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Review

Listening to animal behavior to understand changing ecosystems

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Interpreting sound gives powerful insight into the health of ecosystems. Beyond detecting the presence of wildlife, bioacoustic signals can reveal their behavior. However, behavioral bioacoustic information is underused because identifying the function and context of animals' sounds remains challenging. A growing acoustic toolbox is allowing researchers to begin decoding bioacoustic signals by linking individual and population-level sensing. Yet, studies integrating acoustic tools for behavioral insight across levels of biological organization remain scarce. We aim to catalyze the emerging field of behavioral bioacoustics by synthesizing recent successes and rising analytical, logistical, and ethical challenges. Because behavior typically represents animals' first response to environmental change, we posit that behavioral bioacoustics will provide theoretical and applied insights into animals' adaptations to global change.

Highlights

Behavior represents animals' primary means of responding to environmental variation and adapting to rapid environmental change.

Many animals' presence, let alone behavior, is highly cryptic to human observers, presenting a significant barrier in both theoretical and applied behavioral ecology.

Bioacoustic signals not only reveal animals' presence, but also encode detailed information about the behaviors in which they are engaging.

The study of behavioral bioacoustics has emerged to decipher the context and function of animal sounds and to apply this comprehension to understanding animal behavior across ecological scales and levels of biological organization.

Growing capacity for behavioral bioacoustics represents a profound opportunity to understand animal behavior and steward rapidly changing ecosystems in the Anthropocene.

Bioacoustic signals encode behavior in an era of rapid environmental change

Sound is central to ecosystems and how we perceive them. From Carson (Silent Spring) [1] to Cousteau (The Silent World) [2], foundational works have invoked humans' acoustic perception of animal behavior to inform our understanding of ecosystems and human-induced environmental change. The sounds of survival, reproduction, and communication [3] (hereafter behavioral bioacoustics; see Glossary) are useful to both non-human and human listeners by providing information on the behavior of diverse taxa over a range of spatial scales. For wildlife, behavioral bioacoustic signals provide critical social information [4] which expand the detail, accuracy, and range of how animals sense their environments [5–7], enabling more informed decision making in dynamic ecosystems [8,9]. For human listeners, behavioral bioacoustic signals provide clues into how animals respond to dynamic and changing ecosystems because animals typically first respond to changing conditions by modifying their behavior [10].

However, decoding behavior from sound is challenging because animals' sound-producing behaviors and their context are often cryptic to direct human observation. Most passive acoustic monitoring (PAM) studies rely on detecting the presence of species to generate ecological insight through monitoring individual species and guilds [11], acoustic indices of community composition and biodiversity [12] (although see [13,14] for the limitations of acoustic indices as proxies for biodiversity), and whole-ecosystem soundscapes [15,16]. However, PAM systems can only quantify individuals and species which are producing sound at any given point in time. This bias in detectability based on behavioral state has often been viewed (appropriately, in answering certain ecological questions) as a hindrance to be accounted for in downstream ecological analysis, as in PAM-based density estimates [17–19].

Yet, the behavioral information inherently encoded in bioacoustic signals holds enormous potential in and of itself. Deciphering the behavioral content of bioacoustic signals provides an opportunity to detect and understand behavior at landscape and seascape scales in the Anthropocene.

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but requires ground-truthing observations. A growing body of research is beginning to reveal the unique and meaningful insights to be gained from decoding behavioral bioacoustic signals by linking observations from animal-borne biologging acoustic sensors to landscape and seascape-scale PAM observations (Figure 1). Doing so leverages the power of PAM to enabl quiry across a broad range of spatial scales, at fine temporal resolution, and in the study of otherwise cryptic species and ecological phenomena [20–23]. However, this form of data integra remains uncommon.

Here, we aim to accelerate the emerging field of behavioral bioacoustics by synthesizing recent advances toward gleaning detailed information about diverse animal behaviors from acoustic datasets. We argue that behavioral bioacoustics is poised to enable understanding of wildlife havioral responses to ecosystem variation and rapid change. Realizing this potential requires consideration not only of how to integrate insights across acoustic tools (e.g., biologgers and PAM systems), ecological scales, and levels of biological organization, but also how researchers can enable the widespread, effective, and ethical adoption of behavioral bioacoustics in an era of rapid environmental change.

