An overview of passive acoustic monitoring (PAM) of terrestrial vertebrates and its significance, applications and challenges in urban and natural environments

Sebastian Carvello

Department of Life Sciences, Imperial College London, UK | 16th May 2025

Abstract

Amidst a global biodiversity crisis and unprecedented levels of species loss, effective environmental monitoring is more important than ever, but traditional methods are often labour intensive and subjective. Passive acoustic monitoring (PAM) is rapidly establishing itself as an important non-invasive, scalable and cost-effective tool for surveying sonant fauna in both natural and urban environments. While key challenges remain, particularly around standardisation, data analysis in complex soundscapes, and logistical difficulties in remote study locations, the future for PAM looks bright, with rapid advancements in the field of AI and novel open-source hardware solutions driving progress.

1 | Introduction

Global biodiversity is under severe pressure, with a 73% decrease in the average size of Living Planet Index-monitored populations between 1970 and 2020 (WWF, 2024) and conservative estimates placing the current extinction rates of certain vertebrate taxa at up to 100 times the average background level (Ceballos et al., 2015). This stands to have grave consequences on ecosystem function, stability and, consequently, services (Cardinale et al., 2012). The accurate monitoring of ongoing biodiversity loss and the degree of success of conservation interventions is therefore of significant importance for planning effective future strategies, and this requires accurate, comprehensive and long-term datasets (Magurran et al., 2010).

Traditional, observer assessment methods (such as point counts or transect surveys) present a number of disadvantages. They suffer from the high financial expense

Correspondence: sebastian.carvello23@imperial.ac.uk

of specialist staff remuneration for the entire duration of the recording period and their transportation to and from study locations (Darras et al., 2019a), with these costs increasing with duration of survey and spatial scale (Hoefer et al., 2023). Reliable observations are crucial to obtaining accurate data and, in study regions with especially high or unique diversity of fauna, this can require intensive training to ensure consistent identification between observers (Ralph, Droege & Sauer, 1995); the availability of these skilled experts for a specific region or set of species may itself become limiting (Wheeldon et al., 2019), even before any considerations of cost prohibitiveness are taken into account. Importantly, all human observers are susceptible to human error – although higher levels of observer skill are associated with a lower error rate (Farmer, Leonard & Horn, 2012) – and inter-observer variability remains a fundamental challenge in human observer-based identification of species, especially of those with lower phenotypic distinctiveness (Zett, Stratford & Weise, 2022), hindering data accuracy and cross-study comparability and data compatibility (which are key for collaborative long-term global monitoring). Finally, the physical presence of observers may confound results, negatively impacting the detection of human-sensitive species (Darras et al., 2018).

Remote sensing methods alleviate many of the challenges posed by human-based observation, often requiring little-to-no specialist time spent in the field, with established technologies ranging from camera trapping (O'Connell, Nichols & Karanth, 2011) to the use of high-resolution satellite imagery (Xue, Wang & Skidmore, 2017). Passive acoustic monitoring (PAM) is one such technology that has emerged as a promising method to remotely survey sonant fauna through the use of automated acoustic recording devices (Blumstein et al., 2011). In addition to its non-invasive and remote nature, requiring far fewer hours in the field (which also minimises disturbance to surveyed populations) (Mennill et al., 2012) and enabling data collection over much greater spatiotemporal scales due to relatively low costs of survey upscaling (Blumstein et al., 2011), PAM facilitates the detection of animals in visually-limited areas and situations, such as in dense forest or at night when surveying nocturnal species (Marques et al., 2013). As well as species identity, animal sounds can also convey information relating to abundance and position, body size and condition, and the motivations of the emitter (Wilkins, Seddon & Safran, 2013), making them a highly informative medium.

PAM has seen fairly widespread application for the monitoring of sonant marine life – particularly cetaceans (Gibb et al., 2019) – favoured due to the efficiency with which acoustic signals propagate through water and the challenging nature of traditional observer-based alternatives underwater (Heinicke et al., 2015). Terrestrial PAM, however, can pose additional challenges due to the often complex soundscapes requiring analysis (Heinicke et al., 2015), and research into the degree of its utility as a reliable alternative to traditional methods for most terrestrial vertebrate taxa is somewhat lacking (Hoefer et al., 2023). Notable exceptions are bats and birds (Sugai et al., 2019), which have historically been the predominant focus of terrestrial vertebrate PAM research (Gibb et al., 2019). Analysis of acoustic data from urban environments can be of particular difficulty since anthropogenic sounds (anthropophony) will likely dominate the soundscape (Matsinos et al., 2008). It is, however, of increasing interest, not least due to a growing appreciation for the important direct and indirect impacts of urban biodiversity on the (increasing proportion of the) human population that live in cities (Zari, 2018), and progressive legislation such as the UK Government's Biodiversity Net Gain (BNG) requirements for new developments (Schedule 14 of the Environment Act 2021, although it should be noted that this only mandates monitoring of biodiversity through habitat proxies, and not direct population surveys). PAM in remote natural locations faces its own complexities, however, with maintenance of recording units, such as replacing batteries and memory cards, posing a much greater inconvenience compared to in easily accessible urban locations (Pijanowski et al., 2011a).

This review seeks to provide a high-level introduction to and overview of PAM, examine its potential value in urban and natural environments, the challenges faced in each setting, and potential future solutions to these in our rapidly advancing technological landscape.

