise pollution and land-use change are expected to alter acoustic activity patterns and increase structural similarity among sites (Derryberry et al., 2020; Francis et al., 2017). Testing this hypothesis would establish whether

structural measures detect changes in soundscape organization beyond those captured by compositional measures.

Island biogeography and habitat fragmentation

S4 – Structural acoustic diversity increases with habitat area and decreases with isolation. Following island biogeography theory, larger and less isolated habitats are expected to support greater regional structural diversity and more complex acoustic structures (Fuller et al., 2015; MacArthur & Wilson, 1967; Müller et al., 2020). Testing this hypothesis would reveal whether structural acoustic diversity reflects spatial patterns associated with habitat fragmentation.

Temporal dynamics and global change

S5 – Long-term biodiversity declines are associated with changes in structural acoustic diversity and increased acoustic homogenization. Climate change and other anthropogenic pressures may reduce acoustic niche diversity and alter the organization of acoustic activity (Burivalova et al., 2019, 2022; Morrison et al., 2021). Testing this hypothesis would assess whether long-term acoustic monitoring can detect structural changes associated with biodiversity loss.

2.3 Functional acoustic diversity

Communication involves the production, transmission, reception, and decoding of signals that shape interactions such as mate choice, competition, predation, and parental care. Because communication influences population and community processes, including reproductive output, species coexistence, and trophic dynamics (Erbe & Thomas, 2022; Seki, 2023), it can be framed as an ecosystem process. Acoustic functional diversity quantifies variation in signal strategies (i.e., realised trait expressions) within a community and their effects on communication processes and individual fitness (Zsebők et al., 2021). From a fitness and evolutionary angle, traits like dominant frequency, amplitude, song rate, temporal complexity, and repertoire size are functional because they affect signaling efficacy, mate choice, and rivalry outcomes, often via correlations with morphology (body size, syrinx or larynx structure), physiology (metabolic rate), or foraging strategy. **The acoustic morphological hypothesis** links acoustic traits to morphological and physiological constraints on communication (Gillooly & Ophir, 2010), including body size, beak size, and metabolism. Consequently, acoustic trait optimisation is likely species-specific and constrained by morphology, phylogeny, and associated trade-offs (Ryan, 1986).

Within these constraints, the acoustic adaptation hypothesis describes how species adapt evolutionarily or plastically to their acoustic environment (Farina, 2014), whereas the acoustic niche hypothesis addresses competition among species sharing acoustic space (Krause, 1987). These perspectives relate to response and effect traits, respectively, although their classification depends on the research question. The duration and intensity of noise exposure influence evolutionary adaptation and phenotypic plasticity. Species in naturally noisy habitats (e.g., rivers) may evolve changes in signal frequency or amplitude, whereas animals exposed to anthropogenic noise (e.g., traffic and urbanisation) may rely on plasticity, learning, or cultural transmission to maintain effective communication. These mechanisms are central to the resilience of communication networks under disturbance. By analogy with other ecological networks, acoustic traits are functional when they influence the acoustic space occupied by a species, its temporal and spectral overlap with other species, and the communication network's resilience to disturbance and species loss.

2.3.1 Measuring functional acoustic diversity

Individual and population level

At the individual level, functional acoustic diversity is reflected in the range and plasticity of acoustic traits expressed by a single organism. Key traits include dominant frequency, bandwidth, call duration, amplitude, temporal patterning, repertoire size. These traits are functionally relevant for information exchange, such as signalling individual identity, social status, fitness components, or habitat quality (Arend et al., 2026; García et al., 2024; Jablonszky et al., 2025; Kubacka et al., 2024; Mariette & Buchanan, 2016). They can be linked to morphological characteristics such as body size, mass, or sound-producing organ dimensions, as well as to fitness components including mating success, territory tenure, and survival (Gillooly & Ophir, 2010).

