










REVIEW

Passive acoustic monitoring provides a fresh perspective on fundamental ecological questions

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Abstract

1. Passive acoustic monitoring (PAM) has emerged as a transformative tool for applied ecology, conservation and biodiversity monitoring, but its potential contribution to fundamental ecology is less often discussed, and fundamental PAM studies tend to be descriptive, rather than mechanistic.
2. Here, we chart the most promising directions for ecologists wishing to use the suite of currently available acoustic methods to address long-standing fundamental questions in ecology and explore new avenues of research. In both terrestrial and aquatic habitats, PAM provides an opportunity to ask questions across multiple spatial scales and at fine temporal resolution, and to capture phenomena or species that are difficult to observe. In combination with traditional approaches to data collection, PAM could release ecologists from myriad limitations that have, at times, precluded mechanistic understanding.
3. We discuss several case studies to demonstrate the potential contribution of PAM to biodiversity estimation, population trend analysis, assessing climate change impacts on phenology and distribution, and understanding disturbance and recovery dynamics. We also highlight what is on the horizon for PAM, in terms of near-future technological and methodological developments that have the potential to provide advances in coming years.
4. Overall, we illustrate how ecologists can harness the power of PAM to address fundamental ecological questions in an era of ecology no longer characterised by data limitation.

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KEYWORDS

acoustic index, bioacoustics, biodiversity, ecoacoustics, sensor array, soundscape, spatiotemporal scale

1 | INTRODUCTION

Breakthroughs in ecological research have often resulted from technological advances or integration of methods from other fields (McCallen et al., 2019). Examples include the wide range of ecological subdisciplines that have been shaped by advances in genetic analyses, such as population genetics (Lowe & Allendorf, 2010), the adoption of GPS tagging and biologging in movement ecology studies (Williams et al., 2020) and the use of stable isotope analysis in trophic ecology (Post, 2002). Similarly to how such technological advances continue to move ecology forward as a discipline, so too

does acoustic data collected in the field hold promise for helping to answer some of ecology's major fundamental questions.

Recent developments in data acquisition, storage and processing have led to *Passive acoustic monitoring* (PAM; Box 1) approaches being increasingly adopted for a wide array of ecological applications and conservation management (Burivalova et al., 2019; Elise et al., 2019; Gasc et al., 2017; Lomolino et al., 2015; Sethi, Jones, et al., 2020). PAM allows the study of ecosystems at various ecological scales from individuals and populations to communities and landscapes or *soundscapes* (Sueur & Farina, 2015; Box 1). Soundscapes describe all biological (*biophony*), geophysical (*geophony*) and

BOX 1 Glossary of key terms

Acoustic calibration—the action of comparing a result to a known reference value for a given system (see Alcocer et al., 2022).

Acoustic indices—indices based on mathematical formulae that summarise the soundscape with the goal of extracting ecologically meaningful information (Sueur et al., 2014).

Acoustic localisation—The act of pinpointing the precise spatial location of a target sound source using synchronised data from multiple local sensors, often from an acoustic sensor array (Rhinehart et al., 2020).

Acoustic masking—Masking occurs when an acoustic signal cannot be perceived by the receiver because a non-target sound fills the same frequency and time domain (Krause, 1993). Can be biotic (e.g. masked by a heterospecific or conspecific signal) or abiotic (e.g. masked by rainfall).

Acoustic niche hypothesis—The conceptual framework describing how species are expected to partition the soundscape in frequency and time to avoid acoustic masking by heterospecifics, maximising the likelihood of successful acoustic communication (Krause, 1993).

Acoustic sensor arrays—Spatially distributed networks of multiple passive acoustic sensors, which together form an array across the landscape/seascape (e.g. Van Parijs et al., 2015).

Anthropophony—All human-related sounds in an ecosystem including, for example, noise pollution from construction work or traffic (Pijanowski, Villanueva-Rivera, et al., 2011). Sounds produced by machines are sometimes termed *technophony*.

Biophony—All sound emitted by animals usually excluding humans (Krause, 1987).

Fundamental ecological questions—Theoretical or empirical questions concerning acquisition of knowledge of the underlying foundations of ecological phenomena which do not necessarily have particular applications (Courchamp et al., 2015). Also termed *basic* or *blue-skies research*.

Geophony—Natural, but non-biological ambient sounds, such as climatic events (e.g. wind, rain, thunder) or geologic events (e.g. earthquake, rivers; Krause, 1987).

Passive acoustic monitoring (PAM)—the use of autonomous recording units (e.g. microphones, hydrophones, ultrasound detectors) to record audio data in the field (Gibb et al., 2019).

Reference library—a collection of (annotated) audio recordings with known species identities, used as type-specimen references for identifying species in new recordings (e.g. The Macaulay Library, www.macaulaylibrary.org).

Soundscape—all biological, geophysical and anthropogenic sounds in an ecosystem (Pijanowski, Farina, et al., 2011; Pijanowski, Villanueva-Rivera, et al., 2011).

Species classification algorithms—Automated (e.g. machine learning) algorithms that aim to classify distinct sounds to group species with minimal human input (Zhao et al., 2017), often using reference libraries as training data.

Spectrogram—a visual representation of acoustic energy in the time (x-axis), frequency (y-axis) and amplitude (usually colour) domains (see Pijanowski, Villanueva-Rivera, et al., 2011).

anthropogenic sounds (*anthropophony*) in an ecosystem (Box 1). Furthermore, soundscapes contain rich information about landscape structure and can be indicators of ecological processes or disturbance (Deichmann et al., 2018; Odom et al., 2021; Pijanowski, Farina, et al., 2011; Pijanowski, Villanueva-Rivera, et al., 2011; Sueur & Farina, 2015; Villanueva-Rivera et al., 2011).