2 | Overview of modern PAM methodology and general challenges

2.1 Hardware

While early PAM studies employed repurposed general-use cassette recorders (Riede, 1993) or even seismological and naval equipment (Sousa-Lima, 2013) to collect raw data, dedicated autonomous recording units – commonly referred to as ARUs (Shonfield & Bayne, 2017) – have been commercially available for some time and comparable to, for example, camera traps in terms of durability and user-friendliness (Gibb et al., 2019). A typical ARU consists of an acoustic transducer (a microphone for terrestrial models and a hydrophone for aquatic) and data storage (such as an SD card), contained within a protective waterproof housing (Merchant et al., 2015). Modern ARUs benefit from increased battery life and storage capacity, programmable schedules and, in some cases, real-time data transmission (Aide et al., 2013) however, commercial hardware costs can be high, limiting study scalability (Gibb et al., 2019) – a single Song Meter SM4 unit from market-leader Wildlife Acoustics retails for 699 USD as of Thursday 8th May, 2025 (Wildlife Acoustics, Inc., 2025). A range of sensors are available for both the audible range (for surveying birds, most mammals and amphibians) and ultrasound (bats), although the comparability of data recorded using different ARU models and protocols is unclear (Browning et al., 2017). Indeed, a lack of standardisation is a key challenge in the field; while PAM is now widely considered to be an invaluable tool for environmental monitoring, debate around study design best practice continues (Ross et al., 2023). With respect to hardware standards and data collection methodology, this is very much still a work in progress, and discussion is ongoing regarding potential methods of microphone calibration (Merchant et al., 2015) and metadata collection and organisation (Roch et al., 2016), among many other issues.

2.2 Sensor deployment

There are multiple sensor deployment strategies seen across PAM surveys. While mobile sensors along a transect can be used (Jones et al., 2013), ARUs are increasingly being deployed as static sensors (Gibb et al., 2019) usually as standalone units, although multi-ARU networks and arrays are possible to allow for more precise localisation of sounds in the environment (Blumstein et al., 2011). The optimal combination of ARU type and survey design is considered to be dependent on the focus taxon, spatiotemporal scale and objectives of a given study (Parijs et al., 2009). As an acoustic signal is transmitted from the emitter through its environment, its sound waves will progressively attenuate until they are no longer able to be detected above background ambient noise. The distance at which a signal will no longer be detectable varies according to a number of factors: frequency and amplitude of the sound, environmental medium (with much more efficient transmission through water than air), the position of the emitter relative to the receiver, and features of the surrounding environment (such as topography, vegetation cover, potentially-masking background noise, temperature and pressure) (Farcas, Thompson & Merchant, 2016; Gibb et al., 2019). As such, if unaccounted for, the resulting unintentional differences in effective sampling area around an ARU may ultimately lead to biased estimates of population and/or biodiversity (Gibb et al., 2019).

2.3 Analysis

Collected audio data, whether retrieved manually via returning to the site and removing the memory card or remotely over-the-air, then enters a processing pipeline. Manual analysis (a specialist listening to the recordings and/or visually interpreting the spectrograms) faces many of the same drawbacks as traditional observer-based surveying methods, such as high expert-level time burden (Wimmer et al., 2013) and the risk of subjectiveness leading to bias (Gibb et al., 2019). Additionally, the long deployment periods enabled by PAM can result in very large datasets that would simply not be practical for manual processing (Bittle & Duncan, 2013).

As such, automated analyses are of great potential value, and a prerequisite for the upscaling of PAM studies (Gibb et al., 2019). Examples include the use of algorithms to categorise clips with similar properties (termed 'clustering', and a form of unsupervised learning) (Pirotta et al., 2015; Gibb et al., 2019), the use of species-specific algorithms (termed 'recognisers' or 'classifiers') to identify calls according to similarity to a training dataset (a form of supervised learning) (Gibb et al., 2019; Eichinski et al., 2022; Hoefer et al., 2023), and the use of acoustic indices, of which there are many (Allen-Ankins et al., 2023). Whole soundscape (all sound at a particular location; the sum of biophony (biological), geophony (geophysical) and anthropophony (human) (Pijanowski et al., 2011b)) approaches often employ the latter of these methods, acoustic indices, which are quantitative representations of spectral, amplitudinal and temporal qualities of a soundscape (Sueur, 2018). Examples include: Acoustic Diversity and Acoustic Evenness Indices (ADI and AEI or Aeve – reflecting frequency variation, using the Shannon diversity and Gini evenness indices respectively) (Villanueva-Rivera et al., 2011); Acoustic Complexity Index (ACI – a direct quantification of animal vocalisations, based on the theory that biophony exhibits greater intrinsic variability of intensities compared to anthropophony) (Pieretti, Farina & Morri, 2011); Bioacoustic Index (BI or Bio – a quantification of acoustic energy in the vocalisation range, equivalent to the area under the amplitude spectrum but above a specific cut-off threshold) (Boelman et al., 2007); and Normalised Difference Soundscape Index (NDSI – a comparison of the relative abundances of anthropophony and biophony) (Kasten et al., 2012).

However, automated analyses are not perfect, and accuracy can suffer particularly when vocalisations overlap or a recording has a low signal-to-noise ratio; a 2019 review found manual analysis to still be, by far, the dominant (58% vs 19% fully automated and 15% semi-automated) method used in PAM studies, despite its significant drawbacks (Sugai et al., 2019). While machine learning models are increasingly being employed in PAM analysis, they require access to a rich, clean and accurately labelled set of training data (Eichinski et al., 2022), which should be as similar as possible to the target audio that will be captured in the field, otherwise a mismatch can arise between the reference training data and the unlabelled experimental data. This phenomenon is known as dataset shift (Dockès, Varoquaux & Poline, 2021), and may occur when dealing with regional variation in calls or significantly different environmental features (such as different vegetation cover, leading to an altered background noise profile) (Eichinski et al., 2022).

