

What is soundscape ecology? An introduction and overview of an emerging new science

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Abstract We summarize the foundational elements of a new area of research we call soundscape ecology. The study of sound in landscapes is based on an understanding of how sound, from various sources—biological, geophysical and anthropogenic—can be used to understand coupled natural-human dynamics across different spatial and temporal scales. Useful terms, such as soundscapes, biophony, geophony and anthrophony, are introduced and defined. The intellectual foundations of soundscape ecology are described—those of spatial ecology, bioacoustics, urban environmental acoustics and acoustic ecology. We argue that soundscape ecology differs from the humanities driven focus of acoustic ecology although soundscape ecology will likely need its rich vocabulary and conservation ethic. An integrative

framework is presented that describes how climate, land transformations, biodiversity patterns, timing of life history events and human activities create the dynamic soundscape. We also summarize what is currently known about factors that control temporal soundscape dynamics and variability across spatial gradients. Several different phonic interactions (e.g., how anthrophony affects biophony) are also described. Soundscape ecology tools that will be needed are also discussed along with the several ways in which soundscapes need to be managed. This summary article helps frame the other more application-oriented papers that appear in this special issue.

Keywords Soundscape ecology · Landscape ecology · Bioacoustics · Soundscape conservation · Acoustic ecology · Biophony · Geophony · Anthrophony · Land use change · Climate change

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Introduction

Sounds that emanate from the landscape vary spatially and temporally. Forests, grasslands and wetlands support a diverse array of sounds produced by mammals, birds, amphibians, and insects (Marler and Slabberkoorn 2004). The urban landscape is filled with sounds generated by vehicles, sirens, machines and other human-produced sounds (Botteldooren et al.

2004; Raimbault and Dubois 2005). Geophysical motion of the atmosphere and water create natural sounds, such as those of gushing rivers flowing over the terrain, or rain falling through a canopy (Swanson et al. 1988). The integration of all of these sounds across the landscape creates the “soundscape” (Pijanowski et al. 2011).

In this paper, we provide an introduction and overview of a new field of science we call soundscape ecology—the focus of this special issue of *Landscape Ecology*. First, we present useful terms and describe the history of the term “soundscapes” as it has been used by different disciplines. A review of the intellectual roots of this new field is given. We then present an integrative framework of the underlying causes of soundscape dynamics, with a focus on the drivers of global and regional environmental change (*sensu* Turner et al. 1990). We discuss the tools that we believe will be necessary for soundscape ecology to advance. Finally, we summarize several important considerations that are necessary for the conservation of soundscapes.

Soundscape ecology—a lexicon

Several disciplines have used the term “soundscape”. The etymology of the term “-scape” is reference to an “area, scene, space or view” (Zonneveld and Forman 1990). “Soundscape” is thus “sounds occurring over an area”. The first use of the term was by Southworth (1969), an urban planner who used “soundscape” to

refer to the acoustic properties of cities that help people relate to certain spaces. Southworth tested how blind people used sounds to form a “sonic identity” of unique areas in Boston. Schafer (1977), in his seminal book “Tuning of the World”, formalized the term “soundscape” (Coates 2005) as the “auditory properties of landscapes” (see also Truax 1999). A musician by training, Schafer was concerned about noise pollution and the lack of awareness humans have of their acoustic surroundings. Urban acousticians (e.g., Raimbault and Dubois 2005; Dubois et al. 2006) have used “soundscapes” as a neutral term, to avoid the word noise, in describing the “structuring of categorical space of sounds in cities”.

Our working definition of soundscapes is “the collection of biological, geophysical and anthropogenic sounds that emanate from a landscape and which vary over space and time reflecting important ecosystem processes and human activities” (Pijanowski et al. 2011; see Table 1 for a list of various definitions of the term soundscape). We emphasize the diversity of sound sources, those that are biological, which we call biophony, after Krause (1987), anthrophony (human produced sounds) and geophony (geophysically created sounds) that occur in a landscape (see also Kull 2006). Biophony is the collection of sounds produced by all organisms at a location over a specified time. Geophony are those sounds originating from the geophysical environment, which includes wind, water, thunder, movement of earth, etc. Anthrophony is produced by stationary (e.g., air conditioning units) and moving (e.g., vehicles) human-made objects. We