There is continued debate surrounding methodological best practice, for example in terms of survey design (Desjonquères et al., 2020; Mooney et al., 2020; Sugai et al., 2020), data visualisation (Gage & Axel, 2014; Towsey et al., 2014) and the utility of various analytical approaches for rapidly summarising the soundscape in a management context (Alcocer et al., 2022; Bradfer-Lawrence et al., 2019; Gasc et al., 2015; Ross, Friedman, et al., 2021). Nevertheless, PAM is now widely accepted as an invaluable addition to the environmental monitoring toolkit (Desjonquères et al., 2020; Gibb et al., 2019; Guan et al., 2021). Despite the proliferation of PAM studies in ecology, limited attention has typically been paid to the capacity for acoustic monitoring to provide insight into *fundamental ecological questions* (Box 1); where such work does exist, it is often descriptive rather than mechanistic.

Here, we first discuss the strengths and limitations of PAM methods in the context of fundamental ecological research (Section 2), and then we illustrate how PAM can be applied in conjunction with other methods to address several fundamental questions (Section 3). We aim to demonstrate the broad applicability

of PAM in complementing existing methods by including examples from across subdisciplines, levels of ecological organisation and environments (aquatic and terrestrial). Finally, we discuss some future directions for PAM studies in ecology (Section 4). There exist many excellent reviews on the use of PAM in ecology for beginners and experts alike (e.g. Deichmann et al., 2018; Gibb et al., 2019; Lomolino et al., 2015; Pijanowski, Farina, et al., 2011; Pijanowski, Villanueva-Rivera, et al., 2011; Sueur & Farina, 2015; Sugai et al., 2018). As such, we focus here instead on the use of PAM to tackle long-standing and novel fundamental ecological questions beyond merely descriptive studies, towards process-based studies aiming to answer the 'why' questions that have long captivated ecologists.

2 | WHY IS PAM USEFUL FOR FUNDAMENTAL ECOLOGY?

PAM has clear potential to inform ecological studies by providing opportunities to monitor otherwise difficult-to-access ecosystems (Section 2.1), and by providing long-term and/or high-resolution biodiversity data through time (Section 2.2) that spans broad study regions (Section 2.3). Yet, PAM is limited in its utility by technological and biological constraints (not all species produce sound), the physics of sound propagation and interference from non-target sounds, among others (see Figure 1 and Box 2). As such, results from PAM

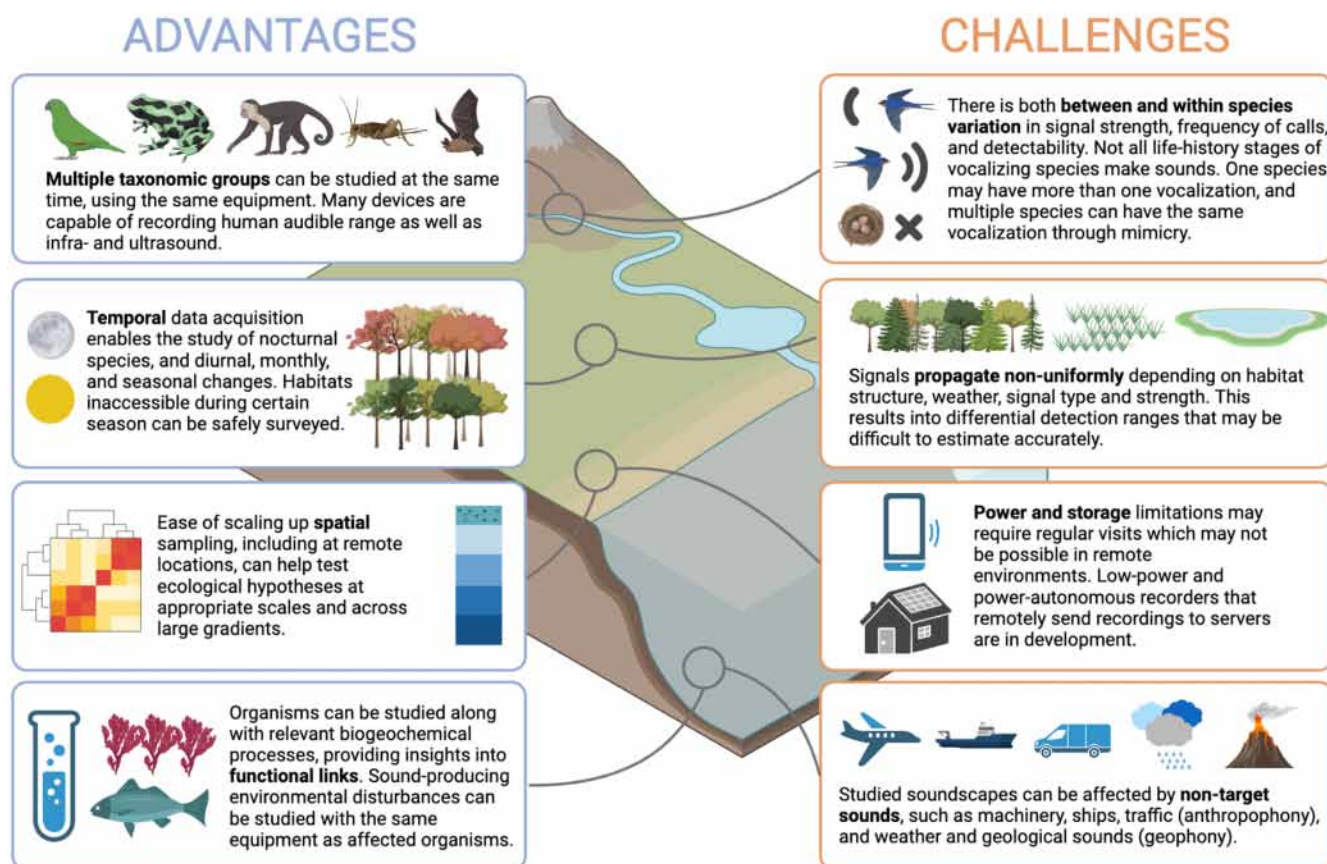


FIGURE 1 Strategic advantages of Passive acoustic monitoring (PAM; left) and current challenges (right), due to different temporal and spatial scales, natural histories of target taxa, as well as human interactions with, and contributions to, the soundscape. Figure created in BioRender.