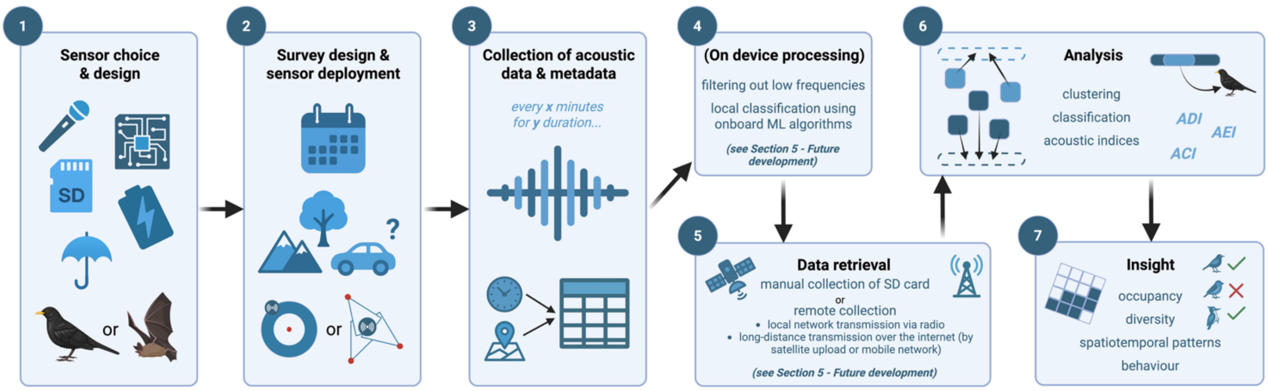

Figure 1. A high-level schematic overview of a typical PAM workflow, including the key considerations at each stage of the process. *Created in BioRender using custom icons.*

3 | PAM in urban environments

55% of the global human population now live in urban areas, a figure that is expected to continue to climb to almost 70% by 2050 (UN Department of Economic and Social Affairs, 2019). Appreciation and evidence for the multiple benefits, direct and indirect, that biodiversity can offer those of us that live in urban areas is growing, including the provision of important ecosystem services such as food supply, air filtration, regulation of pests, and water cycle stability (Elmqvist et al., 2013). Additionally, while urbanisation is rapidly occurring at the expense of natural habitats (Levik et al., 2025), research is increasingly demonstrating that cities are in fact capable of supporting high levels of biodiversity and even endemic species (Aronson et al., 2014).

Green infrastructure (GI) – the (semi-)natural features such parks, roadside trees, gardens, and 'green' walls and roofs (Cvejić et al., 2015) – offer the opportunity to increase local biodiversity (Sadler et al., 2011) and are utilised by many cities to try to improve environmental quality (Fairbrass et al., 2017). However, the suitability of GI to support ecosystems and increase biodiversity is not especially well quantified (Pataki et al., 2011; Fairbrass et al., 2017). In order to efficiently and effectively make future urban planning decisions, strategies should be supported and informed by strong empirical evidence (Fairbrass et al., 2017), requiring greater effort in monitoring and understanding how biodiversity and ecosystems respond to different GI (Kremer et al., 2016). Projects utilising citizen science initiatives, such as NatureWatch and iNaturalist, can harness the high population densities of urban areas to gather biodiversity data on a large scale (Theobald et al., 2015) however, the objectivity and accuracy of data gathered in this way can be questionable (Levik et al., 2025). Urban PAM stands to offer an alternative scalable solution; while this comes with potential challenges such as the risk of theft or vandalism of ARUs (Vidaña-Vila et al., 2020), the key hurdle is technical, being the accurate analysis of data in a challenging background acoustic landscape.

The dominant anthropophony in urban environments can result in acoustically complex soundscapes, and verification studies on the suitability of acoustic indices has historically neglected to include highly disturbed environments such as cities (Fairbrass et al., 2017). A number of anthropogenic sounds have been identified as capable of significantly biasing common acoustic indices, such as traffic noise (Fuller et al., 2015) and human speech (Pieretti, Farina & Morri, 2011). When applying acoustic index analysis to urban acoustic data, consideration should be given to the choice of an appropriate index that is somewhat robust to or considers anthropophony; for example, ACI relies on differences in variability of intensities between biotic and anthropogenic sounds (Pieretti, Farina & Morri, 2011), while NDSI relies on a theoretical split in frequency with the 1-2 kHz band generally representing anthropogenic sound and the 2-8 kHz band biophony (Kasten et al., 2012).

The application of filters to exclude low frequencies is a common preliminary processing step (Sueur et al., 2008; Pieretti et al., 2015) however this, and the general assumption underlying indices such as NDSI that anthrophony is conveniently constrained to a specific low frequency range and biophony to a non-overlapping higher range, are not scientifically sound in an urban context. A 2017 study (Fairbrass et al.) assessing the viability of various acoustic indices at study sites across Greater London found many anthropogenic sounds occupying the same frequencies as biophony (Figure 2) – to remove all anthropogenic-affected frequencies would result in the loss of biophonic data, while filtering at a lower, safer threshold would not sufficiently clean the data. Manual identification and subsequent removal of samples with contaminating sound remains an option (Gasc et al., 2013) however, this results in a decrease in data volume and involves many of the shortcomings (such as subjectivity and labour intensiveness) of human-based methods that automated PAM supposedly overcomes. Fairbrass et al. (2017) ultimately found that all of the common urban-appropriate acoustic indices tested (ACI, ADI, BI and NDSI) were correlated with the presence of anthropogenic sounds (note this is desirable for NDSI), with human speech having the most widespread effect of all anthropophonies considered, independently impacting all four indices. Furthermore, acoustic index bias from geophony, which has also been observed (Towsey et al., 2014), may become more complex to predict due to the high heterogeneity associated with urban environments (Grimm et al., 2008), making the suitability of different indices in urban study settings highly site specific (Fairbrass et al., 2017).

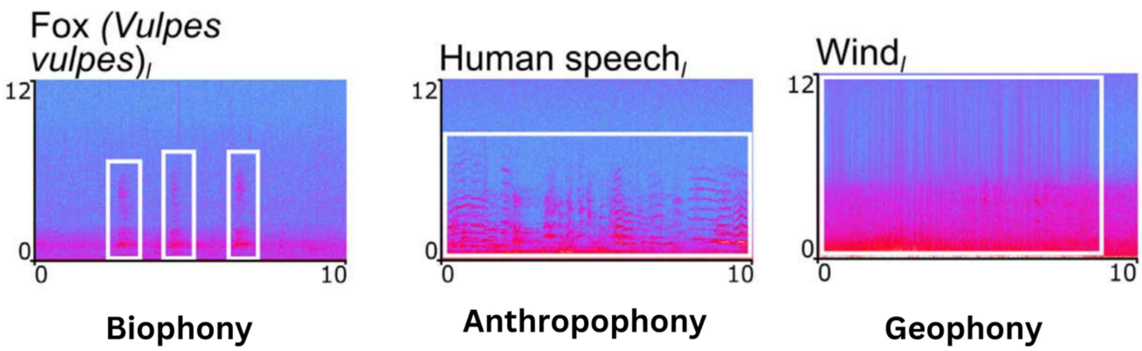

Figure 2. Spectrograms from an urban PAM study in London showing examples of biophony, anthropophony and geophony occupying overlapping frequencies, making filtering challenging. *Adapted from Fairbrass et al., 2017. Frequency (kHz) and time (s) represented on y- and x-axes, respectively.*

