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Source: The Auk, 134(1) : 215-228

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-16-124.1

The Auk
Ornithological Advances
AmericanOrnithology.org

Volume 134, 2017, pp. 215–228
DOI: 10.1642/AUK-16-124.1

PERSPECTIVES

Future directions for soundscape ecology: The importance of ornithological contributions

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Submitted June 17, 2016; Accepted September 26, 2016; Published December 14, 2016

ABSTRACT

Building upon the rich legacies of bioacoustics and animal communication, soundscape ecology represents a new perspective through which ecologists can use the acoustic properties of ecosystems to understand the complex interactions of organisms, geophysical dynamics, and human activities. In this paper, we focus on the potential benefits of a soundscape approach for enhancing ornithological research and of ornithological perspectives for advancing the nascent field of soundscape ecology. We first summarize 4 major grounding principles of soundscape ecology in relation to avian ecology, evolution, and behavior. We then propose 3 research objectives that we envision as future directions for soundscape ecology: development of (1) soundscape metrics and interpretation, (2) understanding of soundscape drivers, and (3) soundscape-based disturbance indicators. Ornithological contributions can help advance the field of soundscape ecology to obtain these research objectives across various spatial, temporal, and organizational scales. Detailed ornithological knowledge can aid in the improvement of soundscape databases, interpretation of soundscape metrics, and validation of soundscape theories. Such contributions should also invite input from other taxonomic-group specialists, further enriching soundscape ecology. Reciprocally, soundscape approaches can enrich ornithology by offering an acoustic-based theoretical framework grounded in a broad ecological context, hosting soundscape collections from diverse ecosystems, and advancing acoustic methodologies. This paper is intended to stimulate further discussion and collaboration between ornithologists, soundscape ecologists, and any researchers studying sound in an ecological context in order to enhance research in these important domains of ecology.

Keywords: bioacoustics, interdisciplinary, ornithology, research perspectives, soundscape ecology

Futures directions pour l'écologie des environnements sonores: l'importance des contributions ornithologiques

RÉSUMÉ

Héritée en grande partie des travaux de recherche en bioacoustique et communication animale, la discipline appelée *soundscape ecology*, ou ⟨⟨ étude écologique des environnements sonores ⟩⟩, représente une nouvelle perspective de recherche pour les écologues. Cette discipline scientifique se base sur l'analyse des propriétés acoustiques émanant d'un écosystème dans le but d'étudier les relations entre organismes, événements géophysiques et activités anthropiques. Dans cet article, nous discuterons des implications d'une telle approche acoustique pour l'avancement de la recherche ornithologique, ainsi que sa réciproque, à savoir les perspectives ornithologiques à faire avancer le domaine naissant de l'écologie des environnements sonores. Dans un premier temps, nous résumerons les principes fondamentaux de cette discipline et ces liens avec les connaissances ornithologiques en écologie, phylogénie et éthologie. Ensuite, nous déclinerons ce que nous considérons comme trois objectifs de recherche importants pour l'avenir de l'écologie des environnements sonores : développer les méthodes et l'interprétation de mesures des environnements sonores, développer la compréhension des processus qui modèlent les environnements sonores et développer des indicateurs des perturbations basés sur l'analyse des environnements sonores. Nous discuterons de l'importance des contributions ornithologiques dans l'atteinte de ces objectifs sur plusieurs échelles temporelles, spatiales et écologiques. L'intégration des larges connaissances ornithologiques devrait permettre l'amélioration des bases de données et l'interprétation des mesures, et permettre la validation des théories sur lesquels repose l'étude des environnements sonores. Une telle contribution devrait également appeler à la collaboration avec des spécialistes d'autres groupes taxonomiques. Réciproquement, l'étude des environnements sonores offre aux études ornithologiques la perspective d'intégrer un contexte écologique large, l'accès à des collections d'environnement sonores émanant de différents écosystèmes et une recherche impliquée dans le développement de nouvelles méthodes d'analyses acoustiques. Cet article encourage la discussion et la collaboration entre chercheurs en ornithologie, écologie des environnements sonores, et plus généralement ceux dont les études sont à l'intersection entre son et écologie.

Mots-clés: bioacoustique, écologie des environnements sonores, interdisciplinarité, ornithologie, perspectives de recherche, soundscape

Over the past half-century, a variety of disciplines—including psychology, the arts, engineering, and ecology—have proposed varying usages and applications of the term *soundscape* (Pijanowski et al. 2011a). In all these disciplines, soundscape has typically referred to the totality of the sounds occurring at any location within a certain time frame, including those that are biological, geophysical, and anthropic. While the concept of the soundscape was grounded in the early works of Southworth (1969), an environmental psychologist, and Schafer (1994), a musician, it has recently been championed as a means of ecological analysis (Dumyahn and Pijanowski 2011, Pijanowski et al. 2011a, 2011b, Farina 2014, Smith and Pijanowski 2014, Lomolino et al. 2015). Indeed, acoustic communication is crucial for many organisms to reproduce, feed, defend territories, and avoid predators (Kroodsma 1982, 2005, Templeton and Greene 2007). In 2011, Pijanowski and colleagues formalized "soundscape ecology" as a discipline that seeks to understand the interaction between living organisms and their environments by relating soundscape composition, patterns, and variability to processes that occur within and across biological, geophysical, and human systems (Pijanowski et al. 2011a, 2011b). Recently, "ecoacoustics" has been suggested as a discipline that considers soundscape ecology alongside other research interests that incorporate sound and ecology (Sueur and Farina 2015).

The foundations of soundscape ecology are derived from a large body of research in disciplines including bioacoustics, landscape ecology, community ecology, and engineering. The principal ecological questions in soundscape ecology are related to the interactions of the biological, geophysical, and anthropic components that shape soundscapes and the temporal and spatial variation of those soundscapes in a landscape context (Pijanowski et al. 2011a, 2011b; "landscape" *sensu* Wu (2012): "spatially heterogeneous geographic areas characterized by diverse interacting patches or ecosystems. [...] Landscape is an ecological criterion whose essence is not its absolute spatial scale but rather its heterogeneity relevant to a particular research question"). Through such analyses, soundscape ecology also seeks to explain the ecological and evolutionary processes related to soundscape patterns (Mazaris et al. 2009). Soundscape ecology is sometimes focused on variation in biophony (i.e. the spectral, temporal, and spatial structure of biological sounds) in relation to large-scale environmental changes such as habitat alteration, climate change, introduction of toxins, and spread of invasive species (Qi et al. 2008, Sueur et al. 2008b, Joo et al. 2011, Pijanowski et al. 2011b, Kuehne et al. 2013, Tucker et al. 2014, Krause and Farina 2016).

