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The Acoustic Habitat Hypothesis: An Ecoacoustics Perspective on Species Habitat Selection

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Abstract Sound is an inherent component of the environment that provides conditions and information necessary for many animal activities. Soniferous species require specific acoustic and physical conditions suitable for their signals to be transmitted, received, and effectively interpreted to successfully identify and utilize resources in their environment and interact with conspecifics and other heterospecific organisms. We propose the *Acoustic Habitat Hypothesis* to explain how the acoustic environment influences habitat selection of sound-dependent species. We postulate that sound-dependent species select and occupy habitats with unique acoustic characteristics that are essential to their functional needs and conducive to the threshold of sound frequency they produce and detect. These *acoustic habitats* are based on the composition of *biophony*, *geophony*, and *technophony* in the soundscape and on the biosemiotics mechanisms described in the *eco-field hypothesis*. The *Acoustic Habitat Hypothesis* initiates questions of habitat selection that go beyond the physical attributes of the environment by applying *ecoacoustics theory*. We outline the theoretical basis of the *Acoustic Habitat Hypothesis* and provide examples from the literature to support its assumptions. The concept of *acoustic habitats* has been documented in the literature for many years but here, we accurately and extensively define *acoustic habitat* and we put this concept into a unified theory. We also include perspectives on how the *Acoustic Habitat Hypothesis* can stimulate a paradigm shift in conservation strategies for threatened and endangered species.

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Introduction

Sound is an inherent component of ecological systems and many animals have evolved organs and physiological processes that generate and utilize sound for a variety of actions ranging from inter- and intraspecific communication to habitat selection (Lanyon and Tavolga 1960; Fay 1988a; Ward and Schlossberg 2004; Hahn and Silverman 2006). *Biophony* is the term used to describe the sounds made by animals in nature and may be as simple as a single note of a raven (*Corvus corax*) or the songs of the dawn and dusk choruses (Krause 1993). *Biophony* is one of three components that make up the soundscape often integrated with sounds made by human technology (*technophony*) and the sounds of the physical environment (*geophony*) (Pijanowski et al. 2011; Farina 2014, p. 7; Gage and Axel 2014; Mullet et al. 2016).

The soundscape encompasses the sounds emitted across the landscape in acoustic space (Schafer 1985) and contains a wealth of information that animals can use to interpret and respond to environmental conditions and inter- and intraspecific interactions given their auditory capabilities (Farina 2014, p. 3). The soundscape is therefore a crucial element of a species' habitat and the abilities that an animal has to transfer, interpret, and respond to information in the acoustic space are contributory adaptations that drive the natural selection process.

The "*eco-field*" is described as the physical space and its associated biotic and abiotic factors that an animal perceives (through its senses) when a specific cognitive or instinctual need for a resource arises (Farina and Belgrano 2006). The concept of the *eco-field* can be linked to the *General Theory of Resources* (Farina 2012) which postulates that animals reduce their energy investment to assimilate into a specific habitat because their genetic predisposition and phenotypic characteristics allow them to effectively assess and select habitats with a sufficient configuration of available resources that are generally scarce, cryptic, and heterogeneously distributed in space and time. In effect, when an individual need emerges, a template of resources essential to fulfill that need is identified by an organism, instinctively or cognitively (via biosemiotics codes), which provides the indispensable information an individual uses for the selection of a suitable habitat where those resources are available. For those species whose survival is significantly dependent on acoustic information, the composition, temporal patterns, and spatial arrangement of the sonic environment within a habitat type is an important source of information a species requires to fulfill its functional needs.

In particular, different sonic patterns can be used to locate specific "*acoustic eco-fields*". For instance, alarm calls can be used to delimit the *eco-field* related to safety (Manser et al. 2001). Also, acoustic information, such as the roosting chorus of common starlings (*Sturnus vulgaris*) has been shown to be a social mechanism to exchange information about food location and abundance (Ward and Zahavi 1973). Hence, the *acoustic eco-field* is the biosemiotics representation of sounds and their spatial and temporal characteristics a species interprets to carry out various functions.

Biophony in the Context of Habitat

The ability of animals to select suitable habitats is vital to their survival. There are many variables that determine the suitability of a habitat. However, each variable or combination of variables must provide adequate resources and/or information for a species to establish a territory, acquire food and shelter, avoid predation, seek mates, and reproduce. Each species has evolved adaptations to utilize specific resources in the environment that are not utilized in exactly the same way by others (Vandermeer 1972). A variety of species have evolved the ability to produce and utilize sounds in the acoustic space. The manner and pattern in which these species produce and utilize sound is linked directly to the physical environment and the community of organisms they interact with in a particular habitat and their accumulated experience.