Fairbrass et al. (2017) highlights improved machine learning algorithms as a potential future solution to some of these issues however, anthropogenic contaminating sounds are likely to increase the likelihood of dataset shifts (Eichinski et al., 2022), posing challenges for the urban application of machine learning models that have perhaps not been trained on exclusively urban-specific reference datasets.

4 | PAM in natural environments

PAM in non-urban settings is arguably of even greater relevance to the growing biodiversity crisis, with tropical and subtropical forests, especially rainforests, dominating the list of biodiversity hotspots (Myers et al., 2000), representing many of the most irreplaceable and threatened communities in the world. In locations such as these, PAM's non-invasive and scalable nature make it a very promising technology. The lack of significant anthropophony compared to an urban setting may, at first, make the analysis of acoustic data from natural environments seem far more straightforward, yet it cannot be assumed that all natural soundscapes have low background noise levels; rainforests, for example, can prove especially challenging, with a high and dramatically variable background noise level (Waser & Waser, 1977; Kalan et al., 2015). Automated classification methods frequently encounter the issue of insufficient expert-verified training data, especially outside of Europe and North America, with existing terrestrial vertebrate datasets being heavily biased towards bats and birds (Gibb et al., 2019).

Logistical challenges are increasingly problematic the more remote a study location is, and the human mental and physical costs to study staff of travelling through potentially harsh conditions and challenging terrain are important to consider (Wood et al., 2023). It follows, therefore, that the more remote a site (and therefore greater the costs of returning to provide maintenance), the longer the desirable continuous ARU deployment duration. Ultimately, power supply duration and hardware durability will determine the upper limit for this, with the former negatively correlated with sampling frequency, leading to an unfortunate trade-off between device longevity and the probability of actually detecting the target species. Lithium batteries may be of help here, offering a larger capacity, more constant rates of power across its full charge range, increased portability thanks to their lighter weight, and a wider range of operating temperatures compared to alkaline however, they are approximately ten times more expensive (impacting study scalability) and not compatible with all circuit boards (Wood et al., 2023). Regarding hardware durability, mounting the microphone internally will increase the ARU's resilience, but at the expense of some recording performance (Darras et al., 2019b; Wood et al., 2023).

Long-term storage of collected data on-device is of particular importance for remote ARU deployments, due to the impracticality of switching out memory cards and the likely lack of any cellular network to transmit recordings back to a central server periodically or in real-time. This is a greater challenge for full-spectrum ultrasound recording (for example, in bat surveys), which can produce extremely large files due to the higher required sampling rate (Gibb et al., 2019). Some specialised ultrasound ARUs use frequency division to reduce storage requirements however, the resulting loss of some frequency and amplitude data can negatively impact the identification of species and behaviours (Walters et al., 2013). Finally, while modern SD cards typically have some form of memory protection in the event of power loss, simultaneous failure of the memory card controller chip and loss of power may interrupt the writing of files, leading corruption of the filesystem; remote studies are more likely to utilise larger capacity SD cards to maximise deployment duration, and these will result in a larger (and harder to re-collect) dataset being lost (Wood et al., 2023).

5 | Potential solutions and areas of future development

In order to fully harness the potential scalability PAM offers, lower cost ARUs are required; open-source alternatives to commercial sensors (Figure 3) are typically a fraction of the cost, with the AudioMoth, for example, being mass-producible for as little as 30 USD (Gibb et al., 2019). Greater cross-study standardisation is also needed – aided by projects such as Bradfer-Lawrence et al. (2019; 2024) – along with the efficient collation and sharing of data (e.g., Villanueva-Rivera & Pijanowski, 2012) to facilitate the global collaboration required to advance the field to its full potential.

As discussed, in remote locations, ARU maintenance can become especially impractical. Solar panels may offer a way to extend deployment time by negating the need for regular battery replacement (Aide et al., 2013), although this increases ARU cost and fragility significantly (Hill, Rogers & Prince, 2017). Another challenge mentioned in remote study sites was that of possible data corruption from sudden power loss; to protect against this, researchers can program the ARU's schedule to 'gracefully' shutdown before projected battery expiration, along with implementing a feature in the device's firmware to initiate a controlled shutdown in the case of a low-power event (Wood et al., 2023). Where deploying a set of static sensors is too physically challenging, drone audition may prove useful, with recent advances making significant progress in overcoming the main historical limitation of drone ego-noise through structural and software adjustments (Wang, Clayton & Rossberg, 2023).

Figure 3. A commercial ARU, the SM4 from Wildlife Acoustics (left), and two open-source units, the AudioMoth (centre; pictured here in low-cost waterproofing) and the Bugg (right).
Images reproduced from: Wildlife Acoustics, Inc., 2025; Hill, Rogers & Prince, 2017; Sethi et al., 2018.

Storing large volumes of audio data along with its accompanying metadata can, as discussed, prove challenging. While some units may apply local filters or utilise frequency division to reduce storage requirements (Walters et al., 2013), the associated loss of data is scientifically undesirable. One possible solution is real-time transmission of data to a central server. In remote locations, radio transmission via a base station (which itself is connected to the internet) may be necessary (e.g., Aide et al., 2013) however, this comes with the associated costs and complexities of setting up a dedicated local network of transmitters and receivers. Satellite upload may be used (e.g., Cyberforest (Saito et al., 2015)) where no other connections to the internet are readily available, but this can also be expensive. Open-source solutions may again offer a solution here, although one that is likely to be far more useful in urban or semi-natural settings, by taking advantage of pre-existing mobile network infrastructure (Sethi et al., 2018). In locations where bandwidth is scarce, onboard machine learning could be employed to perform some classification in the field, only transmitting back scientifically significant data, although this will be constrained by the computational capacity of the ARU (Zaugg et al., 2023).