The large scope of these questions and the data-heavy nature of digital acoustic recording mean that soundscape ecology is dependent on large collections of recordings with associated "big data" challenges of collection, management, and analysis. However, research in soundscape ecology is currently booming (Table 1), and this increase is a testament to technical improvements in acoustic recorders and soundscape analysis tools that have been developed over the past 10 yr (Servick 2014). Programmable recorders now allow for simultaneous, long-term, multisite recording (Acevedo and Villanueva-Rivera 2006, Brandes 2008), and data management systems like Pumilio (Villanueva-Rivera and Pijanowski 2012), the Remote Environmental Assessment Laboratory (REAL) digital library (Kasten et al. 2012), ARBIMON (Aide et al. 2013), and Ecosounds Acoustic Workbench (Truskinger et al. 2014) have facilitated data organization. In addition, necessary research on soundscape dataset visualization has recently advanced (Towsey et al. 2014b). While advances in tools to analyze soundscape recordings are still being made, a set of indices to measure the overall acoustic diversity of a soundscape has been proposed

TABLE 1. Numbers of published and cited papers from the past 20 yr (1995–2015) containing the terms *ornithology*, *soundscape*, *ecology*, and *birds*. Percentages of these papers published and cited within the past 10 yr and 5 yr show the recent increase of interest in the field of soundscape ecology. Source: Web of Science (http://apps.webofknowledge.com, accessed May 31, 2016).

	Number of papers since 1995		Percentage in past 10 yr		Percentage in past 5 yr	
Terms	Published	Cited	Published	Cited	Published	Cited
Ornithology	2,939	5,118	51	61	35	19
Soundscape	1,199	1,086	89	90	70	46
Soundscape and ecology	178	1,086	98	98	85	63
Soundscape and birds	68	748	93	99	85	67