Table 1 Definitions of soundscapes used in the literature

R. M. Schafer (1994): “the soundscape is any acoustic field of study... We can isolate an acoustic environment as a field of study just as we can study the characteristics of a given landscape. However, it is less easy to formulate an exact impression of a soundscape than of a landscape” (p. 7). The soundscape can be any defined acoustic environment
B. Krause (1987, 2002): all of the sounds (biophony, geophony and anthrophony) present in an environment at a given time, soundscape as a finite resource- competing for spectral space (niche hypothesis)
A. Farina (2006): the collection of sounds associated with a given landscape as perceived by organisms (eco-field hypothesis)
National Park Service (2006): on natural soundscapes: “Park natural soundscape resources encompass all the natural sounds that occur in parks, including the physical capacity for transmitting those natural sounds and the interrelationships among park natural sounds of different frequencies and volumes. Natural sounds occur within and beyond the range of sounds that humans can perceive, and they can be transmitted through air, water, or solid materials” (p. 56)
(Pijanowski et al. 2011): complex arrangement of sounds from multiple sources including biophony, geophony and anthrophony that creates acoustical patterns in space and time

posit that sound reflects natural *and* human activities and thus serves as an excellent “universal” variable to consider in any study of a coupled natural-human system (Liu et al. 2007).

Intellectual roots of soundscape ecology

Soundscape ecology shares many parallels with landscape ecology and biogeography (Fig. 1a). Landscape ecology centers on the relationship between spatial pattern and corresponding ecological processes (Forman and Godron 1981; Urban et al. 1987; Turner 1989; Turner and Gardner 1991; Wiens 1992; Turner et al. 2001; Farina 2006). The interaction of pattern and process is generally studied at multiple spatial scales with outcomes directed toward natural resource management or decision making. Land use change (Turner 1987; Hobbs 1993; Dale et al. 1994; Pickett and Cadenasso 1995), and more recently, climate change (Wascher and Opdam 2004; Vos et al. 2008) are frequently studied as major disturbances of the landscape. Soundscapes reflect many ecological processes and are ecological patterns in themselves (Matsinos et al. 2008). Comparison of soundscapes can also occur across large spatial scales and thus soundscape ecology could build from the knowledge generated in the field of biogeography. Biogeographers (cf. Lomolino et al.

2004) have long studied how species distributions and diversity patterns vary across distinct biophysical gradients, such as those found along altitudinal, latitudinal and biogeochemical gradients. Biogeography also considers evolutionary factors that are behavioural (Lomolino et al. 2004). Thus, we believe that landscape ecology and biogeography are fields which will help support integrative soundscape ecology research.

A more comprehensive study of soundscapes should build from several other disciplines including urban environmental acoustics, bioacoustics, and acoustic ecology (Fig. 1). Urban environmental acoustics (Fig. 1b) is the study of “the aggregate of sounds that are interwoven with the built environment” and that “emerge naturally due to the typical activities that take place in the public area” (Hartmann 1997; Botteldooren et al. 2004). Because the acoustic properties of urban areas affect the quality of life of its residents, urban soundscape research has often been extended to include urban planning (Carles et al. 1999; Ouis 2001; Raimbault and Dubois 2005; Adams et al. 2006; Guastavino 2006; Raimbault 2006). Modelling of sound propagation from noisy human-made objects and the development of noise mitigation techniques has been the focus of considerable research by transportation experts who study urban sounds (e.g., Staples 1996; De Coensel et al. 2005; De Coensel and