Beyond presence: decoding behavior from bioacoustic signals

Animals use sound for an array of purposes including, but not limited to, finding food and mat defending territory, coordinating movements, and alerting others to the presence of threats. When human researchers detect these signals and understand their behavioral purpose, they yield information not only on animals' presence (effectively, 'I am here'), but also about anima behavior (effectively, 'I am here, and this is what I am doing'). Studies across diverse ecosyst and taxa have identified behavioral information transmitted via bioacoustic signals, including: (i) movement phase; (ii) predation; (iii) antipredation behavior strategies; (iv) unique individual or group acoustic signatures; (v) collective behavioral processes in animal groups; and (vi) te riality, mating, and fitness displays (Figure 2).

Gleaning such rich behavioral information from bioacoustic signals provides a means of unde standing animals' behavioral responses to ecosystem variation and change, sometimes at ecosystem scale. For example, endangered blue whales (Balaenoptera musculus) in the Nort east Pacific Ocean produce wide-ranging, low-frequency songs that are detectable via PAM over thousands of square kilometers [24]. Deployment of biologging devices on individuals in this population has revealed that individuals' diel patterning of these songs encodes inform tion on their behavioral state (foraging or southward breeding migration [24]). This acoustic si nature enables detection of population-level departure for breeding migration, which tracks interannual variation in foraging habitat phenology [25]. This long-distance acoustic informatic is also likely used by blue whales themselves to better time their collective migration under interannual variation and change in their vast and dynamic foraging habitat [26]. Although blue whales' high-amplitude, low-frequency sounds enable such behavioral insight at ecosystem scale from a single PAM recorder, similar behavioral insights are possible for other taxa via distributed PAM networks [27].

The behavioral content of bioacoustic signals can also enable study of other seasonal behaviors under changing ecosystem phenology. For acoustic signals with known individual-level behavioral context, such monitoring can be conducted via PAM alone. Many taxa (e.g., frogs, fish, ir sects, birds, and mammals) produce seasonal acoustic choruses associated with reproductive activity, in which the mating calls of many individuals overlap and provide an acoustically disc able signal of population-level breeding phenology. By studying mating activity via PAM, researchers have gained ecosystem-scale understanding of whether and how such chorusing

Glossary

Acoustic playback: playing recordings of sounds either to animals or broadcast in ecosystems, typically to infer either the behavioral function of bioacoustic signals, evaluate animals' behavioral responses to sound sources, or to conduct acoustic ecosystem restoration.
Acoustic restoration: active restoration approach in which broadcasting soundscapes or specific animal sounds is used to promote or accelerate recolonization of a degraded ecosystem. Acoustic monitoring can also be used to track the impact of acoustic restoration.
Behavioral bioacoustics: study of bioacoustic signals specifically to understand behavioral processes beyond presence.
Bioacoustic signal: sounds produced by the behavior of organisms.
Biologging: use of archiving instrumentation directly attached to animals to study diverse elements of animals' activities and surroundings. This can include observation of animals' acoustic and other behaviors via sensors including micro/hydrophones, GPS loggers, accelerometers, etc.
Biologging acoustic sensors: passive acoustic recording via recorders directly attached to animals via biologging devices. These tools are typically considered a distinct, animal-borne subset of PAM tools. Here we only refer to passive acoustic biologging instrumentation and not active acoustic instrumentation on biologging platforms.
Ecological scale: scale of ecological processes, ranging from individual organisms to ecological communities and ecosystems.
Eulerian observations: observations of units made from a static frame of reference as these units pass through the fixed region of observation.
Lagrangian observations: observations made by following individual units as they move through space and time.
Levels of biological organization: levels at which biological processes occur and/or are examined, here used in the context of behavioral processes ranging from individual to community or ecosystem.
Passive acoustic monitoring (PAM): passive recording of soundscapes via archival and/or streaming acoustic recorders. PAM stands in contrast to active acoustic tools, in which sound is

populations shift their mating effort under shifting biophysical ecosystem conditions in space and time [28,29].

Analysis of bioacoustic signals has provided additional insight into adaptative behavioral changes in response to more direct anthropogenic ecosystem impacts, such as rapid urbanization. For example, study of túngara frogs (Engystomops pustulosus) has revealed that males adaptively produce more conspicuous bioacoustic mating signals in urbanized habitat [30]. Behavioral bioacoustics can further elucidate wildlife responses to changes in human activity, as in white-crowned sparrows' (Zonotrichia leucophrys) shifts in song characteristics under lower-noise conditions during the coronavirus disease 2019 (COVID-19) pandemic shutdowns [31]. Individually identifying behavioral information from bioacoustic signals can also enable insight into responses to ecosystem change. For example, Indian wolves (Canis lupus pallipes) can be individually identified via unique acoustic properties of their howls. This insight allows for exploration of shifting individual and pack-level space use in increasingly human-dominated landscapes [32].