BOX 2 Current limitations of passive acoustic monitoring.

Beyond the simple observation that not all life on earth produces sound at a detectable level—and therefore cannot be easily detected via passive acoustic monitoring—those implementing PAM in ecological studies currently face a range of additional limitations. Identifying species-specific vocalisations from acoustic recordings provides evidence for species presence at a given time and location, but determining true absences is more challenging. A species might not be vocalising because it is not present, its vocalisation was masked (Box 1), or it was simply too quiet to be detected (Toth et al., 2022). Detectability of certain species also changes with seasonal and environmental factors (Medina & Francis, 2012). For example, during the breeding season, many birds sing more frequently, making detectability higher than during winter. Disentangling behaviour from detectability is thus essential to generate unbiased estimates of occupancy. Estimating species abundance is often challenging, as it can be difficult to disentangle individual vocalisations; the challenge is to understand whether there are multiple individuals versus a single noisy individual vocalising repeatedly. Abundance estimation is increasingly possible using acoustic localisation techniques (Rhinehart et al., 2020; Verreycken et al., 2021), but further methodological progress is needed for generalisable and well-performing abundance estimation to be achieved.

Passive acoustic monitoring also involves considerable practical effort, limiting widespread adoption. Networks of audio recorders generate vast amounts of data (Sethi et al., 2021; Sethi, Ewers, et al., 2020) that can be difficult to store, analyse and archive without sophisticated and expensive server architectures. Similarly, metadata such as time and date, weather and GPS location should be stored alongside recordings, but there is no standardised approach for formatting and storing metadata. The lack of metadata standards ultimately hinders efforts to reanalyse and share datasets (Section 4), slowing progress in developing and evaluating new analysis pipelines. As another example, variation in survey design (Skalak et al., 2012; Wood, Kahl, et al., 2021) and recording equipment (Gibb et al., 2019) can significantly impact the outcomes of analyses, making cross-study synthesis particularly difficult.

studies should be interpreted carefully, and PAM may be best applied in combination with other data collection techniques. Nevertheless, here we outline some of the advantages of PAM as it relates to the study of fundamental ecology.

2.1 | Access to survey locations

Remote, rare or otherwise inaccessible ecosystems and cryptic species are logistically challenging to incorporate in ecological studies. PAM, together with camera traps, provides opportunities to test ecological hypotheses in ecosystems that have previously been restricted to snapshot studies of biodiversity, such as rapid biodiversity assessment during one-off expeditions (Pillay et al., 2019). Beyond geographical remoteness, PAM can also enable data acquisition during seasons of heightened inaccessibility, such as during floods or rainy seasons, which often coincide with important life-history stages for vocalising birds and mammals (Szymański et al., 2021). Similarly, parts of ecosystems that are typically hard to study, such as forest canopies or the deep sea, or areas undergoing dramatic disturbance such as gas exploration or extreme weather events, become more accessible (Deichmann et al., 2017; Gomes et al., 2020; Gottesman et al., 2021; Ross et al., 2023). Such disturbances and other temporary alterations to ecosystems or soundscapes frequently provide invaluable 'natural experiments' for testing ecological hypotheses (Derryberry et al., 2020). Although PAM devices can record 10+ hours per day for many weeks or even months, they still require more frequent visitation for maintenance than camera traps, for example, as they are typically used to record data more consistently, which is more demanding in terms of power and data storage. Solar panels may address this issue (Roe et al., 2021), but solar power is less reliable in habitats with high cloud or canopy cover, such as rainforests, or with limited solar exposure, such as the arctic in winter.

2.2 | Temporal resolution and scale

One of the most important aspects of PAM is the ability to generate both broad-scale and high-resolution acoustic time series. High-resolution acoustic data offer the opportunity for biodiversity monitoring across temporal scales, and the possibility to study fine-scale temporal species dynamics at higher resolution than previously possible (e.g. Desjonquères et al., 2022). As well as capturing the dynamics of individual species, the biotic component of the soundscape is composed of multiple vocalising taxa, spanning trophic levels and taxonomic groups, and thus soundscapes can be analysed as a signal of the whole (vocalising) community in a way that few other monitoring methods currently allow. As long-term PAM data are amassed, recordings will enable study of the temporal variability in detected species and soundscapes due to natural cycles (although this may be confounded by temporal variation in background noise). For example, in many ecosystems, animal vocal activity peaks at dawn and dusk each day, driving a strong diel cycle in the soundscape (Desjonquères et al., 2015; Ruppé et al., 2015; Staicer et al., 2020; but see Gottesman et al., 2020). Despite being a highly researched phenomenon, the reasons for the dawn chorus are still unclear (Gil & Llusia, 2020). Over longer timescales, soundscapes also cycle seasonally (Towsey

et al., 2014), with the lunar phase (Staaterman et al., 2014), and with infrequent climactic events (e.g. Lee et al., 2017). In this area, PAM may help answer valuable ecological questions in chronobiology and temporal ecology, such as how species respond to mass fruiting events, or the role of the lunar cycle in species' natural histories. At the same time, as longer-running studies amass a wider variety of non-target sounds in recordings (such as wind, construction noise, or extreme events such as earthquakes or tropical cyclones), it becomes more difficult to reliably extract biodiversity information from the soundscape (Ross, Friedman, et al., 2021). These sources of variation are both a challenge and an opportunity; high-resolution PAM datasets allow studies to explicitly separate variability from seasonality in both biotic and abiotic sound, and to ask ecological questions on a scale previously restricted to biodiversity datasets collected with considerable effort over many years (Francomano et al., 2020; Staaterman et al., 2014; see also Magurran et al., 2010). PAM offers the potential to bypass some of this recording effort, though replaces this challenge with others such as interpretability and data storage (Box 1). For example, Sueur et al. (2019) attributed erosion of soundscape intensity (amplitude) to weather-related changes in bird diversity across a 14-year period in California, USA. As even longer time series are amassed, the scope of such investigations continues to grow.