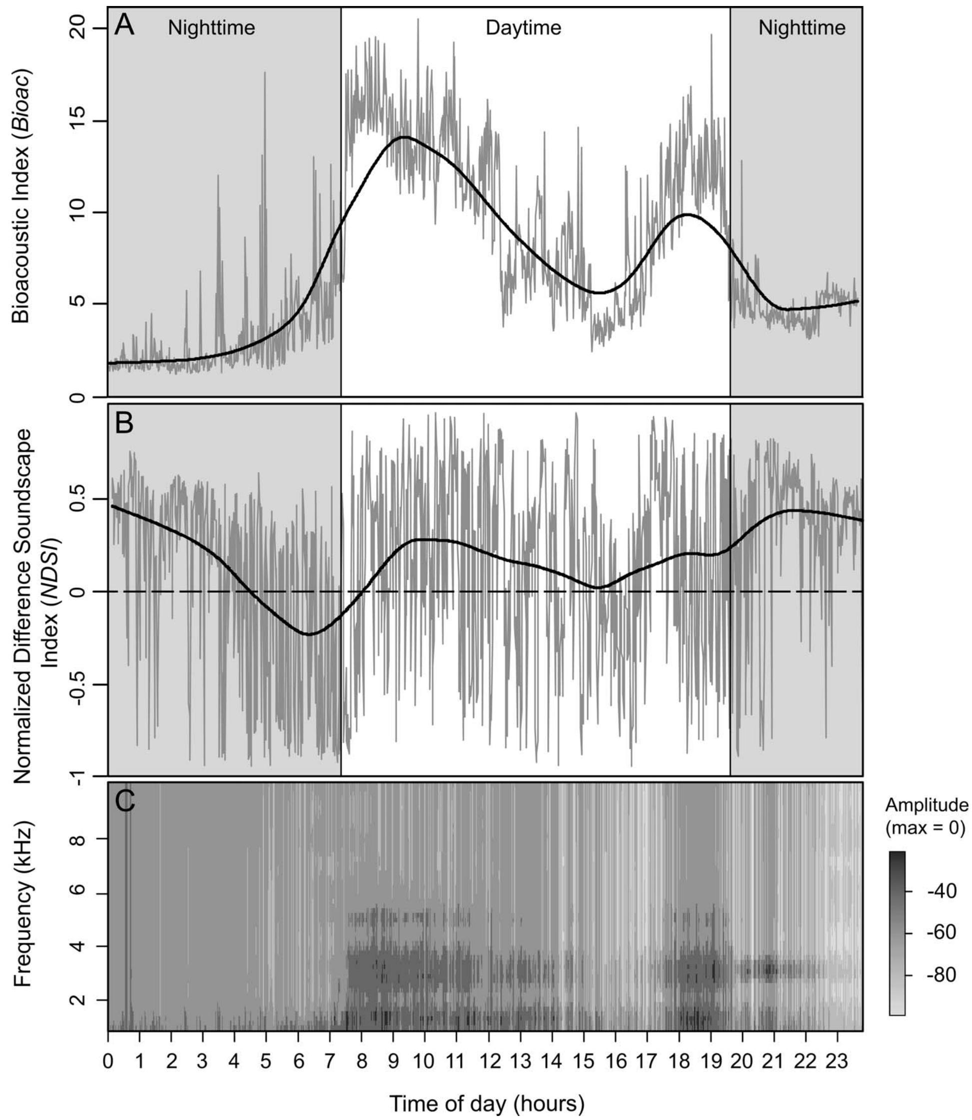

FIGURE 1. Soundscape variation on March 21, 2014, at the Purdue Wildlife Area (coordinates: 40.4517, –87.0524), a forested site at the edge of a pond in Indiana, USA. A Wildlife Acoustics Song Meter SM2+ (sampling rate = 44,100 Hz, bit depth = 16, gain = +36 dB, omnidirectional microphones) recorded continuously throughout the day. High-pass and low-pass filters were applied to the recordings at 1 kHz and 10 kHz, respectively. (**A**) Bioacoustic Index (Bioac; Boelman et al. 2007) values were calculated for each minute using the function "bioacoustic_index" in the R package "soundecology" (Villanueva-Rivera and Pijanowski 2015). A LOWESS curve (bold) was fitted to the points using the function "lowess" in the package "stats" ($f = 0.2$). This index represents the area under the frequency spectrum and above the minimum amplitude of the spectrum. In our example, it responds to the 2 peaks of biophony due to vocal activity of geese and songbirds. (**B**) Normalized Difference Soundscape Index (NDSI; Kasten et al. 2012) values were calculated with the function "ndsi" in "soundecology" (frequency threshold = 2 kHz). A LOWESS curve (bold) was fitted to the points using the function "lowess" in the package "stats" ($f = 0.2$). This index represents the ratio of the acoustic activity occurring between 2 and 10 kHz to the activity between 1 and 2 kHz. The index is normalized between –1 and 1, with positive values indicating high high-frequency:low-frequency ratios and vice versa. (**C**) A 24 hr spectrogram of the same recordings made by (1) using the function "spectro" in the package "seewave" (overlap = 50%, fft windows = 256; Sueur et al. 2008a), (2) averaging the frequency and amplitude content for each minute, and (3) creating an image using the function "image" in the package "graphics." Darker shading indicates higher relative amplitude. Index values and graphics were generated using R 3.1.0 (R Development Core Team 2016).

(Sueur et al. 2014) and integrated in software such as the R packages "seewave" (Sueur et al. 2008a) and "soundecology" (Villanueva-Rivera and Pijanowski 2015). These metrics are highly attractive because they can easily be applied to large collections of recordings without aural evaluation of individual recordings (for an example of soundscape metrics applied to a large number of recordings, see Figure 1).

While these tools are technically helpful, to enhance the theoretical understanding of the drivers of soundscape composition and dynamics, soundscape recordings need to be associated with detailed descriptions of the content and context of these recordings in terms of sound sources (e.g., the sound-producing species) and local context (e.g., land use/cover history, landscape structure, biodiversity, and weather). Soundscape studies addressing "acoustic animal communities" (*sensu* Gasc et al. 2013b, Lellouch et al. 2014, and Farina and James 2016) could exhibit improved interpretive strength through detailed descriptions of sound sources and more thorough consideration of these sources' behavioral, ecological, and evolutionary characteristics. Given that birds dominate soundscapes in a variety of ecosystems, and that ornithological knowledge is notably advanced in bioacoustics, ecology, and evolution, the ornithological community can make significant contributions to the nascent field of soundscape ecology. In turn, soundscape ecology can also promote advances in ornithology and avian conservation. In terms of avian bioacoustics, soundscape ecology offers a wealth of raw natural recordings that can place avian vocalizations in the context of additional acoustic information and nonacoustic metadata. For ecological and behavioral studies, soundscape recordings can be used to examine the phenology of avian activity patterns as well as conspecific and heterospecific acoustic interactions. The geographic diversity of soundscape recordings also offers the potential to conduct large-scale, high-resolution studies of avian ranges and/or habitat preferences. Thus, the value of all these contributions will be greatly enhanced through close collaboration between soundscape ecologists and ornithologists, which will also extend the knowledge boundaries of both disciplines.

Here, we describe how soundscape ecology could benefit from broad participation by the ornithological community and how the ornithological community could benefit from perspectives being advanced by soundscape ecology. We first summarize 4 of the major grounding principles of soundscape ecology as they relate to avian ecology, evolution, and behavior. Then, looking toward the future of soundscape ecology, we propose 3 integrative research objectives that would mutually benefit ornithology and soundscape ecology, while simultaneously promoting biological conservation.

Principles of Soundscape Ecology Related to Avian Ecology, Evolution, and Ethology

Thanks to a remarkable body of work conducted by the ornithological community, Aves is one of the best-known taxonomic groups. More specifically, scholarship on avian acoustics has been impressively prolific, having generated 23,595 papers including the terms *acoustic* and *bird* since 1864 (source: Web of Science, http://apps.webofknowledge.com, accessed May 31, 2016). This body of knowledge has revealed that bird vocalizations contain a wealth of information that researchers can use to advance knowledge about avian ecology (population delineation and density, community diversity, and interactions between species and their environments), evolution (species description, relationships between taxa, and cultural evolution), and ethology (learning processes, mate selection, foraging, flocking, and moving). Because birds are present in most ecosystems, avian acoustic activity often represents an important part of spatiotemporal soundscape variation. In fact, numerous specific case studies in avian ecology, evolution, and ethology have supported principles on which soundscape ecology is largely grounded, as detailed in the following paragraphs.

Principle 1: Sounds interact in a landscape. Sounds composing a soundscape can be characterized in different ways. They can be described by their qualitative acoustic characteristics, such as "pure note" or "whistle"; by their quantitative acoustic characteristics, such as frequency or amplitude; or by their function, such as "distress calls" or "territorial-defense calls." A sound can also be classified by its source (e.g., car, rain, or bird; Schafer 1994). According to this last sound classification, several scientists have proposed grouping sounds into 3 main categories by their biological, geophysical, or human/machine origins. These sounds have been respectively dubbed *biophony*, *geophony*, and *anthrophony* (or synonymously *anthropophony*), with *technophony* existing as a subcategory of anthrophony for "human-made sounds generated from machines and technology" (Krause 1987, Pijanowski et al. 2011a, Mullet et al. 2016).

Biophony can change over time, as community composition can change, and some living organisms that produce sound have the capability to adapt their sounds in response to environmental conditions, including other sounds in the landscape. These sonic interactions can affect the production and/or reception of a biological signal or cue, leading to a change in fitness for the individuals trying to communicate. Soundscape ecology considers interactions between these 3 sound sources, and some of these interactions (i.e. biophony–anthrophony, biophony–biophony, and biophony–geophony) are relevant to ornithology. Geophony–anthrophony interactions are of substantial interest as well (Levin and Edgerton 1999), but to our knowledge they have not been examined in an ornithological context.