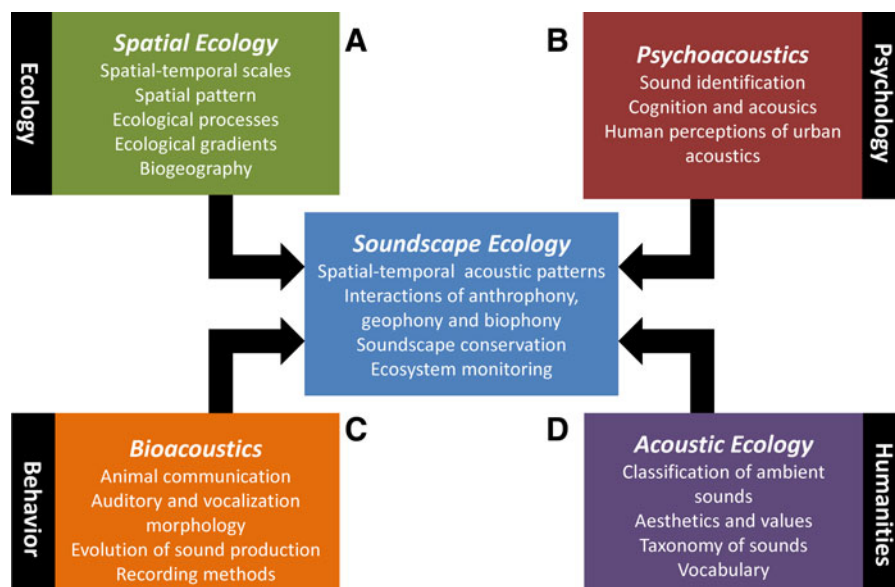


Fig. 1 Intellectual foundations of soundscape ecology. Colors of the boxes are used for the online version to indicate which discipline contributes to the integrative framework contained in Fig. 2

Botteldooren 2006, 2007). Urban environmental acoustic studies also include subjective assessments of different urban sounds, determining how humans perceive and value common urban sounds (e.g., Yang and Kang 2005; Dubois et al. 2006; Lavandier 2006; Jeon et al. 2010). Further research on the role of the built-environment, the patterns of anthrophony, the physics of sound propagation in the environment as well as the role that sound plays in shaping human perceptions of cities (Garrioch 2003), will be necessary as we attempt to understand the role that humans have on soundscape composition.

Bioacoustics (Fig. 1c) has a rich history (for excellent summaries, see Kroodsma et al. 1982; Bradybury et al. 1998; Marler and Slabberkoom 2004; or Fletcher 2007). **Its interdisciplinary focus integrates animal behaviour** (Marten and Marler 1977; Marten et al. 1977; Grafe 1996; Wollerman 1999; Kroodsma and Haver 2005; Barber and Conner 1997), **mechanisms of sound production by animals** (e.g., Walker 1962; Armstrong 1963; Walker 1975), **evolutionary foundations** (e.g., Morton 1975; Greenfield 1994; Mitani and Stuht 1998), **communication and habitat features** (e.g., Ryan and Brenowitz 1985; Boncoraglio and Saino 2007; Barker 2008), **animal physiology and anatomy** (e.g., Greenewalt 1968; Walker 1969; Webster et al. 1992), **and timing of vocalizations** (Allen 1913; Saunders 1947, 1948; Kacelink and Krebs 1982; Cuthill and MacDonald 1990; Hutchinson 2002; Berg et al. 2006; Hardouin et al. 2008), among others. Limited research has been conducted in freshwater systems (Wysocki et al. 2007; Qi et al. 2008; Amoser and Ladich 2010). **Considerable research, however, has been conducted in ocean systems, especially in the area of marine mammal communication and human noise production** (e.g., Payne and Webb 1971; Charif et al. 2001; Croll et al. 2001; Vasconcelos et al. 2007; Amoser and Ladich 2010). In general however, bioacoustics has focused primarily on individual species.

Acoustic ecology (Fig. 1d) also brings to soundscape ecology a rich vocabulary that can assist ecologists in thinking about soundscapes. For example, Schafer (1977), Truax (1978, 1987), and Guastavino (2007), introduced useful terms and taxonomies to describe various types of sounds and soundscapes. **Schafer used the terms “keynotes”, “soundmarks” and “sound signals” to describe background sounds, location specific sounds and foreground sounds, respectively, of landscapes.** The keynote of a natural soundscape is often

wind, whereas in cities it is dominated by traffic. Soundmarks might be spring the chorusing of peepers in Midwestern USA wetlands or the ringing of church bells in small towns in Europe. Soundscapes that contain a large degree of acoustic frequency diversity are referred to as “hi-fi”; these sounds can be heard clearly and are not masked or crowded. In “lo-fi” soundscapes, one frequency spectrum (often low frequencies such as in urban environments) dominates and distant sounds cannot be discerned. Wrightson (2000) describes hi-fi soundscapes as those possessing “acoustic colorization”, meaning that audible sounds bounce, are absorbed, and echo off of the natural features of a landscape so that acoustic size (i.e., sound intensity) and distance from the sound emitter can be interpreted by the listener. Finally, acoustic ecologists encouraged people to take “soundwalks” and be “earwitnesses” in the hope that people would increase the awareness of their acoustic surroundings.