High-resolution PAM data may also be better suited to causal inference than data from traditional field surveys, which are typically of lower temporal resolution. Successful causal inference should deviate as little as possible from an idealised experimental or observational setting controlling for all potentially confounding variables (Kimmel et al., 2021). This makes causal inference data-hungry, and quasi-experimental designs (see Butsic et al., 2017) or statistical approaches to infer causality from observational time series (e.g. empirical dynamic modelling, Ross, Suzuki, et al., 2021) may profit from large PAM datasets. Despite this potential, we emphasise that several important obstacles remain in using PAM for causal inference, including the development of new models that will be able to incorporate uncertainty connected to PAM data at several levels, especially given the natural variation and complex seasonality present in most soundscapes.

2.3 | Spatial resolution and scale

Along with temporal resolution, a major bottleneck to testing fundamental ecological questions in real-world settings has been the difficulty of sampling diverse animals at sufficient spatial resolution. The spatial scale of observation can influence the strength or form of many, perhaps most, modern-day ecological relationships, such as those concerning biodiversity change (Chase et al., 2018), community assembly (Shinohara et al., 2022), ecosystem functioning (Gonzalez et al., 2020) or ecological stability (Ross, Suzuki, et al., 2021). Distributed networks of PAM devices allow sampling across large spatial extents (Sethi et al., 2018), with potential for revealing spatial patterns and processes as envisioned by the discipline

of soundscape ecology (Pijanowski, Villanueva-Rivera, et al., 2011). For example, the US National Park service is using PAM technology to build a national estimate of noise levels (Buxton et al., 2017; Mennitt & Fristrup, 2016). When paired with citizen science count and monitoring data, this PAM data revealed the pervasive impact of anthropogenic noise on bird diversity and breeding (Klingbeil et al., 2020; Senzaki et al., 2020). Such continental-scale approaches, combining PAM data and statistical modelling, provide biodiversity insights at previously elusive spatial scales, and should next be expanded to other vocalising animals (e.g. fish, frogs, insects, mammals) from acoustic recordings at scale. Collaborative efforts using standardised PAM equipment and protocols will help calibrate traditional methods of censusing animals at local, regional and global scales, and across landscape types.

3 | WHERE CAN ACOUSTICS FACILITATE FUNDAMENTAL ECOLOGICAL DISCOVERY?

Despite its limitations (Box 2), the benefits of PAM outlined above allow PAM studies to contribute to answering fundamental ecological questions. Next, we illustrate some cases where PAM, in conjunction with other survey methods and machine learning tools, can provide more temporally and spatially extensive estimates of diversity than ever before (Section 3.1). This, in turn, enables quantification of population change (Section 3.2), assessment of climate change impacts on species and communities (Section 3.3), and broader understanding of ecological responses and recovery (Section 3.4), among other things. Without being exhaustive, we aim to demonstrate some notable fundamental questions to which PAM data can contribute new angles or fresh insight.

3.1 | How much biodiversity is there on planet earth?

The questions of 'how many species are there?' and 'where are they found?' are foundational to natural sciences and remain as important today as they were to the pioneers of ecological research. Our understanding of biodiversity, and the ecological mechanisms underpinning it, depends on accurate estimates of where species are distributed (Brown, 1995). Acoustic surveys have played an important role in filling gaps in understanding, particularly in habitats where other biodiversity survey methods are difficult or impossible. Due to the challenges of working in the marine environment, PAM has historically been most influential in marine biodiversity surveys. Since the 1950s, acoustic surveys have shed light on the diversity and life histories of marine mammals and fish, which would have been otherwise impossible (Rice et al., 2021; van Parijs et al., 2009). In terrestrial systems, PAM is increasingly used to map biodiversity in remote or challenging habitats such as tropical forest (Burivalova et al., 2019; Deichmann et al., 2018). Though PAM is incapable of including non-vocalising taxa in species count estimates (but see

Sethi et al., 2022), it nevertheless provides a powerful approach for rapidly estimating the diversity of several key indicator taxa, such as birds, amphibians and bats (de Camargo et al., 2019; Deichmann et al., 2017; Sugai et al., 2018).

As methods to interpret and analyse acoustic data have evolved, PAM presents unique opportunities for detecting cryptic diversity. In complex ecosystems, behaviourally cryptic (shy and rarely seen) and taxonomically cryptic (unrecognised species, phenotypically similar to a recognised species) may be overlooked, particularly in the highly diverse but relatively understudied tropics (Fišer et al., 2018; Rheindt et al., 2020; Whitmarsh et al., 2018). The unparalleled temporal and spatial survey coverage afforded by PAM, especially in challenging environments, has played a key role in detecting ecologically significant, but behaviourally cryptic species across ecosystems, from marine fish to forest elephants (Picciulin et al., 2019; Wrege et al., 2017). Researchers now often turn to bioacoustics analyses to highlight cryptic species diversity and draw species boundaries in diverse but difficult-to-access ecosystems (Parmentier et al., 2021; Sin et al., 2022), often drawing on publicly available *reference libraries* (Box 1) of vocalising species (e.g. Xeno-canto; the Macaulay Library). This approach is particularly useful for birds and other taxa where vocalisations play an important role in sexual selection (Uy et al., 2009). Demonstrating a bird population has diverged significantly from their source population in the structure or tempo of their vocalisations is a useful indication that there is minimal gene flow between populations and that speciation may have occurred (Ó Marcaigh et al., 2021, 2022; O'Connell et al., 2019). However, to date, these analyses have been species specific and labour intensive, both in terms of collecting targeted recordings and manual extraction of spectral and temporal measurements from *spectrograms* (Box 1). Advances in the analysis of PAM data are likely to alleviate these challenges in the near future. Considerable improvements have already been made in automated identification of species from soundscapes (Sethi, Jones, et al., 2020; Ulloa et al., 2021). For example, the Convolutional Neural Network BirdNET can automatically identify over 3000 species of birds, mammals and amphibians worldwide (Kahl et al., 2021). Researchers are also beginning to identify individual animals, such as in the soundscape fingerprinting of Bornean gibbon individuals using machine learning techniques (e.g. Clink & Klinck, 2021). As analytical methods improve, and type-specimen data for reference libraries of species' vocalisations are curated, it should be possible to isolate and categorise taxonomically cryptic species from soundscape inventories. In turn, this will allow consideration of putative species to be incorporated into biodiversity assessments and highlighted for further investigation and description.