Some ornithologists considering biophony–anthrophony interactions have conducted interesting studies, mostly examining impacts of anthropogenic noise. For example, several studies have demonstrated that birds can modify the frequency and amplitude of their signals, shift their daily temporal activity patterns, and move to different locations in the landscape to avoid the potential masking effects of anthropogenic sound (Brumm and Slabbekoorn 2005, Francis et al. 2011, Dowling et al. 2012).

Some studies have explored biophony–biophony interactions through the concept of the acoustic niche and through exploration of acoustic responses to certain acoustic stimuli. According to the "acoustic niche hypothesis" (ANH; Krause 1987), competition between multiple emitter–receiver couples for limited acoustic space should lead to diversity in acoustic signals (Garcia-Rutledge and Narins 2001, Bradbury and Vehrencamp 2011), defined as diversity in frequency, in daily and seasonal activity patterns, and/or in spatial sound-production locations (Ficken et al. 1985, Gottsberger and Gruber 2004, Diwakar and Balakrishnan 2007). Such competition for acoustic space has been highlighted both between and within bird species. For example, Brumm (2006) examined how Common Nightingales (*Luscinia megarhynchos*) adjust their song timing to avoid overlaps with heterospecifics; Luther (2009) described acoustic differentiation within the avian community of a Neotropical rainforest; and Wasserman (1977) presented evidence that White-throated Sparrows (*Zonotrichia albicollis*) avoid singing at the same time as local conspecifics. Studies on biophony–biophony interactions have also considered the behavior of bird species in relation to the surrounding soundscape. For example, Laiolo et al. (2011) demonstrated the positive effect of surrounding bird diversity on the vocal repertory size of 2 mimicking species, the Crested Lark (*Galerida cristata*) and Thekla Lark (*G. theklae*). Billings et al. (2015) showed that some chickadees (*Poecile* spp.) produce different vocal responses (alarm and mobbing calls) when presented with calls of different raptors that represent different types of predation threats.

Some studies have also highlighted the interaction between biophony and geophony. Lengagne and Slater (2002) showed that in rainy weather, many Tawny Owls (*Strix aluco*) stop their calling activity when heavy rain would largely mask their vocalizations. On the other hand, Lengagne et al. (1999) demonstrated that in windy weather, King Penguins (*Aptenodytes patagonicus*) actually emit more calls and a higher number of syllables per call to increase the probability of successful communication. These contrasting behavioral changes are interesting in that they represent both sides of the ecological trade-off between costs (e.g., energy consumption) and successful communication (Patricelli and Blickley 2006, Warren et al. 2006) and demonstrate that species might be differently affected by changes to their sonic environments. Many of the case studies cited here are focused on single species, but the resultant knowledge provides much of the theoretical basis for soundscape ecology's consideration of all the interactions between biophony, geophony, and anthrophony in a general landscape context.

Principle 2: Sounds are shaped by environmental constraints. Landscape structure can affect sound propagation. For example, vegetation can absorb and reflect sound waves (Wiley and Richards 1978, Slabbekoorn 2004), and ground properties can play a significant role in sound absorption (Attenborough 1988). These effects vary depending on frequency; because absorption is higher for high-frequency sounds, lower frequencies propagate farther, an effect that has been demonstrated in forest, grassland, and edge habitats (Morton 1975, Richards and Wiley 1980). Moreover, topography and geographic orientation can influence soundscapes. As Brumm and Slabbekoorn (2005) say, "many habitats have their own typical pattern of ambient noise." Indeed, wind exposure (which varies by elevation and aspect) in combination with vegetation structure can lead to different patterns of wind sounds. The hypothesized adaptation of biological signals to the acoustic conditions of habitats—the "acoustic adaptation hypothesis" (AAH; Morton 1975)—is supported by several studies (Richards and Wiley 1980, Boncoraglio and Saino 2007, Bradbury and Vehrencamp 2011). Morton (1975) noted differences in frequency components of avian vocalizations between habitat types in Panama, and Wiley (1991) documented habitat-dependent temporal variation in the vocalizations of territorial oscines of eastern North America.

These habitat-based adaptations influence not only the emission but also the reception of avian vocalizations, as Wiley (1991) suggested. Henry and Lucas (2010) explored differences in frequency resolution between woodland and open-habitat species using auditory brainstem responses, and Aubin et al. (2014) adopted a behavioral methodology to show that White-browed Warblers (*Basileuterus leucoblepharus*) in the Brazilian Atlantic forest recognize conspecific songs despite the songs' degradation in forested habitats.

Sound propagation is additionally affected by parameters such as temperature, humidity, and atmospheric pressure, and sounds are also subject to phase modification, which can lead to difficulty in locating emitters (Wiley and Richards 1978). Collectively, these studies suggest that birds (1) tend to produce signals that will propagate well in their natural environments and (2) are adapted to perceive crucial information despite signal degradation that results from environmental constraints. Soundscape ecology is grounded in this knowledge of propagation-based adaptations, and it considers the physical environment as an influence on soundscapes.

Principle 3: Soundscape features can reflect characteristics of animal communities. Several scientists have suggested that the diversity and temporal patterns of biophony could be indicators of the characteristics of acoustic animal communities. A majority of the first works that focused on biophony as a community indicator considered bird communities. These studies can be classified into 2 types. The first type is focused on biodiversity assessment, examining whether the acoustic diversity of a recording can reveal biodiversity facets of the recorded bird community such as species richness (Pieretti et al. 2011, Depraetere et al. 2012, Lellouch et al. 2014, Towsey et al. 2014a, Gasc et al. 2015), functional diversity, and phylogenetic diversity (Gasc et al. 2013a). The results of these works clearly demonstrated that acoustic indices of overall variation in soundscapes composed of bird sounds can contain information reflecting the diversity and activity patterns of avian communities.

The second type of soundscape studies is focused on the interaction between recorded animal communities and some component(s) of their environments. For example, Pekin et al. (2012) demonstrated that the acoustic diversity of a dusk chorus in the tropical forest of La Selva, Costa Rica, was highly correlated with the complexity of vertical forest structure—which, in turn, is thought to be correlated with characteristics of animal communities. While this work considered the entire community of sound-producing animals, other works have focused explicitly on the composition of avian communities. For example, Cardoso and Price (2010) demonstrated an acoustic convergence between avian communities according to habitat characteristics over sites from different continents. Overall, studies on avian communities and their acoustic production support the hypothesis that soundscape characteristics can reflect the diversity and composition of avian communities and related ecological processes. While some of these soundscape-based studies do not explicitly incorporate landscape perspectives, soundscape ecology attempts to draw this knowledge into a landscape context.