There are two hypotheses that attempt to explain the evolution of sounds produced by animals in the context of habitat; these are the *Acoustic Adaptation Hypothesis* and the *Acoustic Niche Hypothesis*. The *Acoustic Adaptation Hypothesis* (Morton 1975; Hansen 1979) states that soniferous animals have evolved adaptations to maximize the propagation of their vocalizations in frequency, modulation, and length due to the influence of a habitat's physical structure on sound attenuation and frequency filtering. This links *biophony* and how animals have evolved to produce specific sounds directly to the *physical* characteristics of their environment. The *Acoustic Niche Hypothesis* (Krause 1993) postulates that the competition between species has led to the diversification of sound signals resulting in sounds produced at specific temporal and frequency intervals in the acoustic space and that these *acoustic niches* are unique to a species. *Biophony* in this case is linked to the complex system of *interactions* within the animal community of a habitat for clear communication. This further implies that each habitat type possesses an available niche in acoustic space that a soniferous species can occupy to carry out its functional role in the ecosystem.

The *Acoustic Adaptation Hypothesis* and the *Acoustic Niche Hypothesis* imply that *biophony* is both influenced by the physical aspects of the environment that has selected specific traits for sound production and the competition for acoustic space between interacting soniferous species. The *Acoustic Niche Hypothesis* could be considered nested within the *Acoustic Adaptation Hypothesis* in that an *acoustic niche* could not be filled without the precursor of soniferous adaptation. Thus, the information generated from *biophony* can serve as an indicator of the physical habitat type and the composition of the animal community within those habitats, neither of which are mutually exclusive.

Sonotopes and Acoustic Communities

The concepts of *sonotopes* (Farina 2014, p. 17) and *acoustic communities* (Farina and James 2016) attempt to explain the heterogeneity of *biophony* in the landscape based on the fundamental aspects of the *Acoustic Adaptation Hypothesis* and the *Acoustic Niche Hypothesis*. A *sonotope* is an acoustic patch of a soundscape resulting from the specific assemblage of *biophony*, *geophony*, and *technophony* within a given habitat on the landscape (Farina 2014, p. 17). Quintessential to the acoustic attributes of habitat types is the assemblage of *biophony* produced by sonifeorus species that form *acoustic communities* within a *sonotope* (Farina and James 2016). As such, an *acoustic community* is defined as an aggregation of species that produces sound by using internal or extra-body soniferous tools (Farina and James 2016). Each habitat type therefore has its own unique *sonotope* based on the composition of sounds produced by *acoustic communities* (*biophony*), geophysical and climatic events (*geophony*), and the activities of humans (*technophony*). Empirical corroboration of the idea of *acoustic communities* is developing (Farina and Salutari 2016; Farina et al. 2016; Farina and Gage 2017) and evidence supporting the *sonotope* concept is growing with empirical observations confirming that there is in fact a significant positive correlation between acoustic heterogeneity and the spatial heterogeneity of habitat types (Bormpoudakis et al. 2013; Fuller et al. 2015), in addition to there being close relationships between *sonotopes* and landscape patterns (Mullet et al. 2016, 2017).

Just as the physical aspects of a habitat influence the presence and success of a species, the *acoustic community* serves as a selective force in the competition for acoustic space but more generously serves as an indicator of habitat condition in space and time (Mönkkönen et al. 1990; Farina and James 2016). Because there is temporal and spatial variation in resource availability, the *acoustic community* may be representative of the time when resources are available (Valone and Templeton 2002; Hahn and Silverman 2006; Betts et al. 2008) and the composition and differential spatial distribution of *sonotopes* can reveal the locations where those resources may be found based on their unique acoustic signatures (Mönkkönen et al. 1990; Ward and Schlossberg 2004; Hahn and Silverman 2006; Betts et al. 2008).

The *sonotope* and *acoustic community* concepts describe the acoustic nature of each habitat as unique and the knowledge gained by an organism through processing the acoustic information contained in a habitat (i.e., *acoustic eco-field*) could be as equally useful to interpreting habitat suitability as it is to its physical characteristics (Betts et al. 2008). As a result, it is likely that acoustic information also drives the selection and occupancy of habitats, perhaps more so for some species than others.

Acoustic Habitat Hypothesis

Given the heterogeneity of information provided by *sonotopes* and *acoustic communities* throughout the landscape, it is conceivable that a species selects a habitat based on the unique acoustic characteristics of a particular area because those acoustic attributes provide differential information about the quality of the environment that affects the success of a species' survival within a habitat. Based on this idea, we define an "*acoustic habitat*" as the explicit composition of *biophony*, *geophony*, and *technophony* present in the acoustic space within a given habitat type that provides a species with the information and conditions they require to fulfill their functional needs.

We put *acoustic habitat* in the context of the *acoustic eco-field* in that an *acoustic habitat* is composed of a variety of sounds and their spatial and temporal dynamics that a species utilizes as cognitive information to fulfill unique functions in the ecosystem. Much like the physical nature of biotic and abiotic factors of the *eco-field*, an *acoustic habitat* is composed of the biotic and abiotic sounds utilized by a species to learn about their environment during the process of tracking resources by using distinct *acoustic eco-fields*. *Acoustic habitats* possess the differential information conducive for sound-dependent species to make decisions on where suitable habitats exist based on their acoustic conditions. In essence, the *acoustic habitat* is the ensemble of all *acoustic eco-fields* that a species requires to survive.