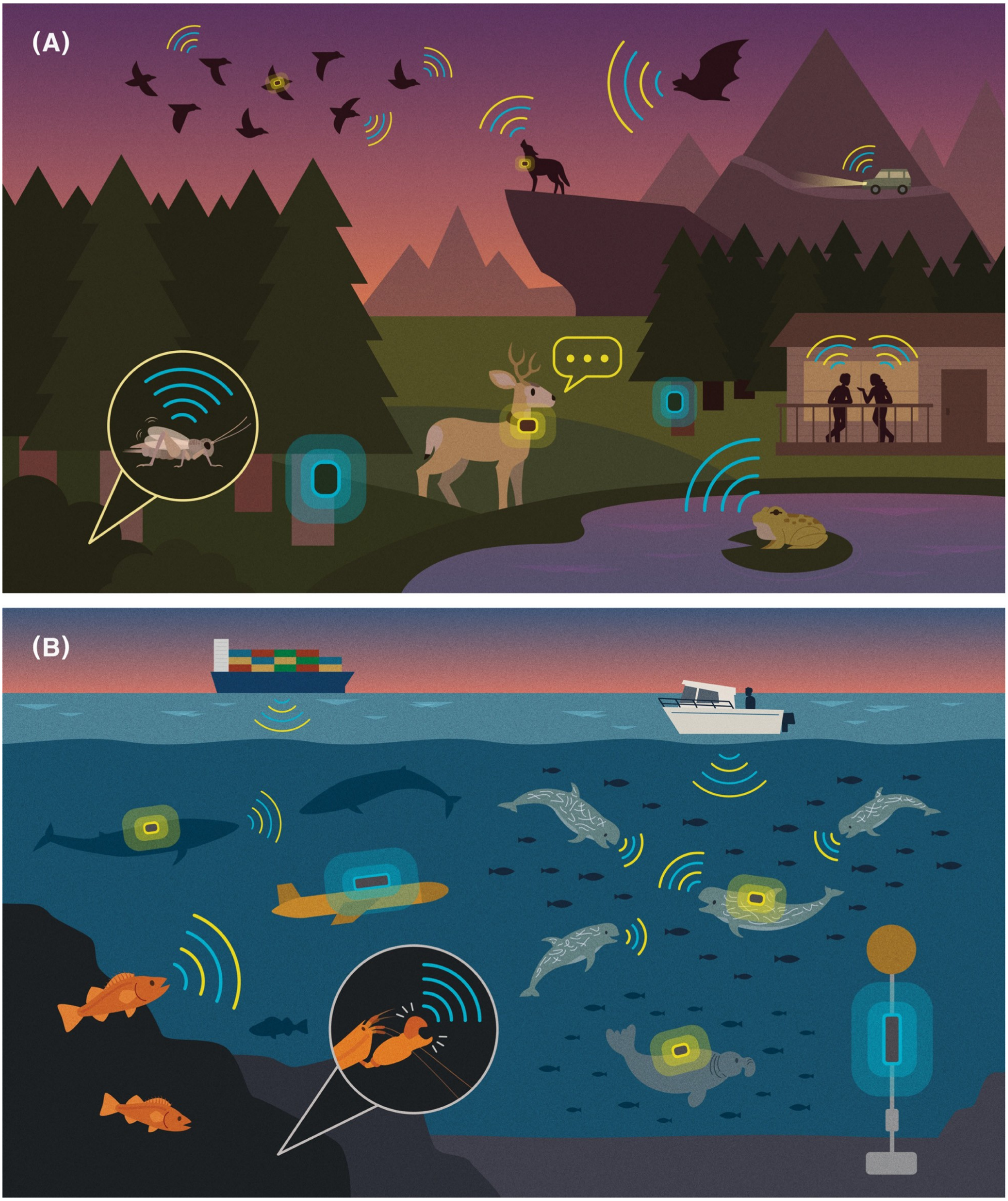
Detailed elements of animals' behaviors detected via bioacoustic signals can be incorporated into future assessments of behavioral response to ecosystem change. The ability to acoustically detect the sounds of life and death, including predation events, antipredation strategies, and mating (Figure 2), makes bioacoustic signals valuable for assessing novel species interactions and fitness under changing ecosystem conditions. For example, biologging acoustic studies have documented the sounds of predation events in both marine and terrestrial ecosystems [33–39]. This enables both individual-level (via biologging acoustics) and population-level (via PAM) assessments of predation rates under interannual ecosystem variation and directional change in ecosystem conditions. Biologging acoustics have also revealed animals' antipredation strategies at the individual level [40], and detection of group and population-level strategies is possible in diverse taxa via PAM (e.g., alarm calls [41–47]). In turn, acoustic monitoring can play a key role in future studies exploring whether specific antipredation strategies are adaptive or maladaptive in the face of novel predator–prey interactions resulting from climate-induced range shifts and species introductions. Transfer of information via acoustic signals can also mediate collective sensing and behavioral processes, including group hunting [48], group vigilance [47], and collective movement decisions [26,49–53]. Collective sensing and behavior can enable animal groups to make better informed decisions in dynamic ecosystems [6,54,55]. Thus, detection and comprehension of such collective behavioral processes via bioacoustic signals can help us understand whether and how animal groups respond adaptively or maladaptively to ecosystem change.