Going forward, PAM should contribute novel measures of biodiversity at the biome level, providing insight into ecological processes and ecosystem functioning (Folliot et al., 2022). Standardised characterisation of biomes is a persistent challenge for ecologists, and typically involves a mixture of expert knowledge, description of environmental factors (e.g. precipitation and temperature regimes),

and intensive survey effort to assess local biodiversity, which is seldom repeatable at scale (Conradi et al., 2020). Acoustic monitoring over broad spatial scales is still relatively rare, but as PAM networks are established in a diversity of biomes, the potential contribution of PAM to ecosystem and biome categorisation is growing (Sethi et al., 2018). Projects aiming to collect long time series of soundscapes globally will allow assessment of whether biomes have typical, repeatable soundscape characteristics, which if identified, could also be applied to compare and monitor biomes more efficiently than traditionally labour-intensive biodiversity surveys (Gottesman et al., 2020; Roe et al., 2021). That said, identification of 'typical' soundscapes using *acoustic indices* (Box 1) requires overcoming the current pitfalls of such approaches, especially their poor transferability across ecosystems and inconsistent relationships with (alpha) diversity (Alcocer et al., 2022; Ross, Friedman, et al., 2021).

3.2 | Why do populations change over time and space?

Acoustic techniques have long supported real-time and periodic population assessments of many marine mammals and fish (Rice et al., 2021; van Parijs et al., 2009), but in terrestrial ecosystems, landscape-scale PAM has only recently gained traction as a means of assessing populations across vast areas. This has enabled more comprehensive population assessments than have previously been possible for many species (Balantic & Donovan, 2019; Banner et al., 2019; Wood, Popescu, et al., 2019). For example, PAM programmes enabled detection of population changes for bats across ~170,000 km² of the Pacific Northwest USA (Rodhouse et al., 2019), and the rapid population growth and subsequent successful removal of an invasive owl species across ~6000 km² in the Sierra Nevada, USA (Hofstadter et al., 2022; Wood, Gutiérrez, et al., 2019). Detection of population responses to spatial variation in environmental conditions has also been fruitful, with PAM used to demonstrate climate-mediated population changes across an elevational gradient spanning 37,600 km² in northern California (Furnas, 2020), and behavioural and population responses of songbirds to logging in tropical forests of Borneo (Pillay et al., 2019), and northern Brazil (de Camargo et al., 2019). Early successes in the applications of PAM for assessing population change suggest much potential for further advances.

Attributes of terrestrial populations are generally estimated either with occupancy models or with demographic studies. Broadly, occupancy models are a means of testing hypotheses concerning how populations respond to environmental variation while accounting for the fact that animals may not always be observed even if they are present (MacKenzie et al., 2003; Tyre et al., 2003). In *occupancy-based* PAM studies, sites are classified as occupied or unoccupied across repeated surveys based on the detection of acoustic signals of a target species (Wood & Peery, 2022). Mechanistic relationships between species and habitat features—and thus a robust understanding of a species' niche—can be established by quantifying the factors affecting extinction and colonisation by

means of multi-season occupancy models (MacKenzie et al., 2003; Yackulic et al., 2015). Another common objective of basic ecological inquiry, quantification of interaction strength between species, can be achieved with multi-species occupancy models (MacKenzie et al., 2004). Occupancy-based population studies are likely to be possible for most PAM projects, since extracting species-specific acoustic signals over multiple survey periods (e.g. days, weeks) is a basic requirement for most analyses.

In *demographic* studies, populations are quantified in terms of abundance, survival or population growth rate or structure, among other parameters. Abundance or density assessments are generally predicated on either the potential occurrence of multiple conspecifics within range of each acoustic recorder to enable analyses of vocalisation counts (reviewed by Marques et al., 2013; Pérez-Granados & Traba, 2021), or on deploying multiple recorders within range of each individual (Rhinehart et al., 2020), which requires careful positioning and precise time synchronisation of recorders. Alternatively, metrics such as age structure or breeding status can be determined with age- or stage-specific vocalisations (e.g. Palacios et al., 2016). Overall, demographic analyses tend to require more detailed data than occupancy-based studies, but they have the potential to provide more ecological nuance.

The trade-off between processing effort and ecological detail need not be a permanent constraint; because audio data are a permanent archive, complex analyses related to more detailed population parameters or secondary objectives can be conducted whenever the necessary resources and analytical tools become available. One particularly exciting prospect is the potential for acoustic-based mark-recapture models. Individual identification has been achieved in a variety of species (e.g. Clink & Klinck, 2021; Odom et al., 2013), and if acoustic mark-recapture can be effectively applied to landscape-scale datasets, valuable population data such as survival estimates should be attainable. For example, post hoc analyses of audio data collected for occupancy-based studies revealed interspecific competition and foraging behaviour of owls (Wood, Klinck, et al., 2021; Wood, Schmidt, et al., 2019). Similarly, Wrege et al. (2017) estimated abundance and spatiotemporal variation in vocal behaviour of elephants using a PAM dataset, and Rice et al. (2021) described seasonal variation in the distribution and behaviour of cetaceans. Intrapopulation variation can be directly studied with acoustic data, supporting robust inference, but is more resource intensive. For instance, animal tracking combined with acoustic recording linked vocal behaviour to foraging strategy in killer whales (Riesch & Deecke, 2011), playback experiments illuminated predator defence strategies in katydids (Symes et al., 2020), and animal-borne acoustic tags have provided incredible detail into the vocal behaviour of marine mammals and birds (Hoffmann et al., 2019; Johnson et al., 2009; Reid et al., 2021).