Sound-dependent species possess genetic specificity to particular *acoustic habitats* in that they have evolved the sense of hearing and use of sound within specific sound frequency thresholds (Calford 1988; Fay 1988b; Rogers et al. 1988). Therefore, an *acoustic habitat* is likely distinct for particular species based on the combination of their threshold of hearing, their physical and physiological abilities to generate sound mechanically or organically, and the ambient sounds present within their environment that directly or indirectly influences their use and/or manipulation of sound.

There are three basic, yet critical, ecological elements that are the foundations of an *acoustic habitat*: (1) there are biotic, abiotic, and anthropogenic sources in the environment that generate sound, (2) the sounds generated by these sources are indicators of resource quality and availability, inter- and intraspecific competitors, and environmental risks (e.g., predation, disturbance), and (3) the resources essential for a species' survival that are detectable through sound are unique. Based on these three elements, we hypothesize that the habitats that sound-dependent species select and occupy have unique acoustic characteristics based on their functional needs and the frequency threshold at which they can produce and detect sounds. We term this theory the *Acoustic Habitat Hypothesis* (Fig. 1).

Soundscape Orientation and Acoustic Habitat Hypothesis

Complimentary to the *Acoustic Habitat Hypothesis* is the concept of *soundscape orientation* (Slabbekoorn and Bouton 2008) which suggests that animals will use the

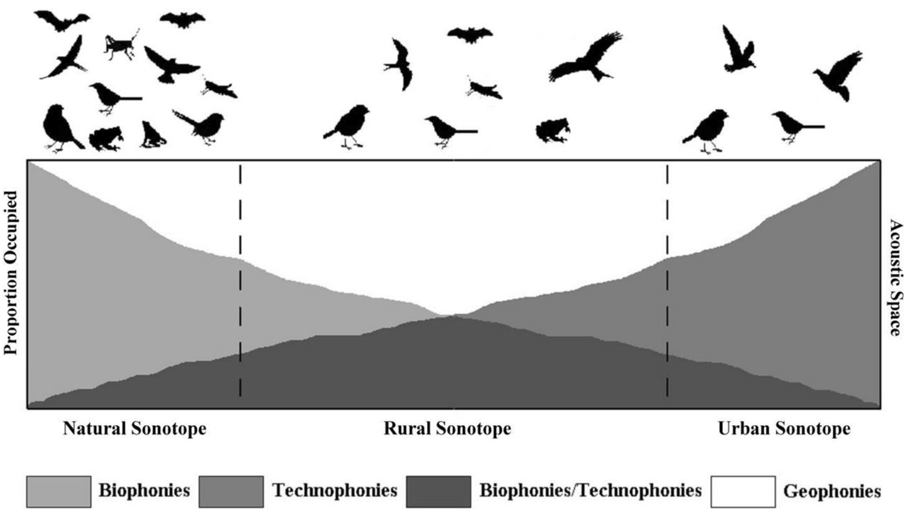

Fig. 1 A theoretic construct of the *Acoustic Habitat Hypothesis* in the context of three *sonotopes* within a soundscape with proportionally different compositions of *biophony*, *geophony*, and *technophony* and the *acoustic communities* of soniferous species occupying and contributing to distinct *acoustic habitats*. Certain aspects of the acoustic space possess instances of both *biophony* and *technophony* where the effects of masking may take place. Some species are *acoustic habitat specialists* and require acoustic characteristics that are specifically structured for a particular *acoustic habitat* type, whereas others may be *acoustic habitat generalists* with the ability to occupy more than one *acoustic habitat* type. Species diversity is expected to decrease in more anthropogenic-based *sonotopes*

characteristics of a soundscape to orient themselves when searching for suitable habitats. *Soundscape orientation* is distinguished from *acoustic habitat* in that *soundscape orientation* emphasizes directionality and sets out to answer the question: what soundscape cues does an animal use to direct them to a specific habitat? What the species is subsequently relying on to identify and select a habitat is acoustic information (i.e., *acoustic eco-field*) generated from their specific *acoustic habitat*. The *Acoustic Habitat Hypothesis* takes the *soundscape orientation* concept a step further with an emphasis on species occupancy with the purpose of answering the questions: what is the soundscape composition of the habitat that a species occupies and is that composition unique to that species? *Soundscape orientation* conceptually explains how species utilize some *acoustic eco-fields* of *acoustic habitats* to locate a suitable location that possesses both physical and acoustic attributes needed to successfully carry out its function in the ecosystem.

Evidence of Acoustic Habitats

Multiple studies have established evidence supporting the *soundscape orientation* concept (Simpson et al. 2008, 2012; Tolimieri et al. 2000) and the *Acoustic Habitat Hypothesis* (e.g., Morton 1975; Blumenrath and Dabelsteen 2004; Both and Grant 2012; Derryberry 2009). However, studies were not based on a consensus that the *Acoustic Habitat Hypothesis* is intended to establish. Likewise, much of the historic and contemporary work that builds support of the *Acoustic Habitat Hypothesis* were focused more so on the individual components of the soundscape (*geophony, biophony*, or *technophony*) rather than providing a holistic perspective of *ecoacoustics theory* (Sueur and Farina 2015) that the *Acoustic Habitat Hypothesis* is founded on.