The lack of transferability of machine learning models in automated PAM analysis (for example, due to the risk of dataset shift) is a recurrent issue however, novel approaches to integrating ML have shown promise. For example, Sethi et al. (2020)

applied a pre-existing general-purpose model (VGGish from Google) to generate acoustic fingerprints, which accurately predicted biodiversity across various scales and ecosystems. This generalisability shows great promise for achieving the goal of real-time global monitoring using PAM, and the current rapid advancements in AI will likely further fuel this by providing even more powerful pre-trained foundation models. Additionally, simulating different acoustic environments by augmenting training data using background noise has also been attempted, to address the issue of limited reference data (Takahashi et al., 2016).

This is undoubtedly an exciting time for the field, with rapid advancements in AI, the continued development of improved hardware, and novel approaches to analysing an ever-growing dataset likely to be key in accelerating success in PAM and its ability to effectively monitor biodiversity across a range of environments, at a time when it is required more than ever. Future progress will likely depend on fostering improved standardisation, collaboration, and embracing open-source solutions, to help realise its full potential as an accurate, low-cost, versatile and scalable tool in remote sensing.

References

Aide, T.M., Corrada-Bravo, C., Campos-Cerqueira, M., Milan, C., Vega, G. & Alvarez, R. (2013) Real-time bioacoustics monitoring and automated species identification. *PeerJ*. 1, e103. doi:10.7717/peerj.103.

Allen-Ankins, S., McKnight, D.T., Nordberg, E.J., Hoefer, S., Roe, P., Watson, D.M., McDonald, P.G., Fuller, R.A. & Schwarzkopf, L. (2023) Effectiveness of acoustic indices as indicators of vertebrate biodiversity. *Ecological Indicators*. 147, 109937. doi:10.1016/j.ecolind.2023.109937.

Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., et al. (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*. 281 (1780), 20133330. doi:10.1098/rspb.2013.3330.

Bittle, M. & Duncan, A. (2013) A review of current marine mammal detection and classification algorithms for use in automated passive acoustic monitoring. In: *A review of current marine mammal detection and classification algorithms for use in automated passive acoustic monitoring*. 2013 Australian Acoustical Society. pp. 1–8. https://espace.curtin.edu.au/handle/20.500.11937/9323.

Blumstein, D.T., Mennill, D.J., Clemins, P., Girod, L., Yao, K., Patricelli, G., Deppe, J.L., Krakauer, A.H., Clark, C., Cortopassi, K.A., Hanser, S.F., McCowan, B., Ali, A.M. & Kirschel, A.N.G. (2011) Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. *Journal of Applied Ecology*. 48 (3), 758–767. doi:10.1111/j.1365-2664.2011.01993.x.

Boelman, N.T., Asner, G.P., Hart, P.J. & Martin, R.E. (2007) Multi-trophic invasion resistance in Hawaii: bioacoustics, field surveys, and airborne remote sensing. *Ecological Applications*. 17 (8), 2137–2144. doi:10.1890/07-0004.1.

Bradfer-Lawrence, T., Duthie, B., Abrahams, C., Adam, M., Barnett, R.J., et al. (2024) The acoustic index user's guide: a practical manual for defining, generating and understanding current and future acoustic indices. *Methods in Ecology and Evolution*. 2041-210X.14357. doi:10.1111/2041-210X.14357.

Bradfer-Lawrence, T., Gardner, N., Bunnefeld, L., Bunnefeld, N., Willis, S.G. & Dent, D.H. (2019) Guidelines for the use of acoustic indices in environmental research. *Methods in Ecology and Evolution*. 10 (10), 1796–1807. doi:10.1111/2041-210X.13254.

Browning, E., Gibb, R., Glover-Kapfer, P. & Jones, K.E. (2017) *Passive acoustic monitoring in ecology and conservation*. doi:10.13140/RG.2.2.18158.46409.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*. 486 (7401), 59–67. doi:10.1038/nature11148.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015) Accelerated modern human–induced species losses: entering the sixth mass extinction. *Science Advances*. 1 (5), e1400253. doi:10.1126/sciadv.1400253.

Cvejić, R., Eler, K., Pintar, M., Železnikar, Š., Haase, D., Kabisch, N. & Strohbach, M. (2015) A typology of urban green spaces. *Ecosystem Services Provisioning Services and Demands*. 7.

Darras, K., Batáry, P., Furnas, B.J., Grass, I., Mulyani, Y.A. & Tscharntke, T. (2019a) Autonomous sound recording outperforms human observation for sampling birds: a systematic map and user guide. *Ecological Applications*. 29 (6), e01954. doi:10.1002/eap.1954.

Darras, K., Furnas, B., Fitriawan, I., Mulyani, Y. & Tscharntke, T. (2018) Estimating bird detection distances in sound recordings for standardizing detection ranges and distance sampling. *Methods in Ecology and Evolution*. 9 (9), 1928–1938. doi:10.1111/2041-210X.13031.

Darras, K., Kolbrek, B., Knorr, A., Meyer, V. & Zippert, M. (2019b) Assembling cheap, high-performance microphones for recording terrestrial wildlife: the Sonitor system. *F1000Research*. 7, 1984. doi:10.12688/f1000research.17511.2.

Dockès, J., Varoquaux, G. & Poline, J.-B. (2021) Preventing dataset shift from breaking machine-learning biomarkers. *GigaScience*. 10 (9), giab055. doi:10.1093/gigascience/giab055.

Eichinski, P., Alexander, C., Roe, P., Parsons, S. & Fuller, S. (2022) A convolutional neural network bird species recognizer built from little data by iteratively training, detecting, and labeling. *Frontiers in Ecology and Evolution*. 10, 810330. doi:10.3389/fevo.2022.810330.