At the population and species level, functional acoustic diversity is captured through the characterization of inter- and intra-individual trait expressions and the quantification of intraspecific variability and plasticity. Species-level acoustic trait vectors—comprising multivariate combinations of spectral, temporal, and amplitude traits—can be used to describe ecological strategies, including habitat use, activity patterns, and communication niches.

Assemblage level

Functional acoustic diversity can be quantified by constructing a multidimensional trait space based on species-level acoustic trait vectors (Bacquelé et al., 2026; Busana et al., 2026). Standard functional diversity metrics, such as functional richness (FRic), evenness (FEve), divergence (FDiv), and dispersion, can then be calculated (Mason et al., 2005). Combining functional trait metrics with structural soundscape descriptors (e.g. spectral and temporal occupancy) makes it possible to ascertain whether observed patterns are driven by changes in species composition or by shifts in the functional organization of acoustic niches (Bohn et al., 2009; Jablonszky et al., 2022, 2025; Luther, 2009; Planqué & Slabbekoorn, 2008; Tobias et al., 2014).

Soundscape level

By mapping acoustic trait distributions and functional diversity indices across landscapes, it is possible to relate variation in acoustic functions to gradients in habitat structure, land use, and ecosystem processes (Busana et al., 2026; Gasc et al., 2016). By comparing trait-based diversity metrics across multiple sites and time periods, this approach also addresses beta and gamma diversity. Multivariate and mixed-effects modelling approaches can be used to partition variation in functional acoustic diversity across spatial and temporal scales, and to test for cross-scale relationships. For example, local functional diversity may influence, or be influenced by, broader landscape-level soundscape patterns (Gabriella et al., 2025; Shaw et al., 2021; Sueur & Farina, 2015). In addition, links between acoustic functional diversity and ecosystem functions (e.g. pollination or herbivory proxies) can provide insight into the ecological significance of acoustic communities (Francis et al., 2012; Martini et al., 2024). This approach has potential to support large scale rewilding and nature recovery projects being implemented in response to EU nature restoration regulation, where the focus is on restoration of ecological process, function and resilience, rather than species (Bullock et al., 2022).

2.3.2 Hypotheses: functional acoustic diversity and ecosystem functioning

Building on biodiversity–ecosystem functioning (BEF) theory, and on previous research recognizing communication as an ecological process, we outline an explicit conceptual framework that links acoustic trait diversity to ecosystem functioning (Bapteste & Papale, 2021; Farina, 2018). This framework yields a set of testable hypotheses connecting variation in acoustic communication to ecological processes and system stability. In doing so, it treats acoustic trait diversity not simply as a

consequence or proxy of biodiversity, but as a functional dimension through which biodiversity can influence organismal fitness, community assembly, and ecosystem resilience.

F1 – Functional acoustic diversity enhances communication performance and the resilience of information exchange to environmental fluctuations.

Communities with higher acoustic functional richness and divergence (i.e. more distinct combinations of frequency, timing, and amplitude traits) will show higher "communication performance," e.g. greater effective signalling range, lower masking, and higher mate encounter rates per unit acoustic activity. Moreover, greater acoustic functional diversity may enhance the **stability of information exchange**, allowing these communication functions to be maintained despite environmental fluctuations. Such fluctuations might arise from disturbances in the form of increased environmental noise, weather events, or invasive and acoustically active species. This can be tested in behavioural studies combining recording arrays, field observations, laboratory experiments with playback experiments, or modelling approaches (Eldridge & Kiefer, 2018; Jablonszky et al., 2022, 2025; Reichert et al., 2024; Staniewicz et al., 2024). Testing this hypothesis would establish whether functional acoustic diversity contributes to communication performance and resilience.