Sensing and understanding behavior across levels of biological organization

Even if we can detect bioacoustic signals persistently over great spatial scales via PAM, how can we discern the behavioral context of these signals? If we can use biologging acoustic sensing to understand the behavioral context of the acoustic signals that animals produce, how can we scale acoustic observation of these behaviors to the population level and ecosystem scale? The answers to these questions lie in the integration of powerful tools and analytical techniques for sensing animal behavior acoustically across levels of biological organization (Figure 3).

Biologging devices equipped with acoustic recorders are increasingly deployed on animals both on land and at sea, providing a detailed view into the lives of individual animals and nearby con- and heterospecifics. By integrating on-animal acoustic, inertial, and/or geolocation data streams, studies on diverse taxa have revealed both the acoustic signatures of key behaviors (e.g., predation events [34]) and the behavioral function of specific acoustic signals (e.g., call patterns associated with collective movement [24]). Such efforts have produced exciting insights about the behavioral content of acoustic signals, but are still in their infancy, with both hardware

both emitted and recorded by acoustic instrumentation.
Soundscape: integrated collection of sounds occurring in a given location at a given time, including human (anthropophony), non-human biological (biophony), and geological (geophony) sounds.



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and software advances holding promise for uncovering a wealth of acoustically transmitted behavioral information across a great diversity of taxa.

For example, novel biologging systems allow researchers to overcome the power limitations of multisensor platforms which include high-sampling-frequency sensors (such as acoustic recorders) [56] and to harness the potential of biologging devices for understanding acoustic communication within animal groups [57]. Analytical advances include methods to discern bioacoustic signals produced by focal and nearby individuals [58–60], which is critical for behavioral interpretation. Further progress in theoretical understanding and analytical methods are enabling researchers to comprehend the significance and information content of complex acoustic sequences produced by wildlife [61]. Developments in machine learning methods for interpreting acoustic signals alongside complex data streams from such multisensor biologging devices, often from multiple individuals simultaneously, provide further promise for understanding the behavioral information encoded in animals' bioacoustic signals [62,63].

Once the behavioral context of a bioacoustic signal is known, the value of detecting said signal at broader ecological scales and higher levels of biological organization is immense for both fundamental and applied science, particularly in the context of behavioral response to ecosystem change. Whereas biologging acoustics typically provides a Lagrangian, individual (or group) level lens on behavior, PAM most often provides a wide-ranging, persistent, population or community-level perspective on behavior from an Eulerian lens (though note that some PAM systems also move their frame of observation in space and time) (Figure 3). While the value of PAM for remote sensing of bioacoustic signals has long been recognized and applied for species monitoring [64], we now have a growing opportunity to integrate behavioral understanding from biologging acoustics with the capacity to observe at ecosystem scales via PAM. As an example, the known acoustic signature of prey capture in sperm whales (Physeter macrocephalus) was discovered via biologging acoustics [34] and has enabled PAM-based study of depredation rates in the Southeast Alaskan demersal longline fishery, helping to mitigate the increased human–wildlife conflict in this ecosystem [65].

Spatially explicit PAM systems [66] that identify the location or bearing of acoustically signaling individuals also provide valuable spatial context for understanding the causes and consequences of population-level behavior, particularly when integrated with Lagrangian tracking of individuals' behavior via biologging acoustics [67]. Such individual-to-population insight via integration of knowledge from biologging acoustics and PAM depends on growing capacity for automated analysis of large PAM datasets across levels of biological organization (Figure 3), from individual-level identification, to species-level detectors, to the use of acoustic indices for analysis at higher levels of biological organization. When deployed in concert, these bioacoustic hardware and software tools provide the capacity for individual-to-ecosystem monitoring of behavior to understand changing ecosystems both on land and at sea (Figure 1).