Elmqvist, T., Fragkias, M., Goodness, J., Güneralp, B., Marcotullio, P.J., McDonald, R.I., Parnell, S., Schewenius, M., Sendstad, M., Seto, K.C. & Wilkinson, C. (2013) *Urbanization, biodiversity and ecosystem services: challenges and opportunities: a global assessment*. Dordrecht, Springer Netherlands. doi:10.1007/978-94-007-7088-1.

Fairbrass, A.J., Rennert, P., Williams, C., Titheridge, H. & Jones, K.E. (2017) Biases of acoustic indices measuring biodiversity in urban areas. *Ecological Indicators*. 83, 169–177. doi:10.1016/j.ecolind.2017.07.064.

Farcas, A., Thompson, P.M. & Merchant, N.D. (2016) Underwater noise modelling for environmental impact assessment. *Environmental Impact Assessment Review*. 57, 114–122. doi:10.1016/j.eiar.2015.11.012.

Farmer, R.G., Leonard, M.L. & Horn, A.G. (2012) Observer effects and avian-call-count survey quality: rare-species biases and overconfidence. *The Auk*. 129 (1), 76–86. doi:10.1525/auk.2012.11129.

Fuller, S., Axel, A.C., Tucker, D. & Gage, S.H. (2015) Connecting soundscape to landscape: which acoustic index best describes landscape configuration? *Ecological Indicators*. 58, 207–215. doi:10.1016/j.ecolind.2015.05.057.

Gasc, A., Sueur, J., Pavoine, S., Pellens, R. & Grandcolas, P. (2013) Biodiversity sampling using a global acoustic approach: contrasting sites with microendemics in New Caledonia. D.L. Roberts (ed.). *PLoS ONE*. 8 (5), e65311. doi:10.1371/journal.pone.0065311.

Gibb, R., Browning, E., Glover-Kapfer, P. & Jones, K.E. (2019) Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods in Ecology and Evolution*. 10 (2), 169–185. doi:10.1111/2041-210X.13101.

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X. & Briggs, J.M. (2008) Global change and the ecology of cities. *Science*. 319 (5864), 756–760. doi:10.1126/science.1150195.

Heinicke, S., Kalan, A.K., Wagner, O.J.J., Mundry, R., Lukashevich, H. & Kühl, H.S. (2015) Assessing the performance of a semi-automated acoustic monitoring system for primates. *Methods in Ecology and Evolution*. 6 (7), 753–763. doi:10.1111/2041-210X.12384.

Hill, A., Rogers, A. & Prince, P. (2017) *AudioMoth*. 1 September 2017. Open Acoustic Devices. https://www.openacousticdevices.info [Accessed: 15 May 2025].

Hoefer, S., McKnight ,Donald T., Allen-Ankins ,Slade, Nordberg ,Eric J. & Schwarzkopf, L. (2023) Passive acoustic monitoring in terrestrial vertebrates: a review. *Bioacoustics*. 32 (5), 506–531. doi:10.1080/09524622.2023.2209052.

Jones, K.E., Russ, J.A., Bashta, A., Bilhari, Z., Catto, C., et al. (2013) Indicator bats program: a system for the global acoustic monitoring of bats. In: B. Collen, N. Pettorelli, J.E.M. Baillie, & S.M. Durant (eds.). *Biodiversity Monitoring and Conservation*. 1st edition. Wiley. pp. 211–247. doi:10.1002/9781118490747.ch10.

Kalan, A.K., Mundry, R., Wagner, O.J.J., Heinicke, S., Boesch, C. & Kühl, H.S. (2015) Towards the automated detection and occupancy estimation of primates using passive acoustic monitoring. *Ecological Indicators*. 54, 217–226. doi:10.1016/j.ecolind.2015.02.023.

Kasten, E.P., Gage, S.H., Fox, J. & Joo, W. (2012) The remote environmental assessment laboratory's acoustic library: an archive for studying soundscape ecology. *Ecological Informatics*. 12, 50–67. doi:10.1016/j.ecoinf.2012.08.001.

Kremer, P., Hamstead, Z., Haase, D., McPhearson, T., Frantzeskaki, N., et al. (2016) Key insights for the future of urban ecosystem services research. *Ecology and Society*. 21 (2). doi:10.5751/ES-08445-210229.

Levik, A., Dobromyslov, I., Goretskaia, M., Matasov, V. & Filyushkina, A. (2025) Ecoacoustic methods application for urban biodiversity monitoring. *Urban Ecosystems*. 28 (2), 4. doi:10.1007/s11252-024-01662-7.

Magurran, A.E., Baillie, S.R., Buckland, S.T., Dick, J.McP., Elston, D.A., Scott, E.M., Smith, R.I., Somerfield, P.J. & Watt, A.D. (2010) Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends in Ecology & Evolution*. 25 (10), 574–582. doi:10.1016/j.tree.2010.06.016.

Marques, T.A., Thomas, L., Martin, S.W., Mellinger, D.K., Ward, J.A., Moretti, D.J., Harris, D. & Tyack, P.L. (2013) Estimating animal population density using passive acoustics. *Biological Reviews*. 88 (2), 287–309. doi:10.1111/brv.12001.

Matsinos, Y.G., Mazaris, A.D., Papadimitriou, K.D., Mniestris, A., Hatzigiannidis, G., Maioglou, D. & Pantis, J.D. (2008) Spatio-temporal variability in human and natural sounds in a rural landscape. *Landscape Ecology*. 23 (8), 945–959. doi:10.1007/s10980-008-9250-7.

Mennill, D.J., Battiston, M., Wilson, D.R., Foote, J.R. & Doucet, S.M. (2012) Field test of an affordable, portable, wireless microphone array for spatial monitoring of animal ecology and behaviour. *Methods in Ecology and Evolution*. 3 (4), 704–712. doi:10.1111/j.2041-210X.2012.00209.x.