F2 – Structural vs functional coupling under disturbance: decreasing structural diversity leads to a decrease in functional diversity

Disturbance (e.g. anthropogenic noise) can decrease structural acoustic diversity (see previous section) while also reducing functional acoustic diversity (loss of distinct acoustic strategies, due to lower availability of acoustic niches, acoustic masking by noise and reduced transmission range), leading to soundscapes that are structurally simplified and functionally degraded in terms of communication (Halfwerk et al., 2018; Staniewicz et al., 2024). Testing this hypothesis would reveal whether structural changes predict functional consequences for communication and whether the two dimensions capture distinct responses to disturbance.

F3 – Acoustic traits form functional syndromes with morphological and ecological traits

Acoustic traits do not evolve in isolation but are constrained and shaped by morphology, behaviour, and ecological context (Morton, 1975; Podos et al., 2004). We hypothesize that species' positions in acoustic functional trait space will covary with morphological and ecological traits, such as body size, vocal apparatus, foraging stratum, and microhabitat use. We use the term *functional syndrome* to refer to a suite of correlated morphological, physiological, behavioural, and ecological traits that jointly shape species' ecological strategies and communication. Such syndromes may arise through reciprocal

relationships among traits, as well as shared evolutionary and ecological constraints, rather than through a single directional causal pathway. Consequently, acoustic functional diversity is expected to partly correspond to patterns of functional diversity in other domains, such as trophic interactions or habitat use, while also retaining unique, non-redundant information. Testing this hypothesis would determine the extent to which acoustic functional diversity provides complementary insight into community assembly and ecosystem functioning beyond what is captured by traditional trait-based approaches.

F4 – Cross-scale propagation of acoustic functional diversity: an increase in functional acoustic diversity relates to an increase in multiple ecosystem functions

Communication is a process that links to several ecosystem functions such as predator-prey interaction, reproduction, coordination of community behaviour etc. We might therefore predict that higher acoustic functional diversity would be associated with higher diversity in other functional domains (e.g. pollination, herbivory). If supported, this hypothesis would suggest that acoustic functional diversity can serve as an integrative indicator of broader ecosystem functioning. For example, acoustically diverse communities may reflect a diversity of habitat structures, diverse species assemblages, and functionally diverse ecological networks. Empirical support for such cross-scale linkages has begun to emerge (Folliot et al., 2022; Francis et al., 2012; Martini et al., 2024), but remains an important frontier for research.

3 Towards an integrated acoustic diversity framework

Distinguishing between compositional, structural, and functional acoustic diversity is not only a conceptual exercise, but also creates opportunities for more targeted and transparent applications in ecological research and monitoring. Rather than proposing a single unified indicator, this framework supports a more considered and targeted use of acoustic data, where different metrics are selected according to specific questions and scales. For example, by recognising ecoacoustic indices as metrics relating to the structure of the acoustic habitat, we can hypothesise that they can serve as proxies for the taxonomic richness of an acoustic assemblage if:

1) the indices are applied to recordings containing only biophony or are at least dominated by biophony (as formulated e.g. in (Bradfer-Lawrence et al., 2023; Metcalf et al., 2020)), **and**
2) there is high acoustic evenness between the species forming the acoustic assemblage, **or**

3) the acoustically dominant species correlate with overall species richness (Müller et al., 2025).

The spatio-temporal structure of the soundscape both reflects and constrains the acoustic communication networks, linking compositional to structural and functional acoustic diversity. Geophony and anthropophony influence species composition and signalling behaviour (García-Navas et al., 2023; Lengagne et al., 1999; Mockford et al., 2011; Ware et al., 2015). A decline in structural acoustic diversity may manifest as i) acoustic homogenization, reduced temporal partitioning, or constrained transmission pathways, or ii) a loss in acoustic species richness. While the former reduces acoustic niche availability and compresses the effective acoustic space, the latter would increase acoustic niche availability. In degraded or noisy habitats, biophonic signals may be masked by abiotic or anthropogenic noise or dominated by a few prominent sound sources, limiting communication and functions such as mate attraction, territory defence, and predator avoidance (del Castillo Domínguez et al., 2021; Diepstraten & Willie, 2021; Francis et al., 2017; Gasc et al., 2018; Ware et al., 2015). Additionally, non-acoustic environmental structures—such as vegetation density, topography, and human-built infrastructure—affect sound propagation and thus influence acoustic connectivity within landscapes (Croci et al., unpublished). High-quality acoustic habitats can therefore be characterised by diverse, well-partitioned acoustic space, low masking, and sufficient signal connectivity, making structural acoustic metrics potential indicators of acoustic habitat quality.