Ultimately, PAM can provide multifaceted information on animal populations, including population dynamics over time, biotic and abiotic determinants of habitat selection, and behavioural variation within survey seasons. An important next challenge is to integrate data about multiple species. Directly comparing population

estimates among taxa would require a nested sampling design to capture differences in space-use and sound propagation (e.g. one wolf compared to thousands of insects), but testing for joint responses to shared environmental change, such as drought or habitat modification, could reveal ecological patterns with a taxonomic breadth previously difficult to attain (Bush et al., 2017).

3.3 | How is climate change affecting phenology and distribution?

Climate change is having profound but still poorly understood impacts on phenology: the timing of lifecycle events (Penuelas et al., 2010). Changing environmental conditions can influence the timing of events such as breeding, migration or post-hibernation emergence (Horton et al., 2020; Samplonius et al., 2018). The consequent mismatches between species can result in asynchronous population dynamics or distributional lags between interacting species (Devictor et al., 2012; Maglianesi et al., 2020). Described as a 'ticking time-bomb' (Simmonds et al., 2020), these mismatches can disrupt important ecological interactions such as pollination and predator-prey dynamics (Renner & Zohner, 2018). Yet, estimating phenology and distribution is costly, and so far is mostly limited to a few intensively studied populations, such as plants (Taylor et al., 2019) or birds (Lack, 1964). Moreover, general, mechanistic understanding is precluded by the potential for phenological responses to differ between species, communities and landscapes, and across spatiotemporal scales (Park et al., 2021). Continuous data at high temporal resolution and from multiple species are thus vital for understanding climate change impacts on species phenology, distribution and interactions. With relatively low effort, PAM data can fill this niche (Desjonquères et al., 2022).

Acoustic monitoring can already provide insight into the link between phenology and climate. For example, Oliver et al. (2018) demonstrated that acoustically estimated dates of songbird arrival at Arctic breeding grounds were linked to snow melt dates, and Farnsworth and Russell (2007) used PAM to detect overnight flight calls of migratory birds from an oil platform, suggesting that the variation in call detections may in part be linked to atmospheric conditions. Similarly, citizen science projects demonstrate the value of tracking bird and insect migration timing at continental scale for both fundamental and applied research (Hurlbert & Liang, 2012; Jeliakov et al., 2016; Newson et al., 2016), but such intensive monitoring is typically restricted in geographical scope (Feldman et al., 2021; La Sorte & Somveille, 2020). Modern recording equipment has expanded citizen science programmes, with initiatives like nocmig (www.nocmig.com) using citizen scientists to track nocturnal avian migration via acoustic monitoring. Large-scale deployment of PAM sensors has potential for tracking phenology in even remote locations (Deichmann et al., 2018; Roe et al., 2021), capturing elevational or latitudinal range shifts with climate change (Lomolino et al., 2015), and climate-induced changes to migration timing (e.g. Oliver et al., 2018).

The timing of foraging and reproduction are key phenological attributes for many species (Renner & Zohner, 2018), and a range of animals, both terrestrial and aquatic, use acoustic signals for reproductive or territorial signalling (Bass & McKibben, 2003; Hou et al., 2017). Leveraging PAM to estimate the timing, intensity and structure of reproductive signals thus allows identification of breeding times and monitoring of potential phenological shifts in breeding (Bruni et al., 2014; Tremain et al., 2008; Vokurková et al., 2018). For example, for fish species from the Sciaenidae family, recent studies suggested that spawning status can be inferred from shifts in call rate and the temporal structure of calls during spawning (Bolgan et al., 2020; Picciulin et al., 2020) addressing fundamental questions concerning life history, and PAM helped locate spawning sites for several fish species of commercial or conservation importance, for example for Gadidae (e.g. Caiger et al., 2020) and Serranidae (e.g. Wilson et al., 2020). Acoustic signals also include alarm calls and contact calls between foraging groups (Benedict & Krakauer, 2013; Fallow et al., 2013), and foraging activity can itself produce characteristic acoustic signals (Desjonquères et al., 2020; Pirota et al., 2014). Where acoustic signals with different purposes are readily distinguishable, separating these signals allows assessment of relative time budgets attributed to reproduction or foraging across seasons and habitats, and PAM could, in this way, contribute towards fundamental understanding of energy balance and allocation (Arranz et al., 2011; Pine et al., 2018).

3.4 | How do ecosystems respond to disturbance?

Because soundscapes encode information on biotic and abiotic aspects of ecosystems, they are useful for detecting changes resulting from disturbances—any change to a system representing a discrete shock (*pulse*) or a sustained alteration (*press*)—as well as post-impact recovery. For example, climate change and subsequent shifts in weather patterns, including extreme weather events, are likely to further modify natural disturbance regimes, interfering with fauna that rely on acoustic information and altering soundscape dynamics (Gottesman et al., 2020; Sueur et al., 2019). Indeed, altered soundscapes are often the first detectable changes in biodiversity noted both by ecologists and the public following ecosystem disturbance (Gottesman et al., 2021; Krause, 1987). Understanding the resistance and resilience of ecosystems facing disturbance has been a core focus of ecologists for many years (McCann, 2000), and this fundamental knowledge is key to informing restoration of heavily altered ecosystems and the robust delivery of ecosystem services (Keyes et al., 2021; Ross, Arnoldi, et al., 2021). Recordings from 'natural' sites can be used as a reference for other sites that are exposed to disturbance but lack a pre-disturbance baseline (soundscape *space-for-time substitution*; Burivalova et al., 2019). Soundscape-level metrics or acoustic indices developed from reference sites can be used as community-scale targets of soundscape restoration (e.g. nocturnal sea birds on the Aleutian Islands: Borker et al., 2020; freshwater ponds in the UK: Greenhalgh et al., 2021), while *species classification*

algorithms (Box 1)—though difficult to obtain in species-rich systems or for rarely vocalising species (but see Ulloa et al., 2018)—can contribute species composition information to develop recovery metrics.