The field of acoustic ecology, as envisioned by Schafer (1977) and Truax (1978), provides several important humanities-based perspectives useful to soundscape ecologists. The term “soundscape ecology” defined by Truax (1978) as the “study of the effects of the acoustic environment on the physical responses or behavior of those living in it.” (p. 127). It was used interchangeably with the term “acoustic ecology” (p. 2). However, the field of study referred to by Truax and Schafer is not ecological in a true sense but rather a study of natural sounds and how people respond and value these properties of the environment. A major contribution that Schafer made was that he emphasized the need to allow nature to create its natural sounds, posing the question “is the soundscape of the world an indeterminate composition over which we have no control, or are *we* its composers and performers, responsible for giving it form and beauty?”. The label of “acoustic ecology” seems appropriate too for the humanities-focussed inquiry as a major synthesizing activity of this group was the support of research and initiatives organized under the auspices of the World Forum for Acoustic Ecology (www.wfae.org).

Underlying processes of soundscape dynamics: an integrative framework

Landscapes are dynamic systems perturbed by natural and anthropogenic factors (Forman and Godron 1981;

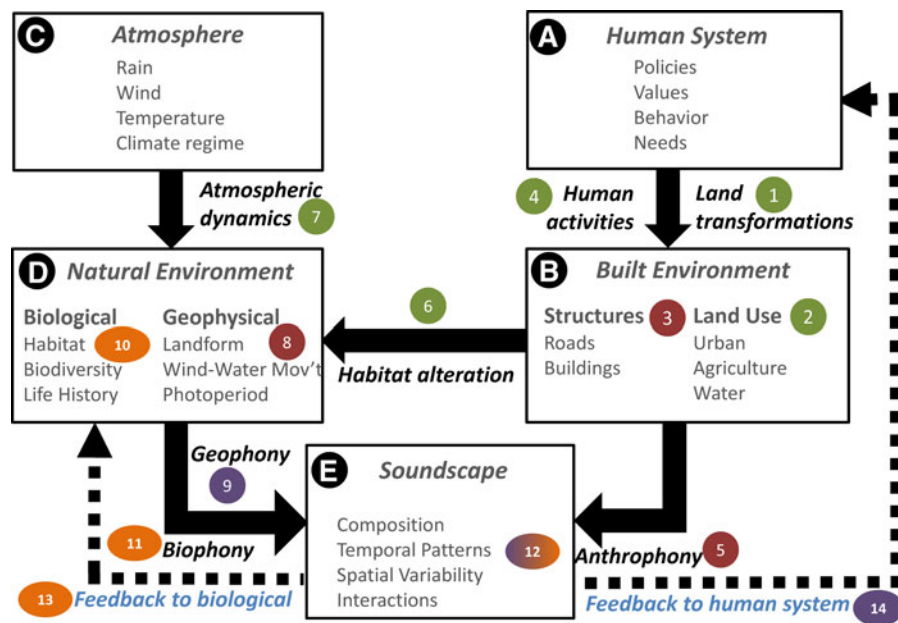


Fig. 2 Conceptual framework describing the underlying processes of the soundscape. Labels and color coding are used for the online version to tie the information presented in Fig. 1

Urban et al. 1987; Turner 1989). A variety of these dynamics relate to sound production. An integrative framework of soundscapes is presented in Fig. 2 that describes how natural and human driven factors influence underlying ecological and social acoustic patterns. We should emphasize that this integrative framework is not exhaustive; our purpose here is to demonstrate how a variety of global environmental change factors influence sound dynamics in landscapes.