3.1 Applications

Acoustic enrichment uses playback to influence habitat selection, recruitment, and settlement, and is increasingly explored in restoration (Gordon et al., 2019; Hahn & Silverman, 2007). Studies have demonstrated its potential to attract fish to degraded reefs, enhance coral settlement and oyster settlement, and improve colonisation of new ponds by frogs and toads (Buxton et al., 2015; Gordon et al., 2019; James et al., 2015; Williams et al., 2022). Biophony, anthropophony, and geophony may also provide cues for species (Mullet et al., 2017; Pijanowski et al., 2011).

Technological advances are enabling new analyses of acoustic communication networks (Logue et al., 2026). These approaches link composition, structure, and function: for example, simulated networks show how the acoustic environment and animal behaviour jointly shape network configuration and functionality (Reichert et al., 2024). Network configuration—who signals to whom and where signals travel—is directly relevant to structural acoustic diversity, whereas signal exchange relates to functional acoustic connectivity and diversity.

Communication networks can be examined at three levels:

- **Population level:** The identity and pattern of acoustic activity and exchanges within a species, such as chorus synchrony in anurans, define a communication network whose topology can be quantified using acoustic interactions among individuals.
- **Community level:** Interacting intra- and interspecific signals generate emergent sonotypes (Guerrero et al., 2025), reflecting the joint activity of multiple taxa and abiotic sound sources.
- **Landscape level:** Mapping sonotypes across space produces an acoustic mosaic of biophony, geophony, and anthropophony (Farina, Eldridge, et al., 2021; Farina & Mullet, 2024). This mosaic both influences signal transmission, masking, and detection and reflects the underlying biological community.

As in other ecological communities, acoustic communication networks may be shaped by environmental filtering, competition, facilitation, and neutral dynamics (Azar & Bell, 2016; Münkemüller et al., 2020; Reichert, 2026; Reichert et al., 2021; Tobias et al., 2014). For example, in addition to competition for acoustic space, experimental evidence suggests that heterospecific social facilitation, or temporal alliance formations against common rivals may play a further role (Goodwin & Podos, 2014; Rossetto & Laiolo, 2024). This is particularly pertinent given that singing activity is enhanced by the presence of heterospecific songs that differ acoustically from one's own (Rossetto & Laiolo, 2024). Such a mechanism of interspecific facilitation using auditory cues from heterospecifics has also been demonstrated from the selection of stopover or breeding habitats by migrant songbirds according to local resident bird density (Forsman et al., 2009; Szymkowiak & Kuczyński, 2017) (Forsman et al., 2009; Szymkowiak and Kuczyński, 2017), while chorusing males of Adelaide's warblers' have been observed to exhibit a higher proportion of song type clustering and matching than chance or competition would explain (Logue et al., 2026).

Perhaps the most urgent application of the proposed framework is in acoustic monitoring for ecological restoration. Passive acoustic monitoring can benchmark restoration success by tracking changes in species composition and acoustic habitat structure, while functional acoustic diversity could provide additional insights into the recovery of ecosystem functioning (Buřivalová et al., 2026; Campos-Cerqueira & Aide, 2016; Hao et al., 2021; Ramesh et al., 2023; Znidersic & Watson, 2022). Further research is needed to understand how acoustic traits function within ecological communities and contribute to ecosystem processes. Integrating compositional, structural, and functional acoustic diversity enables a more differentiated assessment of restoration. Recovery trajectories may differ across dimensions: structurally complex soundscapes may re-emerge before functionally diverse