Soundscape change has long been used to detect response of organisms to ecosystem disturbances, including infrastructure development, habitat fragmentation and introduction of invasive species. For example, in Peruvian rainforests, soundscape analysis demonstrated varying responses of birds, frogs and entire soundscapes to natural gas infrastructure construction and operation (Deichmann et al., 2017), which can have cascading effects on ecosystems that persist even after operations have ceased (Phillips et al., 2021). Similarly, in the North Sea, acoustic monitoring revealed negative short-term harbour porpoise behavioural responses to pile driving for wind farm construction (Graham et al., 2019). Burivalova et al. (2018) compared soundscapes of natural and managed forests in Papua New Guinea, showing that forest fragmentation was associated with reduced soundscape saturation at times of peak biophony. In New Caledonian forests, the invasive ant *Wasmannia auropunctata* caused a reduction of local insect biodiversity, leading to impoverishment of the soundscape (~80% cricket call decline; Gasc, Anso, et al., 2018). With changes in the frequency and intensity of disturbance events in the Anthropocene (Fischer et al., 2021) and the establishment of *acoustic sensor arrays* (Box 1) to generate long-term PAM datasets across ecosystems (e.g. the U.S. Northeast Passive Acoustic Sensing Network [NEPAN]: Van Parijs et al., 2015, the Australian Acoustic Observatory: Roe et al., 2021, and the Okinawa Environmental Observation Network [OKEON]: Ross et al., 2018), there is increasing opportunity to address fundamental questions concerning global environmental change and disturbance ecology through a mechanistic lens (e.g. Gottesman et al., 2021; Ross et al., 2023).

While PAM is helpful for documenting the pre-disturbance state of land and seascapes, the question remains whether recovery to pre-disturbance states is a realistic goal, or whether managing for resilience is a better approach. In either case, how can progress be measured and how does one know when restoration has been achieved? Such applied questions can be readily informed by fundamental science. For example, comparisons of sites under different restoration states in marine (Bertucci et al., 2016; Butler et al., 2016), freshwater (Greenhalgh et al., 2021), island (Borker et al., 2020) and terrestrial systems (Gasc, Gottesman, et al., 2018) highlight the challenges of understanding ecological (re)assembly rules that govern recovery dynamics (Audino et al., 2017). PAM can provide information on succession and community assembly dynamics to aid understanding of restoration trajectories. For example, PAM can detect the arrival of new species to a site or can monitor the recovery of specific functional groups (Rolo et al., 2017), allowing detailed measurement of progress towards a climax community, including in cases where the community may not closely resemble a natural 'control' site (Rossi et al., 2017). There is also potential to monitor patterns of phylogenetic or functional recovery using PAM (Gasc et al., 2013), and to identify incomplete or slow recovery by exposing the mechanisms

limiting recovery (Rossi et al., 2017). In cases where restoration is particularly slow (e.g. decades), it is unlikely that the same experts can remain involved in the restoration effort long term, so securely archived, re-analysable PAM data can help subsequent generations of scientists monitor soundscape change and recovery. For example, wildfire damage was detectable after 3 years in an Arizonan soundscape (Gasc, Gottesman, et al., 2018), and the signature of arctic fox predation persisted in the soundscape of Alaskan bird colonies for decades after predator extirpation (Borker et al., 2020). Whether disturbed soundscapes tend to return to mirror the characteristics of undisturbed sites remains an open question. With the temporal resolution and scale afforded by PAM, future efforts might therefore aim to describe the dynamics and extent of natural soundscape variability (Buscaino et al., 2016; Rodriguez et al., 2014), the potential for non-additive effects of multiple simultaneous stressors or complex temporal disturbance regimes on acoustic communities (Birk et al., 2020; Jackson et al., 2021), and the relevant temporal scales over which ecosystems, through soundscapes, are impacted by disturbance, including transient effects (Hastings et al., 2018) and functional versus compositional disturbance and recovery (e.g. Ross et al., 2022).

4 | APPLICATIONS AND FUTURE DIRECTIONS

PAM is rapidly becoming an attractive way to study biodiversity across ecosystems, with motives from understanding individual vocal behaviour to ecosystem health evaluation. Shared use of similar PAM sensors and data is leading to new collaborations and common research goals with potential to break new ground on existing ecological questions or ask novel ones. In this final section, we discuss the application of PAM to several avenues of research on the horizon, and the challenges that must be overcome to achieve such goals.

4.1 | Global conservation efforts

Addressing the global biodiversity crisis requires multi-scale societal action. The latest Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services report related biodiversity loss, climate change and human quality of life, in an interlinked system with co-benefits (Pörtner et al., 2021). Soundscape metrics should be readily incorporated into monitoring and evaluating the Post-2020 Global Biodiversity Framework indicators and other national and international sustainability frameworks. Identifying changes in threatened populations and in species richness is fundamental to conservation, and the combination of passive acoustic surveys and emerging machine learning tools (e.g. Kahl et al., 2021) will enable such work. Research in ecoacoustics is evaluating the possibility of a robust standard acoustic measurement protocol for use in long-term and global conservation initiatives. Species-level data processed

from PAM recordings are ready to apply in such frameworks, but community-level summaries (typically achieved via acoustic indices) still require work. Even without consensus on validation of acoustic indices using classical biodiversity data (Alcocer et al., 2022), assessing differences between ecosystem conditions and biomes in terms of acoustic composition and rhythm seems promising (Gottesman et al., 2020). Still, considerable challenges remain, including standardisation of acoustic measurements, calibration across ecosystems and data sharing practices (Pijanowski & Brown, 2022). Many PAM efforts to date intend for collected recordings to eventually contribute to global efforts to establish ecosystem baselines for future conservation assessment and management. As such, local databases are being readily amassed, and some national acoustic databases have emerged (Ambrose & Burson, 2004; Roe et al., 2021). However, data sharing remains contingent on personal involvement of local researchers. We envision the emergence of a global ecoacoustics platform that could unite existing local studies (see calls for global reference libraries from e.g. Deichmann et al., 2018; Parsons et al., 2022), opening up study of global-scale processes such as climate change (Sueur et al., 2019). In support of Miksis-Olds et al. (2021) who recently called for a global multipurpose ocean acoustic network, we also advocate for more global collaborative networks of PAM studies, with initiatives such as the Silent Cities Project aiming to collect terrestrial soundscape recordings during the COVID-19 pandemic, and including ~300 participants worldwide (Challéat et al., 2020). For global collaborative efforts such as these to be fruitful, particular effort should be made to amplify underrepresented voices, valuing indigenous knowledge and building globally inclusive networks for effective approaches to addressing big ecological challenges (Nuñez et al., 2021; Ramirez et al., 2018).