Merchant, N.D., Fristrup, K.M., Johnson, M.P., Tyack, P.L., Witt, M.J., Blondel, P. & Parks, S.E. (2015) Measuring acoustic habitats. *Methods in Ecology and Evolution*. 6 (3), 257–265. doi:10.1111/2041-210X.12330.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*. 403 (6772), 853–858. doi:10.1038/35002501.

O'Connell, A.F., Nichols, J.D. & Karanth, K.U. (2011) *Camera traps in animal ecology: methods and analyses*. New York, Springer.

Parijs, S.M.V., Clark, C.W., Sousa-Lima, R.S., Parks, S.E., Rankin, S., Risch, D. & Opzeeland, I.C.V. (2009) Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales. *Marine Ecology Progress Series*. 395, 21–36. doi:10.3354/meps08123.

Pataki, D.E., Carreiro, M.M., Cherrier, J., Grulke, N.E., Jennings, V., Pincetl, S., Pouyat, R.V., Whitlow, T.H. & Zipperer, W.C. (2011) Coupling biogeochemical cycles in urban environments: ecosystem services, green solutions, and misconceptions. *Frontiers in Ecology and the Environment*. 9 (1), 27–36. doi:10.1890/090220.

Pieretti, N., Duarte, M.H.L., Sousa-Lima, R.S., Rodrigues, M., Young, R.J. & Farina, A. (2015) Determining temporal sampling schemes for passive acoustic studies in different tropical ecosystems. *Tropical Conservation Science*. 8 (1), 215–234. doi:10.1177/194008291500800117.

Pieretti, N., Farina, A. & Morri, D. (2011) A new methodology to infer the singing activity of an avian community: the acoustic complexity index (ACI). *Ecological Indicators*. 11 (3), 868–873. doi:10.1016/j.ecolind.2010.11.005.

Pijanowski, B.C., Farina, A., Gage, S.H., Dumyahn, S.L. & Krause, B.L. (2011a) What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology*. 26 (9), 1213–1232. doi:10.1007/s10980-011-9600-8.

Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H. & Pieretti, N. (2011b) Soundscape ecology: the science of sound in the landscape. *BioScience*. 61 (3), 203–216. doi:10.1525/bio.2011.61.3.6.

Pirotta, E., Merchant, N.D., Thompson, P.M., Barton, T.R. & Lusseau, D. (2015) Quantifying the effect of boat disturbance on bottlenose dolphin foraging activity. *Biological Conservation*. 181, 82–89. doi:10.1016/j.biocon.2014.11.003.

Ralph, C.J., Droege, S. & Sauer, J.R. (1995) Managing and monitoring birds using point counts: standards and applications. *In: Ralph, C. John; Sauer, John R.; Droege, Sam, technical editors. 1995. Monitoring bird populations by point counts. Gen. Tech. Rep. PSW-GTR-149. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: p. 161-168*. 149. https://research.fs.usda.gov/treesearch/31755.

Riede, K. (1993) Monitoring biodiversity: analysis of Amazonian rainforest sounds. *Ambio*. 22 (8), 546–548.

Roch, M.A., Batchelor, H., Baumann-Pickering, S., Berchok, C.L., Cholewiak, D., Fujioka, E., Garland, E.C., Herbert, S., Hildebrand, J.A., Oleson, E.M., Van Parijs, S., Risch, D., Širović, A. & Soldevilla, M.S. (2016) Management of acoustic metadata for bioacoustics. *Ecological Informatics*. 31, 122–136. doi:10.1016/j.ecoinf.2015.12.002.

Ross, S.R.P.-J., O'Connell, D.P., Deichmann, J.L., Desjonquères, C., Gasc, A., Phillips, J.N., Sethi, S.S., Wood, C.M. & Burivalova, Z. (2023) Passive acoustic monitoring provides a fresh perspective on fundamental ecological questions. *Functional Ecology*. 37 (4), 959–975. doi:10.1111/1365-2435.14275.

Sadler, J., Bates, A., Donovan, R. & Bodnar, S. (2011) Building for biodiversity: accommodating people and wildlife in cities. In: J.H. Breuste, T. Elmqvist, G. Guntenspergen, P. James, & N.E. McIntyre (eds.). *Urban Ecology*. Oxford University Press. pp. 286–297. doi:10.1093/acprof:oso/9780199563562.003.0034.

Saito, K., Nakamura, K., Ueta, M., Kurosawa, R., Fujiwara, A., Kobayashi, H.H., Nakayama, M., Toko, A. & Nagahama, K. (2015) Utilizing the Cyberforest live sound system with social media to remotely conduct woodland bird censuses in central Japan. *Ambio*. 44 (4), 572–583. doi:10.1007/s13280-015-0708-y.

Sethi, S.S., Ewers, R.M., Jones, N.S., Orme, C.D.L. & Picinali, L. (2018) *Bugg | Intelligent real-time eco acoustic monitoring*. 7 September 2018. Bugg. https://www.bugg.xyz [Accessed: 15 May 2025].

Sethi, S.S., Ewers, R.M., Jones, N.S., Orme, C.D.L. & Picinali, L. (2018) Robust, real-time and autonomous monitoring of ecosystems with an open, low-cost, networked device. *Methods in Ecology and Evolution*. 9 (12), 2383–2387. doi:10.1111/2041-210X.13089.

Sethi, S.S., Jones, N.S., Fulcher, B.D., Picinali, L., Clink, D.J., Klinck, H., Orme, C.D.L., Wrege, P.H. & Ewers, R.M. (2020) Characterizing soundscapes across diverse ecosystems using a universal acoustic feature set. *Proceedings of the National Academy of Sciences*. 117 (29), 17049–17055. doi:10.1073/pnas.2004702117.

Shonfield, J. & Bayne, E.M. (2017) Autonomous recording units in avian ecological research: current use and future applications. *Avian Conservation and Ecology*. 12 (1), art14. doi:10.5751/ACE-00974-120114.

Sousa-Lima, R. (2013) A review and inventory of fixed autonomous recorders for passive acoustic monitoring of marine mammals. *Aquatic Mammals*. 39 (1), 23–53. doi:10.1578/AM.39.1.2013.23.