signalling strategies, or similar structures and functions may arise from different acoustic communities with redundant traits and behaviours. Distinguishing these dimensions can improve the interpretation of restoration outcomes and the definition of targets. It can also support the integration of acoustic data into Essential Biodiversity Variables (EBVs): ecoacoustic indices relate more closely to ecosystem structure and processes, whereas species-level approaches better represent compositional variables. Functional acoustic diversity may bridge these domains, but its operationalisation in monitoring remains an important research priority (Ducrettet et al., 2025). Finally, a more speculative application lies in legal representation of ecological status within the emerging earth jurisprudence frameworks. Whilst only constitutionally recognised in Ecuador, Rights of Nature are increasingly being recognised across the globe.

4 Conclusion

By distinguishing between the compositional, structural, and functional dimensions of acoustic diversity, we provide a framework that clarifies the ecological meaning of acoustic variation and increases the interpretability of soundscape analysis. By decoupling **what** is present (composition), **how** it is arranged (structure), and **what** it achieves (function), we move away from the ambiguous use of acoustic indices as general biodiversity proxies.

This approach allows researchers to test explicit hypotheses regarding community assembly and ecosystem resilience. It highlights that soundscapes are not merely aggregates of different sounds, but dynamic communication networks where structural and functional integrity are as critical as taxonomic richness. Integrating these dimensions provides a scalable, non-invasive pathway to monitor not only the presence of species but also the rate and structure of information flow, resulting in cascading effects on other ecosystem properties. This framework thus provides a necessary conceptual foundation for the next generation of ecoacoustic research, shifting the focus from descriptive patterns to functional ecological insights.

Author contributions

Sandra Müller, Luc Barbaro, Solène Croci, Alice Eldridge, [5]Frédéric Sèbe and Jean-Yves Barnagaud conceived the ideas and led the writing of the manuscript. All authors contributed critically to

drafts and gave final approval for publication. Jean-Yves Barnagaud and Solène Croci were responsible of funding acquisition and project administration of the 'ACOUCENE' group. As this study is an integrative review proposing a new conceptual framework for acoustic diversity, no primary local data collection was required. The authorship team was assembled to ensure a broad interdisciplinary perspective, incorporating researchers from diverse ecological disciplines, a range of career stages (from early-career to senior researchers), and a diverse representation of genders and European countries. This diversity of expertise was critical to the development and validation of the proposed framework.

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Conflict of interest statement

The authors declare no competing interests.

Data availability statement

There is no archived data associated with this manuscript.

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Supplementary information

Glossary

Soundscape: The term soundscape is used differently across disciplines. The ISO standard defines it as the acoustic environment, as perceived by a person or people, in context (ISO 12913, 2014). As such the soundscape is part of the sensory landscape (senus Granö, 1929 in Pijanowski, 2024).
Farina et al. (2021) and Grinfeder et al. (2022) broaden this definition to all organisms, distinguishing between:

- the sensed soundscape — the sounds an organism is sensitive to, regardless of behavioural effect;
- the interpreted soundscape — the subset of sounds that influence behaviour or physiology.

Sound propagation and environmental filtering create differences between the distal soundscape (all sounds in the environment) and the proximal soundscape (sounds reaching a receiver, including recorders). Farina's acoustic habitat is conceptually similar to the distal soundscape and has strong overlaps to Pijanowski´s (2024) definition of a soundscape as "the collection of all biological, geophysical and anthropogenic sounds that emanate from a landscape". In this paper, "soundscape" generally refers to the distal soundscape, which – without a receiver - remains a theoretical construct, and cannot be measured in the field. In

practice soundscapes are often quantified as the proximal soundscape captured by a specific recording device.

Biophony: Sounds produced by living organisms, either intentionally (e.g. vocalizations, stridulations) or incidentally (body movements, wing beats, friction) (Farina, Eldridge, et al., 2021). In Sueur et al. (2021) sounds generated by vegetation interacting with wind are additionally considered as biophony, although these are otherwise often classified as geophony.