Biophony in Acoustic Habitats

Biophony is a form of information that is transmitted, received, and interpreted between and among species and is considered to be a type of “social information” that animals use as cues to select habitats (e.g. Danchin et al. 2004). These social cues may be one of the most effective ways for an individual to investigate multiple candidate habitats and select the one best suited for its needs (Boulinier and Danchin 1997; Valone and Templeton 2002). Several studies have revealed how important social cues can be for some sound-dependent species (e.g., birds) in the process of selecting habitats.

For example, migrating American redstarts (*Setophaga ruticilla*) have been found to use the social cues of conspecifics to select a suitable breeding habitat despite their experience with the physical attributes of the area (Hahn and Silverman 2006). Black-capped vireos (*Vireo atricapilla*) and black-throated blue warblers (*Dendroica caerulescens*) have also been known to use social cues of conspecifics to identify successful breeding habitats while avoiding equally suitable habitat without those social cues (Ward and Schlossberg 2004; Hahn and Silverman 2007). Similarly, female black-throated blue warblers have even been observed selecting low-quality habitats when conspecific call playbacks are played and neglecting high-quality habitats where conspecific vocalizations were absent (Betts et al. 2008), indicating that these animals significantly relied on social information to select their breeding sites.

Social cues can also extend beyond conspecifics to the larger community of sound-utilizing species. Chaffinch (*Fringilla coelebs*) and willow warbler (*Phylloscopus trochilus*) abundance has been strongly positively associated with the density of island-resident tits (*Parus* spp.) in northern boreal forests (Mönkkönen et al. 1990). In this instance, interspecific competition for food was of minor importance in these bird community assemblages which suggests that habitat generalist migrants use the presence of resident species (detected by their *biophony*) as an indicator of safe and/or productive breeding sites in locations where environmental circumstances are unpredictable (Mönkkönen et al. 1990).

Conversely, the *biophony* of some species can have differential effects on heterospecific habitat selection. American redstarts, for instance, have been found to avoid habitats where the calls of the more dominant and aggressive least flycatchers (*Empidonax minimus*) were played, while least flycatchers were equally attracted to conspecific and heterospecifc call playbacks (Fletcher 2007). Similarly, migrant species abundance has been known to decrease by ~30% in habitats where least flycatcher calls were played resulting in a restructuring of the bird community, whereas American redstart playbacks did not influence species richness or community structure of migrant species.

These studies suggest that there is, indeed, an *acoustic habitat* where *biophony* plays an important role. The use of the *acoustic eco-field* not only orients sound-dependent species to a particular habitat but also provides information on whether the habitat conditions are conducive to their reproductive success as occupants. In circumstances where studies found birds selecting unsuitable habitats through conspecific social cues, it appears that some species "trust" the semiotic information of their own kind to inform them on habitat quality (Harcourt 1991).

Geophony in Acoustic Habitats

Geophony encompasses all sounds that are generated by geophysical events (Qi et al. 2008; Pijanowski et al. 2011; Farina 2014, p. 8). Examples of *geophony* include thunder, the sound of rain impacting leaves, water, and the ground, wind blowing through leaves, the rumbling of Earth's tectonic plates during an earthquake, and so on. *Geophonic* activity is nearly ever-present and more variable than other acoustic phenomena (Farina and Gage 2017). Although many studies have shown that geophony can have a significant influence on animal vocalizations (Brumm and Slater 2006; Preininger et al. 2007; Brumm and Naguib 2009; Samarra et al. 2009; Vargas-Salinas et al. 2014) and their evolution (Ryan and Brenowitz 1985; Brumm and Slabbekoorn 2005), very little is known about how geophony influences species habitat selection. However, we suspect that geophony provides a form of information that an animal can use to identify resources (e.g., the flow of water in a stream), areas to avoid (e.g., high wind), or locations to feed (e.g., the cracking of shifting ice revealing open water).

One study provides an example of how important *geophony* is in a species' habitat and how various *geophonic* attributes can distinguish habitats between species. Goutte et al. (2013) tested whether sound pressure level (SPL), the measure of loudness, could be used to differentiate the habitats of anuran species throughout Southeast Asia. They discovered three discrete clusters of *geophonic*-based acoustic habitats among 10 species. Of these, anurans showed distinct habitat selections that were differentiated through the SPL of the physical habitat type: (1) Torrents: very loud streams; (2) Ponds: quiet, small bodies of water; and (3) Rivers/Lakes: large bodies of water quieter than torrents but louder than ponds. When interpreting their results using SPL with six other physical attributes of these habitat types, they found that removing SPL from their models resulted in less clearly discriminated groupings of species habitats. Their results implicate that using SPL included information about multiple aspects of the environment that generate sound that are likely of prime importance to these species. In this example and for these species in particular, *geophony* was an important aspect of their habitat and evidently provided specific acoustic conditions they preferred for settling within those habitats.