Principle 4: Soundscapes vary across ecological and human disturbance gradients. Knowledge resulting from ornithological studies is extremely useful in the evaluation of vertebrate population trends and the impacts of global-scale changes on these trends. Gage and Miller (1978) used human acoustic observations to document avian responses to spruce budworm over 22 yr; Inger et al. (2014) used a 30 yr dataset on 144 bird species to demonstrate the decline of common bird populations in Europe; and Gregory et al. (2005) demonstrated the decline of farmland birds with data collected from 18 countries between 1980 and 2004. Given the availability of high-quality bird data and the fact that birds exhibit wide geographic and habitat distribution and play diverse roles in ecosystem functioning, bird population trends are often used as indicators of environmental change (Sekercioglu 2006, Gregory et al. 2008, Sheehan et al. 2010). For example, the Wild Bird Index (WBI) was developed to evaluate progress toward the international goal of reducing the global rate of biodiversity loss (Butchart et al. 2010, Sheehan et al. 2010). Indices such as the WBI are based on data from species-centered monitoring programs. However, biological conservation would benefit from complementary indicators that directly reflect community composition and dynamics in a landscape context.

Soundscape approaches seem well suited to address this monitoring gap (Pijanowski et al. 2011b, Krause and Farina 2016). Because soundscape monitoring can be largely automated and conducted with minimal ecosystem impacts, it enables measurements that are currently approaching the spatial resolution of remote sensing imagery while exceeding the latter's temporal resolution. Whereas visual remote sensing is used to extract information about land use/cover and vegetation, soundscape approaches add complementary information concerning diversity and/or dynamics of animal communities, weather patterns, and other environmental conditions.

Soundscape measurements would contribute to the avian conservation effort by promoting a more global vision of avian community dynamics and of the relationship between those dynamics and the disturbed environments that shape them. Imitating population-trend research conducted in avian ecology, some long-term (>1 yr) soundscape recording programs have already been initiated to describe the temporal variation of soundscapes. For example, Gage and Axel (2014) published a record of the temporal variation of biophony over a 4 yr period at 30 min recording intervals, thus providing the ability to analyze daily and yearly soundscape patterns. Other long-term recording programs have been conducted by the REAL (Kasten et al. 2012; recordings available at http://dev4.real.msu.edu). Similarly, Pijanowski et al. (2011b) initiated an ongoing, long-term monitoring project in 2008 to describe the soundscape phenology of various Indiana habitats (the collected recordings are available in a database at http://soundscape01.rcac.purdue.edu/pumilio).

Also, some ecosystem disturbances can be revealed by soundscape variation or elements' addition to or removal from soundscapes. For example, soundscapes of fragmented vs. nonfragmented forest in Tanzania showed differences in sound composition due to differences in animal species composition in the 2 locations (Sueur et al. 2008b). Pijanowski et al. (2011b) conducted a study on 8 sites in Indiana and showed that within Tippecanoe County, biophony was less diverse in urban and agricultural sites than in protected forest sites. Joo et al. (2011) showed a negative relationship between urbanization levels and biophony intensity in an urban–rural landscape. Duarte et al. (2015) investigated the effects of mining on biophony and found that nightly wet-season biological acoustic activity levels were higher at a greater distance from a mine, suggesting a negative effect of mining activity on the diversity and/or behavior of soniferous species. Laiolo and colleagues investigated the relationship between acoustic repertory size and geographic isolation of avian populations, showing that (1) the acoustic diversity within populations of Dupont's Lark (*Chersophilus duponti*) decreased with landscape patchiness (Laiolo and Tella 2006) and (2) this acoustic diversity could be positively related to bird population viability and could thus serve as an indicator of that viability (Laiolo et al. 2008). This research supports the hypothesis that landscape characteristics affect soundscape composition and dynamics; more broadly, these studies demonstrate the potential of applying soundscape approaches to biological conservation. Much of the groundwork for such application has been laid. What is now necessary is the further development and integration of this knowledge in a larger context, and soundscape ecology provides a theoretical framework for such integration.

Ornithological Contributions to the Future of Soundscape Ecology

The application of soundscape ecology approaches to biological conservation has gained acceptance within the research community, and such application is presented in various seminal papers (Pijanowski et al. 2011a, 2011b, Sueur and Farina 2015, Ritts et al. 2016). It is clear that the future of applied soundscape ecology resides in the development of soundscape-based disturbance indicators that are calibrated for application in different ecosystems and environmental conditions. Such application depends on the development of detailed and objective soundscape measurement and interpretation and an improved understanding of the drivers of soundscape variation in diverse ecosystems and habitat types (Figure 2). The following proposal comprises 3 research objectives, some of which may be shared throughout ecoacoustics. Together, these objectives address important current challenges for soundscape ecology, and both soundscape ecology and ornithology would benefit from the resultant research advances.

Research objective 1: Develop soundscape metrics and interpretation (measurement). The first research objective is focused on the development of soundscape measurements that enable intelligible, informative, and objective soundscape descriptions. Bird sounds are found in a high proportion of soundscape recordings, and although metrics that measure the global variation of acoustic activity within avian communities exist, their interpretation remains imprecise and would benefit from detailed description of the avian communities in the recordings. For example, Gasc et al. (2013b) demonstrated soundscape differences between areas hosting different animal communities; however, they did not investigate the composition and dynamics of the communities in enough detail to determine how these factors shaped the soundscapes. Beyond simply determining the number of sound-producing species in a soundscape recording, identifying the species in that recording will allow more in-depth analysis of the recording, based on information about species ecology and behavior as well as community structure and dynamics. Describing species' sounds within the broader soundscape would allow scientists to understand how those sounds exhibit mutually influential relationships with their contexts (for examples of research questions, see Table 2).