Sueur, J. (2018) *Sound analysis and synthesis with R*. Use R! Cham, Springer International Publishing. doi:10.1007/978-3-319-77647-7.

Sueur, J., Pavoine, S., Hamerlynck, O. & Duvail, S. (2008) Rapid acoustic survey for biodiversity appraisal. D. Reby (ed.). *PLoS ONE*. 3 (12), e4065. doi:10.1371/journal.pone.0004065.

Sugai, L.S.M., Silva, T.S.F., Ribeiro, J.W., Jr & Llusia, D. (2019) Terrestrial passive acoustic monitoring: review and perspectives. *BioScience*. 69 (1), 15–25. doi:10.1093/biosci/biy147.

Takahashi, N., Gygli, M., Pfister, B. & Gool, L.V. (2016) *Deep convolutional neural networks and data augmentation for acoustic event detection*. doi:10.48550/arXiv.1604.07160.

Theobald, E.J., Ettinger, A.K., Burgess, H.K., DeBey, L.B., Schmidt, N.R., Froehlich, H.E., Wagner, C., HilleRisLambers, J., Tewksbury, J., Harsch, M.A. & Parrish, J.K. (2015) Global change and local solutions: tapping the unrealized potential of citizen science for biodiversity research. *Biological Conservation*. 181, 236–244. doi:10.1016/j.biocon.2014.10.021.

Towsey, M., Wimmer, J., Williamson, I. & Roe, P. (2014) The use of acoustic indices to determine avian species richness in audio-recordings of the environment. *Ecological Informatics*. 21, 110–119. doi:10.1016/j.ecoinf.2013.11.007.

United Nations Department of Economic and Social Affairs (2019) *World urbanization prospects: the 2018 revision*. UN. doi:10.18356/b9e995fe-en.

Vidaña-Vila, E., Navarro, J., Borda-Fortuny, C., Stowell, D. & Alsina-Pagès, R.M. (2020) Low-cost distributed acoustic sensor network for real-time urban sound monitoring. *Electronics*. 9 (12), 2119. doi:10.3390/electronics9122119.

Villanueva-Rivera, L.J. & Pijanowski, B.C. (2012) Pumilio: A web-based management system for ecological recordings. *The Bulletin of the Ecological Society of America*. 93 (1), 71–81. doi:10.1890/0012-9623-93.1.71.

Villanueva-Rivera, L.J., Pijanowski, B.C., Doucette, J. & Pekin, B. (2011) A primer of acoustic analysis for landscape ecologists. *Landscape Ecology*. 26 (9), 1233–1246. doi:10.1007/s10980-011-9636-9.

Walters, C.L., Collen, A., Lucas, T., Mroz, K., Sayer, C.A. & Jones, K.E. (2013) Challenges of using bioacoustics to globally monitor bats. In: R.A. Adams & S.C. Pedersen (eds.). *Bat Evolution, Ecology, and Conservation*. New York, NY, Springer. pp. 479–499. doi:10.1007/978-1-4614-7397-8_23.

Wang, L., Clayton, M. & Rossberg, A.G. (2023) Drone audition for bioacoustic monitoring. *Methods in Ecology and Evolution*. 14 (12), 3068–3082. doi:10.1111/2041-210X.14234.

Waser, P.M. & Waser, M.S. (1977) Experimental studies of primate vocalization: specializations for long-distance propagation. *Zeitschrift für Tierpsychologie*. 43 (3), 239–263. doi:10.1111/j.1439-0310.1977.tb00073.x.

Wheeldon, A., Mossman, H.L., Sullivan, M.J.P., Mathenge, J. & de Kort, S.R. (2019) Comparison of acoustic and traditional point count methods to assess bird diversity and composition in the Aberdare National Park, Kenya. *African Journal of Ecology*. 57 (2), 168–176. doi:10.1111/aje.12596.

Wildlife Acoustics, Inc. (2025) *Song Meter SM4 wildlife audio recorder*. 8 May 2025. Wildlife Acoustics. https://www.wildlifeacoustics.com/products/song-meter-sm4 [Accessed: 8 May 2025].

Wilkins, M.R., Seddon, N. & Safran, R.J. (2013) Evolutionary divergence in acoustic signals: causes and consequences. *Trends in Ecology & Evolution*. 28 (3), 156–166. doi:10.1016/j.tree.2012.10.002.

Wimmer, J., Towsey, M., Roe, P. & Williamson, I. (2013) Sampling environmental acoustic recordings to determine bird species richness. *Ecological Applications*. 23 (6), 1419–1428. doi:10.1890/12-2088.1.

Wood, C.M., Champion, J., Brown, C., Brommelsiek, W., Laredo, I., Rogers, R. & Chaopricha, P. (2023) Challenges and opportunities for bioacoustics in the study of rare species in remote environments. *Conservation Science and Practice*. 5 (6), e12941. doi:10.1111/csp2.12941.

WWF (2024) *Living planet report 2024 – a system in peril*.

Xue, Y., Wang, T. & Skidmore, A.K. (2017) Automatic counting of large mammals from very high resolution panchromatic satellite imagery. *Remote Sensing*. 9 (9), 878. doi:10.3390/rs9090878.

Zari, M.P. (2018) The importance of urban biodiversity – an ecosystem services approach. *Biodiversity International Journal*. 2 (4), 357–360. doi:10.15406/bij.2018.02.00087.

Zaugg, S., van der Schaar, M., Erbs, F., Sanchez, A., Castell, J.V., Ramallo, E. & André, M. (2023) *Towards small and accurate convolutional neural networks for acoustic biodiversity monitoring*. doi:10.48550/ARXIV.2312.03666.

Zett, T., Stratford, K.J. & Weise, F.J. (2022) Inter-observer variance and agreement of wildlife information extracted from camera trap images. *Biodiversity and Conservation*. 31 (12), 3019–3037. doi:10.1007/s10531-022-02472-z.

Imperial College London

Department of Life Sciences, Imperial College Road, London, SW7 2AZ, United Kingdom

Correspondence: sebastian.carvello23@imperial.ac.uk seb@carvello.me | www.sebc.me