4.2 | The challenge of calibration

Whether the focus is on a single species, a community or a soundscape, ecological studies require replication of comparable measurements for validity. The PAM literature mostly lacks calibration methodology, especially when establishing networks of PAM recorders assumed to be comparable. Yet, calibration is especially needed as established PAM sensors age or show discrepancy with new low-cost sensors (which may perform worse than higher-end equipment in terms of signal quality or ability to capture quiet or distant signals), and as microphones deteriorate over time at extreme temperatures or if frequently exposed to moisture (Darras et al., 2018). *Acoustic calibration* (Box 1) mostly compares Sound Pressure Levels (SPLs) obtained by a particular sensor setup (microphone and recorder) with a reference SPL value (Llusia et al., 2011; Merchant et al., 2015). Alternatively, calibration can refer to the entire model of acoustic measurement, from microphone and recorder to acoustic data processing. For example, using remotely sensed images to monitor agricultural fields requires 'ground truthing' by collecting reference measurements under different crop covers and meteorological conditions. This is equivalent to considering the impact of environment

context in PAM studies (e.g. habitat structure, non-target sounds) on sound propagation and detection, as well as comparing acoustic data to meaningful biological reference values (Couldridge & van Staaden, 2004; Ross, Friedman, et al., 2021). We envision increasing use of calibration techniques based on in situ recordings prior to data collection.

4.3 | Soundscape ecology

The conceptual framework for soundscape ecology was introduced over a decade ago, defining soundscape ecology as the study of all sound produced in a landscape, including biophony, geophony and anthropophony, which together create unique acoustic patterns across spatial and temporal scales (Pijanowski, Villanueva-Rivera, et al., 2011). With the recent development of low cost and small autonomous recording units (Hill et al., 2018; Sethi et al., 2018), quantification of spatial landscape characteristics on soundscape structure and dynamics is finally within reach. Soundscape ecology now has the means to address classical questions in landscape ecology and biogeography (Fuller et al., 2015; Lomolino et al., 2015), including connectivity, source–sink dynamics, as well as macroecological questions using PAM data from across ecosystems and biomes via global collaborative networks as discussed above. The continued growth of soundscape ecology will likely rely on its ability to map not only hotspots, but also ‘hot times’ of biodiversity (Holgate et al., 2021).

4.4 | Acoustic localisation and machine learning for sound recognition

Deep learning has enabled tremendous progress in the automated assessment of PAM datasets, dominated by use of Convolutional Neural Networks (Stowell, 2022). Already, tools exist that can identify over 3000 species globally, including >95% of the bird species in North America and Europe (Kahl et al., 2021), and between new algorithms and extensions of existing ones, a far greater proportion of all bird species, as well as acoustically active mammals, amphibians and insects are likely to be identifiable. A key challenge of automated sound recognition is the identification of sound signals in complex acoustic environments, where multiple biotic, environmental and human sounds interact. Long duration PAM studies (e.g. many weeks per season) can improve the chance of recording a resident species with sufficient quality (i.e. minimal interference) for identification. Coupling machine learning with multi-channel sound localisation systems is emerging as a potential solution (Dawson & Efford, 2009; Yip et al., 2020). Future research will likely offer the precise three-dimensional location of individual sound sources using *acoustic localisation* (Box 1) to incorporate information on distance and direction of vocalising animals (Rhinehart et al., 2020). Using acoustic sensor arrays to provide spatial information in this way not only allows precise localisation of sounds, but can also be used to improve data quality by removing noise and amplifying signal strength across multiple

time-synchronised recordings of a target sound. Acoustic localisation involves synchronising recordings across sensors, producing high-dimensional data that may be challenging for observers to visualise or process. Such data could be analysed by deep learning algorithms to improve measurement of vocalisation propensity of identified individuals or species, and their interaction in time and space. In turn, this should open new doors for investigating niche partitioning, including the partitioning of acoustic space as described by the *acoustic niche hypothesis* (Krause, 1993; Box 1). Improved automated species classification stemming from availability of reference libraries should further facilitate progress for each of the research areas discussed in Section 3, allowing reanalysis of existing PAM datasets with new methods, furthering ecological discovery even more.

5 | CONCLUSION

Though PAM remains a powerful applied tool for population, community and ecosystem monitoring, ecologists are increasingly recognising its potential to contribute to fundamental ecology. Though not every example presented here may be considered a truly ‘fundamental’ problem, we aimed to highlight a range of examples that directly or indirectly showcased the utility of PAM in advancing fundamental ecology. To make such contributions in the future, PAM studies must build not only on fundamental work, but also on applied studies which often set methodological best practices for acoustic monitoring (e.g. Bradfer-Lawrence et al., 2020). When building on past work in this way, and only when acknowledging and accounting for the practical limitations discussed herein (Figure 1 and Box 2) does PAM have the potential to overcome many such challenges. In doing so, PAM can ultimately contribute fundamental ecological knowledge to a range of long-standing and emerging questions of broad scientific interest.

AUTHOR CONTRIBUTIONS

Samuel R. P.-J. Ross, Darren P. O’Connell and Zuzana Burivalova conceived the ideas and led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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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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