Challenges and opportunities for realizing behavioral bioacoustics at scale

Understanding wildlife behavior at scale via bioacoustics requires overcoming logistical and analytical challenges, which can be addressed via interconnected immediate, short-term, and longer-term actions (Box 1). Among these challenges is the need for infrastructure to store and

Figure 1. A vision for integrated acoustic monitoring of animal behavior in both (A) terrestrial and (B) marine ecosystems. Yellow rounded rectangles represent biologging acoustic devices and blue rounded rectangles represent passive acoustic monitoring devices. Sounds emanating from various sources are colored according to the primary acoustic devices by which they are detected.

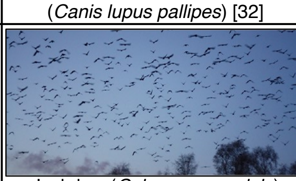
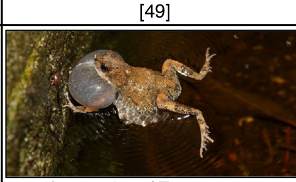
Behavioral category	Example taxon	Bioacoustic tool(s)	Ecological scale	Behavioral information encoded in detected acoustic signal(s)	Additional examples
Movement phase	 Blue whale (*Balaenoptera musculus*) [24]	Bio-logging acoustics, stationary passive acoustics	Individual, population	Foraging vs. migratory behavioral state, enabling inquiring into migratory plasticity under ecosystem variation and change	[11, 27, 111-116]
Predation	 Canada lynx (*Lynx canadensis*) [33]	Bio-logging acoustics	Individual	Successful & unsuccessful prey pursuits	[34-39]
Vigilance, alarm, & anti-predation	 Mule deer (*Odocoileus hemionus*) [40]	Bio-logging acoustics	Individual	Anti-predation vigilance in the absence of sound from individuals wearing bio-logging collars	[41-47]
Unique individual and group identifiers	 Indian wolf (*Canis lupus pallipes*) [32]	Stationary passive acoustics	Individual	Acoustically-distinguishable individual-level identity	[117-127]
Collective behavior & group decision processes	 Jackdaw (*Coloeus monedula*) [49]	Stationary passive acoustics	Group	Coordinated departure from winter roosts	[26,48,50-53]
Territoriality, fitness displays, & mating	 Túngara frog (*Engystomops pustulosus*) [30]	Stationary passive acoustics	Individual, group, population	Male mating signals have adaptive increased conspicuousness under rapid urbanization	[27-29,128-130]

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Figure 2. The diverse and detailed behavioral information encoded in bioacoustic signals. Image credits: Balaenoptera musculus by William Oestreich CC BY 2.0; Lynx canadensis public domain; Odocoileus hemionus public domain; Canis lupus pallipes by Rupal Vaidya CC BY 2.0; Coloeus monedula public domain; Engystomops pustulosus by Brian Gratwicke CC BY 2.0. See [11,24,26–30,32–53,111–130].

access large volumes of heterogeneous data, as well as to support flexible integration with classification algorithms. Ideally, researchers would be able to access an interactive platform underpinned by a library of audio recordings contributed by the community from which acoustic features, species identity, and behavioral state could be extracted. As greater volumes of

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acoustic data are continuously collected, remarkable archives of audio data have emerged (https://www.gbif.org/dataset/b1047888-ae52-4179-9dd5-5448ea342a24) [68–70]. However, these archives remain relatively siloed, despite growing interest from the research community to create more comprehensive platforms for sharing [71–73], which would be critical to identifying behavioral states as well as species occurrences.

Moving beyond archiving, the bioacoustics research community has begun to develop integrated platforms to support species identification (see [70,74,75] as early examples), but has yet to incorporate behavioral classification. As automated approaches for identifying both species and behavioral state rapidly evolve, it will be critical to create flexible platforms which can incorporate new techniques as they emerge. While these (often artificial intelligence; AI) methods are applied to a greater diversity of taxa, sounds, and behaviors, it will also be crucial to correct for systematic errors and biases that arise and which can influence ecological inference. Behaviors extracted from raw audio recordings would constitute a data set in their own right, which could be shared with others for further applications including integration with other data types for generating ecological insight.