Technophony in Acoustic Habitats

The rapid increase and expansion of mechanized human activity has led to an escalation in anthropogenic noise (i.e., *technophony*) in the environment (Krause 2012). *Technophony* is a form of *anthrophony* (i.e., human-generated sound) (Gage et al. 2004; Pijanowski et al. 2011) and refers to the sounds made by human technology (Gage and Axel 2014; Mullet et al. 2016). *Technophony* is expected in areas of human development but there is evidence that it is encroaching evermore into natural areas (Krause 2002; Barber et al. 2010) and can create a significant acoustic footprint in wilderness areas as well (Mullet et al. 2017).

Technophony is a relatively novel soundscape component that has expanded across the Earth in the wake of the Industrial Revolution, the invention of internal combustion engines, and the progressive use of oil and gas (Barber et al. 2010; Mullet et al. 2017). Thus, it has been a relatively short time period for species to sufficiently adapt genetically to a *technophonically*-influenced environment. As a result, the intrusion of *technophony* into more natural areas has forced sound-dependent species to adapt behaviorally to changes in their acoustic environment (Slabbekoorn and Ripmeester 2008). There is an exceptional growing body of work on this subject from marine environments to terrestrial ecosystems. This subject is both of scientific interest and of conservation concern for its practical implications for ecosystem management (Barber et al. 2010; Ortega 2012; Ritts et al. 2016).

Technophony is low-frequency sound (typically <2000 Hz) emitted from a variety of sources (Gage and Axel 2014; Mullet et al. 2016). In terrestrial environments, many studies have focused on the effects of *technophony* associated with roads, oil and gas development activities, and mining activity. Sound-dependent organisms have responded to these *technophonically*-influenced habitats in different ways and although *technophony* can have detrimental effects on species' abilities to transmit their signals (Barber et al. 2010; Ortega 2012; Ortega and Francis 2012), it may also be a source of information that animals use to decide whether to settle within or avoid a habitat.

Bird occupancy and population densities have been found to be significantly lower in areas of road noise compared to areas without road noise (Forman and Deblinger 2000; Stone 2000; Brotons and Herrando 2001; Fernandez-Juricic 2001). Even when correcting for the visual disturbance of road activity, bird densities are known to be much lower in areas of road noise (Reijnen et al. 1995) and can decrease bird occupancy up to 300 m from the source (Forman and Deblinger 2000). Insectivorous birds have been observed avoiding noisy habitats within 500 m from roads associated with oil development activities (Canaday and Rivadeneyra 2001) and evidence has shown that the presence of grassland birds can be significantly lower in areas up to 700 m from roads due to traffic noise

(Forman et al. 2002). There is also some indication that birds may avoid habitats affected by road noise independently from the type of land use (Stone 2000) or whether it is suitable habitat (McClure et al. 2013).

Analogous behavior in birds has been documented empirically in experiments associated with gas-well-compressor noise. For instance, Francis et al. (2009) found that mourning doves (*Zenaida macroura*), gray flycatchers (*Empidonax wrightii*), gray vireos (*Vireo vicinior*), black-throated gray warblers, and spotted towhees (*Pipilo maculatus*) all avoided areas of gas-well-compressor noise in northwestern New Mexico. Nest predators, such as the western scrub jay (*Aphelocoma californica*), have been detected significantly less in habitats with gas-well-compressor noise than in quieter areas presumably because they could detect potential prey in more natural soundscapes devoid of the masking effects of low-frequency noise on prey sound signals (Francis et al. 2012). Red-eyed vireos (*Vireo olivaceus*), yellow-rumped warblers (*Setophaga coronate*), and white-throated sparrows (*Zonotrichia albicollis*) have all displayed avoidance behavior to gas-well-compressor noise where breeding bird densities were one-and-a-half times lower than densities in more natural soundscapes (Bayne et al. 2008). Similarly, significantly higher species richness and more complex species compositions have been documented in areas further from mining noise in the Atlantic forests of Brazil (Duarte et al. 2015).

Perhaps equally as interesting are the findings of several studies that documented some species appearing to "prefer" or tolerate noisy habitats. For example, Peris and Pescador (2004) discovered higher breeding densities of corn buntings (*Miliaria calandra*), house sparrows (*Passer domesticus*), and rock sparrows (*Petronia petronia*) in noisier, high-traffic areas than quieter, low traffic areas of a Mediterranean wood pasture. Francis et al. (2009) found distinct community compositions of birds in noisy habitats in gas-well-compressor fields versus non-noisy habitats most likely because these species were more tolerant to noise than other species and perhaps gained a fitness advantage as a result of low nest predation (Francis et al. 2012).