Geophony: Sounds emitted from the abiotic natural environment, such as wind, rain, running water and thunder. The ecological role of these sounds is described by Farina, Mullet, et al. (2021), Francis et al. (2023), and Mullet et al. (2017).

Anthropophony: Sounds produced by humans and their machines. Sounds from combustion engines are a specific type of anthropophony known as technophony. Technophony has a profound impact on animals, including humans, as discussed in reviews by Francis et al. (2017, 2023) and Shannon et al. (2016).

Acoustic diversity: Acoustic diversity is the variation of all sounds (biotic and abiotic) at a given place over a specific time. Also referred to as ecoacoustic diversity in Farina, Eldridge, et al. (2021). When focusing on biodiversity and the biophony, bioacoustic diversity or biophonic diversity has been defined as: “The variation (…) of sounds emanating intentionally or involuntarily from living organisms (…)” (Sueur et al., 2021). Farina, Eldridge, et al. (2021) advocate the term biophonic diversity and restrict the concept to sounds produced from animals excluding vegetation (that is sounds emitted from vegetation interacting with e.g. wind). Riede (1997) used the term bioacoustic diversity to characterise the diversity of the acoustic assemblage. Correspondingly geoacoustic diversity and anthroacoustic diversity could be defined. In this paper, we use the term 'bioacoustic diversity' rather than 'biophonic diversity', as the former is currently more prevalent in the literature, although both terms are generally used synonymously. Here, we restrict its usage to sounds generated by animals, encompassing both intentional acoustic signals and involuntary sounds associated, for example, with activity or movement.

Acoustic habitat: Acoustic dimension of a species habitat, that is the geographical area selected as favourable by a species for living (Farina, Eldridge, et al., 2021). This concept of the acoustic habitat closely aligns with the Pijanowski et al.´s (2011) definition of the soundscape, as both refer to the objective, listener-independent sonic environment composed of biophony, geophony, and anthropophony and structured in space and time. The main distinction lies in emphasis: Farina, Eldridge, et al. (2021) frame the acoustic habitat as a functional and semiotic component of ecological niches, whereas Pijanowski et al. (2011) conceptualize the soundscape primarily as an emergent landscape property suitable for measurement, monitoring, and environmental assessment.

Acoustic community: A set of acoustically interacting species that produce sounds using internal or external body parts and recur regularly in time, potentially giving rise to emergent acoustic properties such as sound diversity or complexity through space (Gasc et al., 2013; Rossetto et al., 2026). In contrast an acoustic assemblage would describe all coexisting animals that are acoustically active, even ephemerally, at a given time and place, without necessarily implying any regularly emergent patterns of acoustic properties (sensu Stroud et al., 2015).

Acoustic information: Acoustic signals encode critical biological and ecological information. In animal behaviour, they carry individual- and species-specific signatures, group dialects, and labile motivational and emotional cues, all embedded within social and environmental

contexts. When considered collectively across space and time, these signals contribute to the acoustic structure of communities and generate soundscapes that reflect the interactions between organisms and their environment. At the ecosystem scale, these acoustic patterns are shaped by landscape configuration, community composition, and the characteristics of the acoustic habitat, providing a potential window into underlying ecological processes (Farina, 2018; Sueur & Farina, 2015).

Soundscape metric: Numerical description of the whole soundscape. These include low level features (RMS/ loudness etc.), acoustic indices based on the spectral and temporal properties of soundscapes as well as learned descriptions (i.e. latent space representations or embedding dimensions learned through supervised or self-supervised machine learning algorithms).

Acoustic traits: are measurable properties of signals (e.g., frequency, amplitude, temporal patterning, and spectral structure), which can be quantified across individuals, species, and communities, without reference to the environmental context and that effectively participate to signal coding in acoustic communication.

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