While a platform for sharing data, developing methods, and enabling ecological insights is a grand vision, several elements to support the necessary infrastructure are already emerging within the

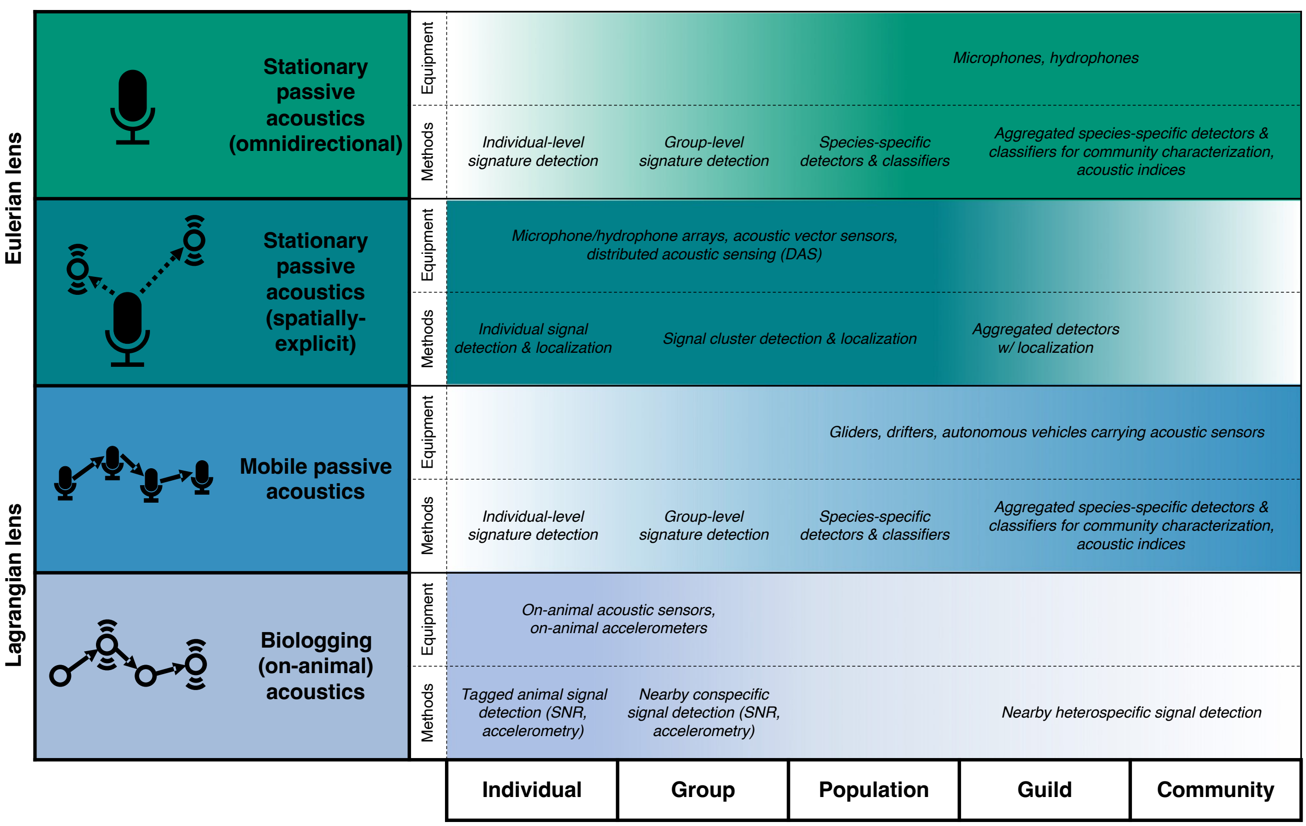

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Figure 3. Sensing acoustic behavior across levels of biological organization. Four major categories of tools for sensing bioacoustic signals provide insight into animal behavior across levels of biological organization (horizontal axis). Darker shading indicates the primary levels at which each tool is applied. Biologging acoustics and mobile passive acoustics provide a Lagrangian lens on behavior, whereas spatially explicit and omnidirectional stationary passive acoustics provide an Eulerian lens. For each category, analytical and signal processing methods and equipment are typically associated with detecting behaviors at specific levels of biological organization. Abbreviation: SNR, signal-to-noise ratio.

bioacoustics world. There is recognition of the need for standardized data models for acoustic data, such as Tethys [76], which could be extended to include behavioral classification. A handful of powerful open-source tools for extracting ecologically meaningful information (https://github.com/lifewatch/pypam) [77–79] or species-level identification [75,80] for a growing list of taxa (thanks to advances in deep learning [79]) have been highly successful in empowering analysis from a wide range of users and could serve as the foundation for identifying and classifying acoustic behaviors.