Within the human system (component A), human needs, values, policies and behaviors lead to land transformations (label #1) in the form of land use patterns (label #2). The built environment (component B) is composed of artificial structures and surfaces (label #3) used for shelter and for transportation which shape human activity patterns (label #4). These human activities give rise to the spatial and temporal patterns of human generated sound or anthrophony (label #5). The built environment alters natural habitat structure (label #6) which is considered the greatest threat to biodiversity over the next century (Chapin et al. 2000). The atmosphere (component C) is highly dynamic, creating rain and air movement patterns (label #7) that, upon interactions with the geophysical features (label #8) of the natural environment (component D), give

rise to sounds derived by water and wind (label #9). Climate patterns influence plant community structure (Gaston 2000; Parmesan 2006) which in turn influences diversity patterns of animals (label #10). Changing climate could also alter geophony patterns; even the increase in frequency of extreme events (e.g., thunder, high precipitation periods) could interfere with animal communication. Biophony (label #11) created from these biodiversity patterns (label #10) and the timing of life history events (label #10) interact with sound inputs from the geophysical (label #9) and built environment (label #5) interface to create the soundscape.

A soundscape (component E) possesses four (label #12) measureable properties which are explored further in “[Soundscape dynamics](#)” section: acoustic composition, temporal patterns, spatial variability, and acoustic interactions. Composition is the acoustic frequency (subjectively what humans perceive as pitch) and amplitude (sound level) of all sounds occurring at the same time and location (“[Acoustic frequency patterns](#)” section). Temporal patterns are numerous and reflect certain biological events (e.g., breeding) that occur in the landscape (“[Temporal patterns in soundscapes: rhythms of nature](#)” section). Spatial variability results from the heterogeneity of the

biophysical landscape (“[Spatial dimensions of soundscapes](#)” section). Finally, a large array of natural and human-induced interactions occurs between biophony, geophony, and anthrophony to create the integrated soundscape (“[Phonic interactions](#)” section).

Soundscape dynamics feedback to natural and human systems (Fig. 2). For example, the interactions between species and their competition for acoustic space (Greenfield 1994) influences mate selection and predator prey interactions (Barber et al. 2010), and thus have the potential to affect population and community dynamics (label #13). Soundscapes affect a variety of human social components (label #14) including human health (e.g., Stansfeld and Matheson 2003), natural resource management of common spaces (Dumyahn and Pijanowski, in review b) and their sense of place (Dumyahn and Pijanowski, in review a).

Recording and measuring a soundscape

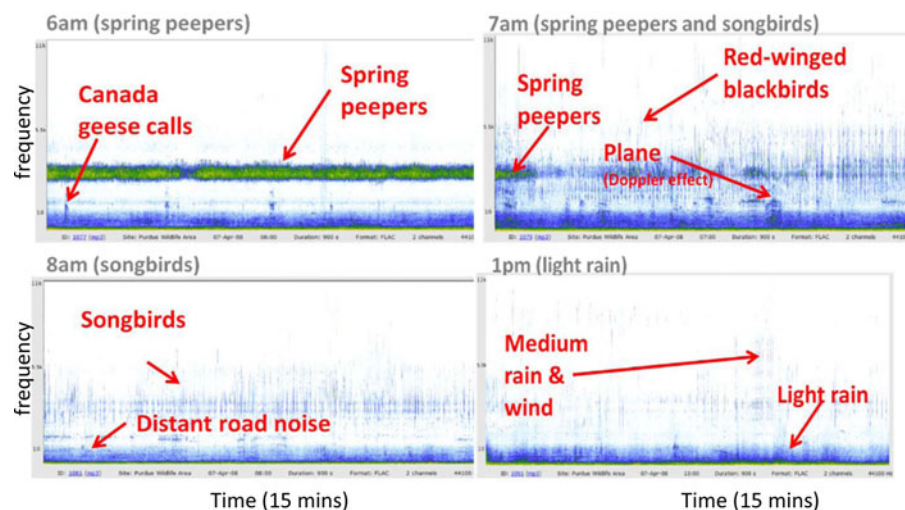
Krause (2002) summarized in detail many different ways to record natural soundscapes. The paper by Villanueva-River et al. (in review) serves as an introduction to sound for ecologists and details about the physical properties of sound, the ways that sound is recorded, stored and analysed can be found there.