There is also evidence that birds with song frequencies above low-frequency *technophony* are less likely to be affected and tend to stay in noisy areas compared to birds whose songs may be masked at such frequencies (Stone 2000; Rheindt 2003; Francis et al. 2012). Some species of birds are known to adapt to noisy habitats by increasing the pitch of their songs above *technophony* frequencies, effectively enabling them to stay in noisy locations (Slabbekoorn and Peet 2003; Halfwerk and Slabbekoorn 2009; Wood and Yezerinac 2006; Mockford and Marshall 2009).

Technophony is certainly a selective force that modulates how species orient themselves to and settle within habitats despite their physical attributes. It is unlikely that *technophony* will decrease in the future. Rather, the expansion of human populations and mechanization will increase and thus expose more species to the effects of *technophony*. With an *ecoacoustics* perspective, identifying and interpreting these effects will be possible (Sueur and Farina 2015).

Discussion

The evidence presented here provides support for the *Acoustic Habitat Hypothesis* which is intended to open a discussion on how the soundscape as a whole influences the behavior of individuals, populations, communities, and entire ecosystems with a perspective founded on *ecoacoustics theory* (Sueur and Farina 2015). Not dissimilar to how species and communities interact with their physical environment, an *acoustic habitat* is likely an additional driver of the natural selection process for traits and behaviors that increase an individual's ability to successfully survive and reproduce. Circumstantially, some species will thrive in specific *acoustic habitats* more so than others causing a differential preference for particular *acoustic eco-fields* that distinguish the selective function of a species' for a distinct habitat type. Thus, the acoustic characteristics of the environment may have considerable sway on the success of a species within a given area.

Acoustic Habitat Specialists and Generalists

Remarkably, some study results indicate that particular soniferous species are more tolerant of certain acoustic environments than others and therefore, *acoustic habitat* quality may be species-specific in the selection of habitat types. *Geophony* has played an important role in the evolution of signals generated by species dependent on sound for establishing territories and mate attraction (Ryan and Brenowitz 1985; Brumm and Slabbekoorn 2005). Studies have shown that *geophony* and *technophony* have significant influence on species' signal adaptations in order to enhance noise-to-signal ratio for sound propagation and distinction in noisy environments (see Brumm and Slabbekoorn 2005).

Some populations of soniferous species have been found to experience a divergence in phenotypes that are associated with their acoustic signals when the population is distributed across different types of *acoustic habitats* (Brumm and Slabbekoorn 2005; Vargas-Salinas and Amezquita 2013). Additionally, there is evidence that certain species exhibit an affinity to natural soundscapes and others to noisy soundscapes (Sec. 6.3). However, studies have also shown that species can show no discernable preference for specific acoustic conditions and may be able to take advantage of almost any acoustic environment (Peris and Pescador 2004; Mockford and Marshall 2009). Hence, species who display specific acoustic preferences can be termed "*acoustic habitat specialists*" and those species with no discernable preference can be considered as "*acoustic habitat generalists*" (Fig. 1).

A study conducted by Vargas-Salinas and Amezquita (2013) may provide an example of how *acoustic habitats* with strong *geophonic* influence possibly result in microevolution within a population. What they found was that a microgeographic-divergent population of poison frogs (*Oophaga histrionica*) showed distinct acoustic and morphological differences depending on their location next to streams. Frogs next to streams emitted higher call frequencies above the background *geophony* and exhibited significantly smaller body sizes than frogs that positioned themselves away from streams. They suggested that this acoustic-morphological interaction was possibly driving a speciation event in that smaller-bodied frogs generally have the ability to call above low-frequency stream *geophony* (Martin 1972; Nevo and Schneider 1976; Gerhardt and Huber 2002) enabling them to successfully attract mates and reproduce additional offspring with similar traits (Vargas-Salinas and Amezquita 2013).

In the context of *acoustic habitats*, Vargas-Salinas and Amezquita (2013) provide evidence that even particular individuals within the same population can find selective advantages in particular acoustic conditions. As such, these differences may result in acoustically-driven speciation where there are differences in allele frequencies that are linked between morphologically-attributed and soniferous-related alleles. Coupled with geographic differences in the orientation and reproductive success of these traits with that of other individuals within conspecific populations not located in similar *acoustic habitats*, it is conceivable that these conditions would result in the appearance of new subspecies whose cultural evolution (Laiolo and Tella 2007) is driven by *acoustic habitats*.

Other studies have found distinctions between species that have shown preferences towards habitats with specific acoustic conditions. Peris and Pescador (2004), Bayne et al. (2008), Francis et al. (2009), and Ortega and Francis (2012) found that some bird species had significantly higher breeding densities in habitats with high amounts of *technophony* while other species had higher densities in more natural, quieter soundscapes. Hoskin et al. (2009) also found distinct separations in habitat types between 116 Australian frog species based on the acoustic characteristics of the habitats and on animal body size and the sound frequency of their calls.