Developing an exhaustive catalog of sound-producing species in soundscape recordings is not a novel challenge (Wimmer et al. 2013), and a sizable body of literature is developing on the use of acoustic recordings as a way of remotely cataloging avian communities (e.g., Dawson and Efford 2009, Venier et al. 2012, Alquezar and Machado 2015). In addition, several scientists are advancing the technical borders of automatic species identification in field recordings (Duan et al. 2011, Towsey et al. 2012, Potamitis 2014, Potamitis et al. 2014). Recordings of nearly all bird species are publicly available; for example, see:

- Xeno-canto: http://xeno-canto.org
- Borror Laboratory of Bioacoustics: http://blb.osu.edu
- Macaulay Library: http://macaulaylibrary.org
- British Library collection of wildlife and environmental sounds: http://bl.uk/collection-guides/wildlife-and-environmental-sounds
- Commonwealth Scientific and Industrial Research Organisation: http://csiro.au/en/Research/Collections/ANWC/About-ANWC/Our-wildlife-sound-archive

These recordings could ideally be used as training samples to enable automatic species identification in complex field recordings. However, these catalogs sometimes fail to adequately capture within-species variation, and they rarely associate sounds with their environmental contexts (Brandes 2008).

In the future, automatic recognition of all species producing sound in a recording might be possible in all environments and conditions. Testing of such automatic recognition will likely have some degree of focus on birds, given the high scientific and conservation interest in this taxon. Accurate manual description of some "intelligent subsamples"—subsamples of soundscape recordings that represent different community compositions, temporal dynamics, and habitat and weather/climate conditions—would facilitate this development. Developing an "acoustic animal community catalog"—a large body of soundscape recordings with detailed descriptions of the recordings' sound-producing species and their interactions—will require substantial contributions from ornithologists. By comparing soundscape features to these community descriptions, ornithologists will help (1) validate existing soundscape measurements as reflecting avian community characteristics, (2) design new ways of objectively measuring soundscape variation that reflect avian community characteristics (such as activity and biodiversity levels of sound-producing birds), and (3) prepare a robust dataset on which to test future automatic recognition methods. Because birds are not the only soniferous animals, further collaboration

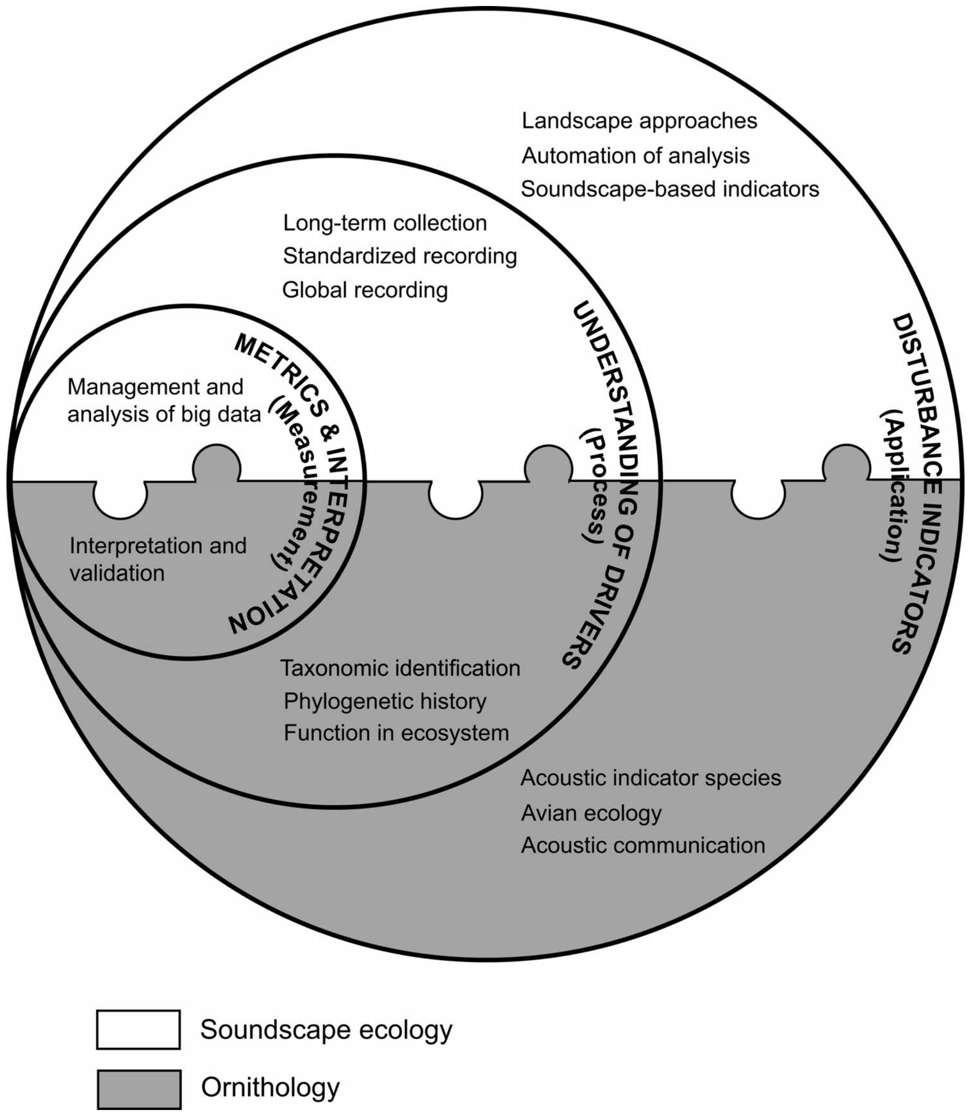

FIGURE 2. Three future research objectives and the complementarity of skills and knowledge from soundscape ecology and ornithology. Nesting of circles represents the cumulative contribution of requisite knowledge to address each objective.

with specialists on other taxa (including entomologists, mammologists, and herpetologists) will be necessary to describe the entire soundscape and develop robust acoustic metrics that consider its multi-taxon assemblages.

Research objective 2: Develop understanding of soundscape drivers (process). Based on the findings of research objective 1, the second objective is to develop an understanding of the drivers of soundscape variation by examining (1) different taxonomic groups' acoustic activities in their soundscape contexts in various ecosystems and environmental conditions and (2) the patterns and processes explaining these differences (for examples of research questions, see Table 2).