There are a variety of tools and techniques for processing and analyzing digital sound files. One familiar visual acoustic tool used by ornithologists is the spectrogram (Stephens and Bate 1966). Spectrograms display acoustic frequencies along the y-axis,

time on the x-axis and colors are used to denote intensity. A series of recordings in a central Indiana wetland illustrate the usefulness of the spectrogram (Fig. 3). Note that at 6 am, spring peepers chorus constantly with Canada geese calling occasionally. At 7 am, songbirds begin their dawn chorus, spring peepers chorus but not as intensely and a plane flies over the wetland about 10 min into the 15-min recording. At 8 am, distant road noise is present and songbirds sing less intensely. A mid-afternoon rain shower creates several geophonic sounds.

There are a variety of ways to analyze a spectrogram (see Chap. 3 in Bradybury et al. 1998 for an excellent introduction to spectrogram analysis). Pijanowski et al. (2011) parsed acoustic frequencies into bands, and then measured the amount of sound occurring above an intensity threshold. Using 10 acoustic frequency bands, measures of acoustic diversity, evenness and dominance were calculated and plotted over time for seven locations differing in land use. They found that (1) dawn and dusk chorus were prominent in natural landscapes exhibiting the diversity of acoustic signals; (2) seasonal patterns were evident where high frequencies are most dominant frequencies in late summer; and (3) acoustic frequency evenness is lowest in human dominated landscapes. In addition, researchers could measure the total acoustic frequency breadth and average intensity. Villanueva-Rivera et al. (in review) were able to discretize a spectrogram into small parts and then input these data into a GIS and calculate sound patch statistics (size, shape). They found that forested

Fig. 3 Spectrograms for 15-min recordings from a wetland in central Indiana. Recordings were made on April 8, 2008 and acoustic sensor set to start at the top of every hour. Readers can listen to these recordings and view interactive spectrograms at http://www.purdue.edu/soundscapes/landscape_ecology



landscapes contain the greatest diversity of sound signals, followed by urban landscapes.

Soundscape dynamics

To address questions in soundscape ecology (Table 2), we must measure soundscapes in a variety of ways: acoustically, temporally and spatially. We describe approaches to each in this section.

Acoustic frequency patterns

Organisms produce a broad spectrum of sounds, and their composition has several suspected ecological causes. Krause (1987) proposed the Acoustic Niche Hypothesis (ANH) which predicts that competitive exclusion will cause species to adjust their signals to minimize interference from sounds produced by other species. Similar arguments have been made by other bioacousticians. For example, Endler (1992, 1993) and Greenfield (1994) emphasized reproductive importance in acoustic signalling and argued that sounds should evolve to maximize effectiveness of intraspecific communication; therefore the timing, frequency and spatial location of sound production should be adapted to reduce acoustic interference from other species. Acoustic partitioning has been demonstrated in crickets (Walker 1974; Otte 1992; Sueur 2002), birds (Ficken et al. 1974; Seddon and Tobias 2007), and anurans (Grafe 1996; Feng and Schul 2006).

Considerable research has also focussed on the acoustic adaptation hypothesis, which predicts that species should evolve the structure of their calls or songs so that it maximizes transmission fidelity (Forrest 1994). Several researchers (e.g., Morton 1975; Richards and Wiley 1980; Brown et al. 1995) have found that bird songs differ according to the habitat where the signaller lives. However, one large comparative study of 121 species of Australian birds (e.g., Blumstein and Turner 2005) showed only modest support for the acoustic adaptation hypothesis; the researchers suggest that factors such as visual cues, are important to communication in birds and decrease selective pressure on acoustic modification to optimize transmission. A second large comparative study by Boncoraglio and Saino (2007) found weak associations of maximum, minimum, peak frequency

and frequency range with habitat type for 26 studies on bird song and habitat structure.

There are several important implications to acoustic niche hypothesis and acoustic adaptation hypothesis which influence our interpretation of sound in landscapes. First, the **soundscape of a habitat that has been present long enough to provide its native species sufficient time to optimize their vocalizations, should exhibit much more spectral-temporal complexity and signal diversity than a habitat that has been recently disturbed or altered by human activity** (Gage et al. 2001; Krause 2002). Second, the **acoustic niche hypothesis also implies that species removed from an “acoustically optimized” habitat should leave readily detectable acoustic gaps which could serve as a “warning system” that the ecosystem is being altered in a significant way** (*sensu* Sueur et al. 2008a, b; see also Riede 1993). Finally, acoustic adaptation hypothesis predicts that not all frequencies and sound structures (e.g., modulation patterns) should be present in all habitats.