Valuable logistical lessons could be learned from other ecological sensing communities. Image-based approaches face similar challenges in deploying algorithmic identification of ecologically

Box 1. Operationalizing behavioral bioacoustics at scale: next steps

Realizing the potential of behavioral bioacoustics for advancing behavioral ecology, understanding wildlife responses to ecosystem change, and enacting effective and equitable management requires coordinated efforts in the bioacoustics research community. Here we provide a nonexhaustive list of key next steps—across timescales and both analytical and logistical—that will accelerate the study of behavioral bioacoustics.

Immediate

- Researchers can publicly share new passive acoustic recordings, biologging data, and analysis work flows to enhance methods development, reproducibility, and reuse of datasets for multiple taxa, ecological questions, and management applications. This includes back catalogs of older PAM and biologging datasets.
- Many existing bioacoustic datasets have been analyzed for presence of particular sound sources, but can be reanalyzed for insights about behavior.

Short to medium term

- Although existing repositories [70] already support automated detection of species alongside data storage and sharing capabilities, such platforms could also provide capacity to include and/or detect behavioral context.
- The bioacoustics community can learn from and collaborate with other disciplines (e.g., other ecological disciplines, genomics, and geosciences) to avoid common logistical pitfalls and accelerate organization.
- The bioacoustics community can learn from and collaborate with other disciplines (e.g., AI and linguistics) to accelerate discovery of the behavioral context and function of bioacoustic signals.
- Researchers can build software packages to not only synchronize data streams from biologging devices deployed simultaneously on multiple individuals, but also to synchronize with other behavioral bioacoustic tools (e.g., PAM) and other key sensors providing conspecific, heterospecific, or ecosystem context.
- The bioacoustics community can provide training opportunities to promote equity and efficacy in opportunities to make behavioral bioacoustics discoveries. This could mirror training opportunities provided in adjacent disciplines (e.g., Animove, Bioacoustic Summer School, Computer Vision for Ecology Workshop).
- More broadly, researchers working in this space can foster greater collaboration across the core disciplines intersecting within behavioral bioacoustics: behavioral ecology, acoustics, biologging, movement ecology, AI, data science, and resource management.

Long term

In the long term, the actions described earlier can contribute to moving the study of behavioral bioacoustics toward a platform that allows for:

- multiple linked and synchronized bioacoustic data streams
- automated species detection
- automated behavioral detection
- methods development for animal sounds with unknown behavioral context
- removal of human sounds
- public sharing or private collaboration with community partners

And which is interoperable with other ecological and environmental data sharing, analysis, and integration platforms and tools; for example:

- Animal movement data [100]
- Ecosystem remote sensing data [83]
- Camera trapping data [81]

relevant information from complex data streams. Wildlife Insights supports camera trap studies by providing AI-generated species identification, built-in statistical analyses, and encouraging data sharing [81]. The development of this platform is particularly relevant for the bioacoustics community given that many bioacoustic analysis techniques also image-based, making use of visual representations of sound [75]. Arbimon [70] represents a similar platform for the bioacoustics community, and could continue advancing behavioral bioacoustics research by enabling integration of PAM and biologging acoustics, as well as linking to other critical data streams for behavioral context (Box 1). Similarly, there are likely lessons to be learned from how the Geosciences have coped with the rapid explosion of remote sensing data, including the development of searchable metadata for data discovery [82] and open-source software ecosystems to support analysis [83]. Like the technical challenges discussed earlier, many of the ethical considerations of operationalizing bioacoustics at scale parallel other remote sensing technologies (Box 2).

Behavioral bioacoustics for ecosystem stewardship

Integrating animal behavior into the conservation decision-making process has proven benefits [84]; including this type of information provides a deeper understanding of biotic interactions and potentially more robust predictors of risk in a changing world [85]. For example, acoustic monitoring after translocation via both biologging acoustics [86] and PAM [87] can assist in assessing behavioral adaptation and the success of this conservation action. Using real-time or near real-time acoustic detection of behavior to adaptively manage a habitat, species of concern, or protected area remains a developing field [88], and applications are needed to support emerging resource management needs such as climate-smart fisheries [89] and sustainable offshore wind development [64]. With the rapid growth in big data solutions for data management, processing, and sharing, behavioral bioacoustics may emerge as a key tool for informing resource management decisions and dynamic management approaches. Behavioral bioacoustics via

Box 2. Engaging with ethical challenges and opportunities

Behavioral bioacoustics is poised to advance our understanding of animals' behavioral responses to changing ecosystems, yet there are a number of ethical considerations when implementing these monitoring technologies at scale. These considerations parallel other ecosystem monitoring technologies. For example, the analysis of environmental DNA samples has raised concerns about misuse of human genetic information captured in these samples [101]. Similar concerns arise in capturing images of people on camera traps [102]. When detecting non-human activity and behavior through acoustic monitoring we also, intentionally or inadvertently, detect human activities. This raises privacy concerns in the use (or misuse) of bioacoustic data, which can be ameliorated at least in part via automated detection and anonymization of human voices [103]. In some cases, detecting human activity may help to understand the behavioral changes of species in response to anthropogenic pressures. For example, PAM has been used to understand both shifts in human behavior [31,104] and the behavioral responses of wildlife to such shifts [31,105]. However, detecting human activities also has implications for policing natural resources and their use. For example, acoustic monitoring is used to detect illegal deforestation [106], fishing [107], and poaching [108].