Conversely, some species appear to display no affinity for particular *acoustic habitats* when comparing noisy and natural soundscapes. Great tits (*Parus major*) for instance, have been found to occur in no significantly different number when occupying *technophonically*-dominated urban areas and more natural soundscapes (Mockford and Marshall 2009). Similarly, Peris and Pescador (2004) found that black redstarts (*Phoenicurus ochruros*), blue tits (*Cyanistes caeruleus*), crested larks (*Galerida cristata*), European goldfinches (*Carduelis carduelis*), great tits, European greenfinches (*Chloris chloris*), Eurasian nuthatches (*Sitta europaea*), European serins (*Serinus serinus*), short-toed treecreepers (*Certhia brachydactyla*), and European starlings (*Sturnus vulgaris*) had no significant differences in their abundance and occupancy of natural soundscapes versus soundscapes with abundant *technophony*.

Although these studies do not necessarily provide definitive conclusions that support the concept of *acoustic habitat specialists* and *acoustic habitat generalists*, they do suggest that such a hypothesis may explain the differences in habitat selection of sound-dependent species given the acoustic characteristics of their environment (Fig. 1). The postulates of the *Acoustic Habitat Hypothesis* provides a foundation of hypothesis testing that can be used to determine whether a species does in fact occupy a specific *acoustic habitat*. This can be achieved through comparative experiments in natural environments, under controlled conditions through manipulation of the acoustic environment, or any other novel study design intended on identifying the relationship between a species and its acoustic environment. Through continued hypothesis testing and experimentation using established and innovative methodologies (e.g., Blumstein et al. 2011; Merchant et al. 2015; Pieretti et al. 2015; Farina and Salutari 2016) we suspect that *acoustic habitat specialists* and *acoustic habitat generalists* will eventually reveal themselves.

Acoustic Habitats and Conservation

The conservation and recovery of threatened and endangered species requires an extensive amount of knowledge of species-habitat relationships. Despite an exceptional body of research on how species use sound, its influence on habitat selection, and even the physiological effects of noise on animal behavior and reproductive success (Maxwell 1993; Spreng 2000; Campo et al. 2005; Crino et al. 2013), acoustic conditions are rarely considered when identifying a species' essential habitat. If the conditions of the acoustic environment are imperative to a species' survival, then it is also imperative that the *acoustic habitat* be given just as much consideration in the species' conservation as its physical habitat needs. Such consideration would then also warrant the preservation of *acoustic habitats* for ensuring a species' fitness and longevity.

The concepts of the *Acoustic Habitat Hypothesis* can be useful when identifying suitable habitats and evaluating conservation efforts for at-risk *acoustic habitat specialists*. If an *acoustic habitat* is specific to an at-risk species, then it is possible to determine the suitability of any particular habitat and the success of restoration projects through acoustic monitoring and analysis. Multiple soundscape indices have been developed to answer a variety of *ecoacoustics* questions (Farina 2014, p. 239). These indices can be used to test the *Acoustic Habitat Hypothesis* by quantifiably identifying the *acoustic habitat* characteristics for any target species or suite of species (Pieretti et al. 2011; Fuller et al. 2015; Gasc et al. 2015).

In cases where the *acoustic habitat* is identified for the target species, additional monitoring can be efficiently conducted across a variety of spatial and temporal scales with minimal and non-invasive effort (Farina et al. 2014; Merchant et al. 2015; Pieretti et al. 2015). While acoustic recordings provide a great deal of information on the condition of an environment, it can also provide a means of identifying species of interest within the sample area. Considering there is a strong association between *acoustic habitats* and the physical environment (Fuller et al. 2015; Mullet et al. 2016), any manipulation of an area for restoration or creation of a physical habitat type for a species can be evaluated for its suitability and effectiveness through acoustic monitoring. Based on this premise, acoustic monitoring can provide data used to identify a species' *acoustic habitat* through non-invasive methods that can also be applied to monitoring plans and the assessment of conservation efforts (Bobryk et al. 2015; Merchant et al. 2015; Bertucci et al. 2016).

Conclusion

Although there is adequate evidence to conclude that *biophony*, *geophony*, and *technophony* individually influence species habitat orientation and site occupancy, it is not yet clear how the composition of all three soundscape components together affect a species' habitat selection, occupancy, behavior, and fitness. Based on the basic principles of ecology, it is conceivable that more than one soundscape component plays a role in species orientation and occupancy and these components are closely linked to the physical attributes of the environment (Fuller et al. 2015; Mullet et al. 2016). Despite the concept of *acoustic habitats* being around for some time in different forms and the term "acoustic habitat" even appearing in the recent literature (Chavarría et al. 2015; Merchant et al. 2015; Hatch et al. 2016) there has been no clear, ecologically-based definition of an "acoustic habitat". Here we set the stage by clearly defining an *acoustic habitat* in the context of a species' ecology and its semiosis with clear connections with other legitimate hypotheses (i.e., *Acoustic Adaptation Hypothesis*, *Acoustic Niche Hypothesis*, *Soundscape Orientation*, *Acoustic Communities*, *Eco-field Hypothesis*) and the *General Theory of Resources* (Table 1). We have also presented evidence from a number of studies that provide some support of the *Acoustic Habitat Hypothesis* and have proposed a hypothetical explanation of why there is differential habitat selection among sound-dependent species in the context of their acoustic environment in the form of *acoustic habitat specialists* and *acoustic habitat generalists*.