The evolutionary drivers that explain the soundscape contributions of avian communities may differ between ecosystems and communities. The ANH predicts a diversification of biophysical structures and behaviors involved in acoustic emission and reception, due to potential competition for acoustic space. All biological taxa contribute to biophony, and their interactions must be considered because they can have a great influence on bird sounds. In contrast, the AAH predicts the homogenization of these sound-related structures and behaviors, due to environmental constraints on acoustic propagation and thus on signal transmission. Additionally, the environmental and historical context of the community certainly influences its sounds; the evolutionary history and resulting morphology and behavior of each species must be considered as additional drivers (Figure 3). For example, the differences in soundscapes between ecosystems such as

TABLE 2. Examples of research questions at individual, species, community, and ecosystem levels linked to 3 research objectives. There is substantial overlap between the ecological levels at which we have placed each question, so some questions may apply to more than one level.

Research objective 1: Develop soundscape metrics and interpretation (measurement)
- Individual: To what degree can an individual affect soundscape metrics?
- Species: How do certain bird species exhibit differing influences on soundscape metrics?
- Community: Which soundscape metrics best capture differences (e.g., composition and dynamics) in avian and multi-taxon communities?
- Ecosystem: How can soundscape metrics be used to compare ecosystems in which soundscapes are dominated by bird vocalizations?

Research objective 2: Develop understanding of soundscape drivers (process)
- Individual: How do individual variations in behavior affect soundscape composition and dynamics of a place, and vice versa?
- Species: How do avian species-specific activity periods (e.g., mating and migration) affect soundscape dynamics?
- Community: How do interspecies avian interactions drive soundscape variability?
- Ecosystem: To what extent are the acoustic niche and acoustic adaptation hypotheses supported by the nature of avian vocalizations in relation to local environments, local sound-producing species, and evolutionary histories of species?
  - How could one model the degree of importance of avian acoustic communities in soundscapes of different ecosystems?

Research objective 3: Develop soundscape-based disturbance indicators (application)
- Individual: How is individual fitness affected by the soundscapes of a place?
- Species: Are sound-producing bird species indicative of various disturbances in various ecosystems?
- Community: How can soundscape differences be used to infer community-level effects (e.g., changes in species richness or abundance)?
- Ecosystem: What is the time lag between the onset of an ecosystem-level disturbance and any detectable soundscape changes?
  - Are indicators of non-sonic disturbances applicable to ecosystems with varying levels of anthrophony and geophony in the soundscape?

the forest in the Sky Islands of the Sonoran Desert and the tropical forest of Costa Rica could result from differences in acoustic competition between the sound-producing species, which would theoretically be higher in the species-dense tropical forest. Also, the differing vegetation densities and structures would appear to promote different types of sounds in each ecosystem.

The effects of these interacting drivers of biophony remain poorly studied at the community and ecosystem levels. As stated by Lomolino et al. (2015), biogeography

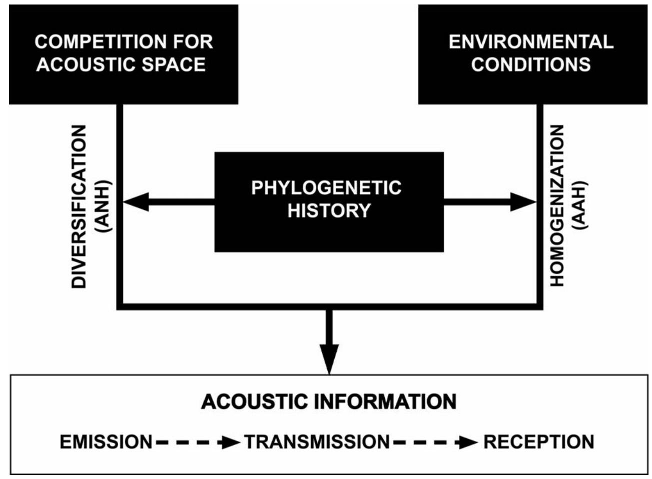

FIGURE 3. Schematic representation of 3 evolutionary drivers (black boxes) that exert pressure on acoustic information transfer (white box), resulting in the diversification (acoustic niche hypothesis [ANH]) or homogenization (acoustic adaptation hypothesis [AAH]) of both emission and reception.

has rarely considered environments' soundscapes. Soundscape-based research on the acoustically active avian community in diverse ecosystems could offer valuable insight into the processes shaping global patterns of biodiversity and ecological dynamics within and beyond that community. Considering each acoustic avian community within its broader soundscape would also help us better understand the evolutionary processes behind the acoustic diversity of those bird communities. Additionally, this research could help determine (1) the degree to which the ANH and AAH are supported in different conditions and (2) how invasive species and anthropogenic noise might potentially disrupt soundscape structures. These findings would also help calibrate the measurement and interpretation of biophony in different ecological conditions.

Murray Schafer's (1994:33) statement about the need for ornithological knowledge in a soundscape context may still hold true: "Ornithologists have not yet measured the statistical density of birds' singing in different parts of the world in sufficient detail for us to make objective comparisons—comparisons that would be helpful in mapping the complex rhythms of the natural soundscape." Ornithologists could contribute to this proposed research by developing a reference framework describing acoustic communities over space and time in different ecosystems and environmental conditions. In addition, to link the composition and dynamics of biophony with biological and ecological processes, ornithologists would bring valuable knowledge concerning species behavior, phylogenetic history, and ecology. Soundscape ecology would bring complementary knowledge about landscape contexts

(Tucker et al. 2014, Fuller et al. 2015). Extensive, currently accessible soundscape libraries from which such data could be derived include those of the Center for Global Soundscapes (http://centerforglobalsoundscapes.org) and the REAL (Kasten et al. 2012). Soundscape and species-specific sound libraries are as valuable as museum specimens (see the sound library of the Muséum national d'Histoire naturelle of France: http://sonotheque.mnhn.fr) in that they represent historical archives from which information can be gleaned as new recordings are made and analytical techniques are further developed.

Scientists will have to confront big data challenges when working with spatially and temporally extensive soundscape libraries. Recordings must be accompanied by thorough contextual metadata for appropriate analysis. Some forms of automation, such as the search-and-filtering interface developed by Kasten et al. (2012), may also have to be applied or developed in order for ornithologists to consider representative samples from any given dataset. Collaboration with technicians and engineers will be necessary in this regard. This research could result in the creation of an acoustic distribution map based on a model of avian acoustic activity including such factors as landscape structure, animal community composition, season, time of day, weather conditions, and other sounds. Correlational and causational analyses could then link soundscape differences to various drivers.