Data infrastructures themselves also raise ethical challenges. The computational infrastructures needed to store and process bioacoustic data are reliant on mineral mining and fossil fuel industries with large environmental impacts. Further, large computational demands and data storage needs risk consolidating data ownership and processing capacity exclusively within technology corporations with sufficient resources.

Many of these challenges are also being confronted by other societal domains (e.g., policing, healthcare, and finance). Removing individually identifying data [103], ensuring community consent for the use of these technologies, and engaging with communities to define the scope of data use [109] and codes of conduct [102] will be critical in order to realize behavioral bioacoustics' potential in an ethical manner.

Beyond anthropocentric considerations, we must also confront wildlife-centric ethical quandaries in conducting and applying behavioral bioacoustics research. Biologging devices can negatively impact the individuals bearing these sensors [110]. In using biologging devices, we must carefully consider necessary sample sizes and whether less-invasive methods of discerning the behavioral context of acoustic signals are feasible. As the insights gained from behavioral bioacoustic studies are applied to ecosystem management, it will also be crucial to consider when, where, and how it is ethical to manipulate animals' behaviors via acoustic playbacks [98].

PAM represents a particularly appealing means of monitoring ecosystems due to its relatively noninvasive nature.

Behavioral bioacoustics can also be applied in the acoustic restoration of ecosystems. As eco systems face rapid change and multifaceted threats, more active approaches to managemen and restoration such as acoustic playbacks are emerging [90,91]. Acoustic playbacks of conspecifics or heterospecifics can be used to attract animals [92–94], and represent a growing t for managing animals' distribution and behavior [95,96]. Returning the behavioral function of sound back into degraded habitats (e.g., playbacks of biological sounds) can help kickstart restoration of ecosystems [90]. In practicing acoustic restoration, we must also carefully assess p tential restoration sites to mitigate threats (e.g., climate impacts, invasive species) and improv success [97], address ethical considerations [98] (Box 2), and promote just, community-led res toration programs [99].

Concluding remarks and future directions

We live in an exciting time for the study of behavioral bioacoustics. Researchers are beginning to decode the rich behavioral content of bioacoustic signals by integrating acoustic sensing tech ogies. Growing computational infrastructure is enabling monitoring of behavior via bioacoustic scale, which can support active stewardship of ecosystems. Still, significant theoretical, analy cal, logistical, and ethical challenges remain (see Outstanding questions). These recent adva are concurrent with widespread human-induced rapid environmental change, underscoring the urgency of answering these outstanding questions. By listening to animal behavior, we now have the capacity to understand the behavioral context and function of animal sounds. This understanding creates an opportunity for landscape-scale understanding of animals' behavioral sponses in rapidly changing ecosystems and enhances our capacity to implement solutions f ecological restoration.

Outstanding questions

To what extent do bioacoustic signals reveal adaptive or maladaptive behavioral responses to ecosystem change?

How do animals use the behavioral content of bioacoustic signals from both conspecifics and heterospecifics to make choices in the face of ecosystem variation and change?

How can advances in AI (e.g., large language models, natural language processing, transformers, etc.) be applied to discern behavioral information from biologging and PAM data?

Can we integrate behavioral bioacoustics and ecoacoustics to discern ecosystem-level acoustic behavior-scapes and their variation through time? As discussed in this article, behavioral bioacoustics enable tracking of populations' behaviors across landscapes and seascapes; similarly, tracking community-level shifts in behavior at ecosystem scale may be possible.

What does ethical acoustic monitoring and data sharing look like when human behavior is detected or detectable?

Can behavioral understanding of bioacoustic signals be used to facilitate behavioral adaptation to ecosystem change (e.g., re-introductions, relearning of lost migrations, etc.)?

How can bioacoustic signals and their behavioral connections be shared with and collectively experienced by human communities to advance community-led solutions for biodiversity conservation?

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Declaration of interests

No interests are declared.

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