Table 1 Definition and literature sources of key terms and hypotheses relevant to the *Acoustic Habitat Hypothesis*

Term/Hypothesis	Definition	Source
Eco-field	"An ecological space, or a carrier of meaning, in which every living function interacts semiotically with the surrounding world"	(Farina and Belgrano 2006)
General Theory of Resources	A hypothesis explaining how resources are foundationally the most important mechanism for the survival of an individual or group and that organisms maximize their ability to assess the availability of resources by utilizing the *eco-field*	(Farina 2012)
Ecoacoustics	A theoretical and applied discipline that studies sound across a variety of temporal and spatial scales to address ecological questions where sound plays a role	(Sueur and Farina 2015)
Acoustic Space	The medium in which all sounds are or can be present	Schafer (1985)
Acoustic Niche	The unique frequency and/or time interval occupied by the sounds of a soniferous animal in the *acoustic space*	Krause (1993)
Acoustic Adaptation Hypothesis	A hypothesis postulating that animals have evolved adaptations to maximize the propagation of their vocalizations due to the influence of the physical structure of their habitats on sound attenuation and frequency filtering	Morton (1975); Hansen (1979)
Acoustic Niche Hypothesis	A hypothesis postulating that the competition between species has naturally selected for animals to produce sounds within an *acoustic niche*	Krause (1993)
Soundscape	The temporal and spatial composition of *biophony*, *geophony*, and *technophony* in the landscape	Pijanowski et al. (2011)
Biophony	Sound(s) produced by biological organisms	Krause (1993)
Geophony	Sound(s) produced by geophysical activities	Qi et al. (2008); Pijanowski et al. (2011)
Anthrophony	Sound(s) produced by humans	Gage et al. (2004); Pijanowski et al. (2011)
Technophony	Sounds(s) produced by human technology/machines, a subcategory of *anthrophony*	Gage and Axel (2014); Mullet et al. (2016)
Sonotope	An acoustic patch of a soundscape resulting from the specific assemblage of *biophony*, *geophony*, and *technophony* within a given habitat	Farina (2014)
Acoustic Community	An aggregation of species that produces sound by using internal or extra-body soniferous tools	Farina and James (2016)
Acoustic Eco-field [a]	The *acoustic space* of information an animal cognitively uses to fulfill some functional needs in the environment	
Soundscape Orientation	An animal's use of *soundscape* characteristics (*acoustic eco-fields*) to orient themselves when searching for suitable habitats	Slabbekoorn and Bouton (2008)
Acoustic Habitat[a]	The explicit composition of *biophony*, *geophony*, and *technophony* present in the *acoustic space* within a given habitat type that provides a species with the acoustic information and conditions they require to fulfill their functional needs	
Acoustic Habitat Hypothesis[a]	A hypothesis postulating that the habitats sound-dependent species select and occupy have unique acoustic characteristics that are based on their functional needs and threshold of their sound frequency production and detection	

Table 1 (continued)

Term/Hypothesis	Definition	Source
Acoustic Habitat Specialist[a]	A species whose *acoustic habitat* is significantly distinct and unlike any other acoustic environment and is vital to its functionality in the ecosystem	
Acoustic Habitat Generalist[a]	A species whose *acoustic habitat* is not significantly distinct from other acoustic environments but remains important to its functionality in the ecosystem	

[a] Term/hypothesis introduced in this article

Finally, we have asserted that rigorous experimentation and investigation of the *Acoustic Habitat Hypothesis* can be useful in the conservation of threatened and endangered species.

Although, we have focused our examples on terrestrial systems, we recognize that a considerable amount of work relevant to this subject has been done in marine environments. We postulate that the concepts of the *Acoustic Habitat Hypothesis* can undoubtedly be extended to marine systems as well (see Richardson et al. 1999; Lillis et al. 2013; Monaco et al. 2016). We encourage others that have a better understanding of these systems to investigate the literature and conduct independent research to test the *Acoustic Habitat Hypothesis* in these environments.

In conclusion, the *Acoustic Habitat Hypothesis* combines what is already known about the relationships between sound-dependent animals and the soundscape and places that knowledge into a more unified theory and with a holistic approach to explain animal behavior and ecological interactions. The *Acoustic Habitat Hypothesis* completes the *eco-field* concept which creates an important bridge between biosemiotics and the ecology of populations and communities. Pragmatic investigations of the *Acoustic Habitat Hypothesis* will certainly lead to a deeper understanding of the natural world and initiate more critical thinking and analysis on species-habitat relationships, in addition to having great potential in the efficacy of conservation practices. This can be achieved by adopting the theoretical foundations, methodologies, and tools established in the fields of biosemiotics and *ecoacoustics*.

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