Research objective 3: Develop soundscape-based disturbance indicators (application). When soundscapes can be intelligibly, informatively, and objectively described (research objective 1) and when the drivers of soundscape change in diverse ecosystems and environmental conditions can be identified (research objective 2), it will be possible to measure ecosystems' baseline soundscapes and use soundscape changes as indicators of other changing environmental conditions (for examples of research questions, see Table 2). If the knowledge generated through the pursuit of objectives 1 and 2 is sufficiently detailed, it may even be possible to identify specific causes of soundscape variation. Given the large role of birds in many soundscapes, fulfillment of objective 3 will be dependent on the application of ornithological knowledge to objectives 1 and 2. Only after the development of soundscape metrics that capture avian diversity and dynamics and the determination of the drivers of changes in avian contributions to soundscapes might scientists be able to ascertain the implications of soundscape changes for avian conservation.

Achievement of objective 3 will be especially relevant to those who monitor relationships between avian species, populations, and communities and their environments. Soundscape monitoring could represent a first line of detection for disturbances affecting birds. Soundscape approaches possess several key qualities that are desirable for ecosystem monitoring at both local and global levels. First, soundscape monitoring can be conducted with high temporal resolution. While biodiversity indices have typically been based on periodic inventories conducted only during specific biological periods (e.g., breeding season for birds), soundscape approaches allow for continuous data collection and exploration of processes occurring outside traditional monitoring windows. For example, winter soundscape monitoring, as pioneered by Mullet et al. (2016), could allow for the development of more detailed yearly phenologies of bird activity. Additionally, automated measurement of archived recordings supports high-volume analyses, but it also facilitates standardization of measurements across datasets, which is necessary for large-scale comparative analyses. Soundscapes contain information about various aspects of biodiversity, including species richness and abundance and community dynamics and composition. Consequently, changes in soundscape characteristics could be indicators of changes in community and ecosystem function. The implementation of a high-resolution, high-coverage, soundscape-based monitoring system would be highly valuable for many scientists and land managers interested in monitoring across heterogeneous ecosystems.

One of the principal domains in which ornithologists might help develop soundscape-based indicators is the consideration of behavior, which has been largely ignored in the current corpus of soundscape literature. Any understanding of soundscape variability is incomplete without the inclusion of behavioral knowledge because animal behavior can account for much observed soundscape variability. Integrating soundscape approaches with behavior (e.g., migration, group cohesion, mating, and interactions with other species) in response to disturbances would provide a significant advance in soundscape ecology. The development of a set of metrics that would use soundscape recordings to highlight the dynamics of acoustic avian indicator species could be modeled after the Index of Biotic Integrity for stream biota (Karr 1986) or indices developed across taxa, such as AMOEBA (ten Brink et al. 1991). The application of such metrics over large spatial and/or temporal scales and in complex heterogeneous systems would be highly relevant, especially in systems where exhaustive taxonomic identification is excessively laborious. Such an approach would have to be evaluated for relevance to management and/or policy concerns (see reviews in Dale and Beyeler 2001, Niemi and McDonald 2004, Turnhout et al. 2007), but it is certainly promising. Soundscape approaches to assessing ecosystem health require sensible application, and careful planning is important—especially before deploying recorders in remote sites, over large spatial areas, or in sensitive sites. Ornithologists and other taxonomic specialists should play a significant role in such study planning.

Conclusion

Soundscape ecology approaches offer (1) a theoretical framework grounded in a broad ecological context with large temporal and spatial scope, (2) a wealth of long-term soundscape collections from around the world, and (3) methodological innovations such as acoustic monitoring protocol development, programmable recorder improvement, and management and analysis of acoustic big data. To these successes, ornithology is poised to contribute (1) interpretive power to validate soundscape theories, (2) improvement of soundscape collections through detailed description, and (3) development of soundscape metrics and application of soundscape approaches. It is clear that both disciplines would accrue tremendous benefits through increased integration. Ornithologists can contribute to their own field as well as the field of soundscape ecology by capitalizing on the existing collections of soundscape recordings to enhance the interpretation of sounds in the environment. The application of ornithological expertise to soundscape ecology would promote worthy recognition of that expertise, and it would also provide an opportunity for soundscape ecologists, ornithologists, experts on other taxa, and engineers to collaborate on the challenges of interpreting the meaning of the soundscape.

So far, the scientists interested in soundscape ecology and in ecoacoustic questions more generally have interacted and exchanged information and techniques through organizations such as the Global Sustainable Soundscape Network (GSSN) and the International Society of Ecoacoustics (ISE). These organizations have hosted events that unite biologists, ecologists, naturalists, engineers, and even musicians who consider soundscapes in an ecological context. This relatively small community would benefit greatly from an increased presence of ornithologists, and such collaboration would present mutual opportunities for advancing study designs and analytic approaches. The opportunities for integration are broad and exciting, and the proposed linkages can form useful collaborations to build a more knowledgeable scientific community.

ACKNOWLEDGMENTS

We thank K. Bellisario, M. Ghadiry, B. Gottesman, M. Harris, and L. Villanueva-Rivera, all members of the Center for Global Soundscapes (Purdue University, West Lafayette, Indiana, USA); and P. Grandcolas, F. Legendre, and J. Sueur of the Institut de Systématique, Evolution, Biodiversité (Museum national d'Histoire naturelle of Paris, France) for fruitful discussions. We thank two anonymous reviewers for helpful and constructive comments, and P. Gasc for help in conceptualizing and designing a diagram.

Funding statement: This work was partially funded by the Wright Forestry Fund of the Department of Forestry and Natural Resources, the Purdue University Graduate School, National Science Foundation [NSF] RCN (no. 1114945), NSF IIS (no. 0705836), Purdue University's Center for the Environment, the U.S. Department of Education's Graduate Area of National Needs Program, the McIntire-Stennis Cooperative Forestry Research Program of the U.S. Department of Agriculture, and the College of Agriculture at Purdue University. None of our funders had any influence on the content of the submitted or published manuscript. None of our funders require approval of the final manuscript to be published.

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