Temporal patterns in soundscapes: rhythms of nature

There are many recognized temporal cycles of communication in animals; the most well studied are those of birds, amphibians and insects. These temporal patterns will reflect the timing of life histories of animals that live in these habitats. Birds are known to start singing each spring (Saunders 1947) in the mid to high latitudes. Birds also have their most intense singing sessions early in the morning and at dusk (Saunders 1948; Leopold and Eynon 1961; Brown and Handford 2000). Several hypotheses have been proposed (see Kacelink and Krebs 1982 for review) that attempt to describe the underlying mechanisms of the dawn chorus in birds; the dusk chorus is likely under different controls (Hardouin et al. 2008). In mid-latitude locations in the spring, biophony may be composed of birds from local breeding populations and as migrants, so biophony might be greatest in the spring. There are also many birds that call at night, such as whippoorwills and owls, thus monitoring of biophony patterns during an entire day may help assess impacts of environmental change on nocturnal animals as well.

The most common acoustic insects are crickets, katydids, grasshoppers and cicadas. For example,

Table 2 Sample research questions for soundscape ecology organized into the four categories discussed in “**Soundscape dynamics**” section

Dimension	Natural dynamics	Human impacts
Frequency patterns (6.1)	How common is acoustic niche partitioning? Is acoustic niche separation more important in the tropics where species richness is greatest? How can we measure acoustic niches?	How does habitat alteration by humans impact acoustic partitioning? As climate will re-order species at the local scale, how will that affect acoustic niches? Are empty acoustic niches a sign of disturbance?
Temporal patterns (6.2)	What are characteristic of dawn and dusk choruses? How do these vary across different habitats? With latitude? Over a season? What are the natural seasonal patterns of biophony?	How do human activities affect dawn and dusk choruses via habitat alteration and/or introduction of anthrophony? How does climate change alter the timing and composition of the dawn and dusk chorus? How does climate change alter timing of biophony patterns?
Vegetation/land use gradient (6.3)	How does biophony and geophony vary with the complexity of vegetation structure? Is biophony greatest in areas with the tallest canopies? Does vegetation strata correlate with biophony?	How does biophony, geophony and anthrophony vary across a gradient of human disturbance like land use? In what ways does anthrophony alter biophony in urban, agricultural and other human dominated systems? What is the effect of topographic features on the distribution of anthrophony? How can land use planning be improved to increase biophony and decrease anthrophony?
Altitudinal gradients (6.3)	How does biophony and geophony vary across the altitudinal gradient? Is there any evidence for shifts in the composition of soundscapes with isoclines that occur along elevational gradients? Are soundscape patterns the same in tropical mountains versus mountains in mid- and high-latitudes?	Given that species altitudinal ranges are smaller in tropical mountain areas, how do human sounds (e.g., roads) along altitudinal gradients affect animal communication?
Core–edge habitat gradients (6.3)	How does biophony vary across edges? How does biophony vary across sharp versus soft edges? How far into the core does wind-generated geophony decrease? How does biophony vary over time at an edge compared to the core?	How does the composition of biophony, geophony and anthrophony differ in interior habitats versus those along edges? How does the composition of the soundscape vary from center to edge of a patch? How does habitat fragmentation affect soundscapes across the landscape?
Flow gradients (6.3)	How variable are river acoustic fluxes? How does river morphology (channel structure) impact geophonies? How do animals adjust their sound production along rivers during low flow, moderate flow and peak flow periods?	How might changes in land use in a river basin affect stream flow, geophony and then biophony? How might climate change impact river geophonies in ways that negatively impact animal communication?
Latitudinal gradients (6.3)	How does the dawn and dusk chorus vary with latitude? What are the consistent elements of the dawn and dusk chorus across all latitudes? Do certain taxonomic groups (e.g., insects) become more prominent as one moves northward? How does the dawn and dusk chorus intensity vary with latitude? In very high latitudes, how does the dawn and dusk chorus “play out” during the summer solstice?	Are there certain latitudes that are most sensitive to human generated noise? Are there times of the year where, at a given latitude, that anthrophony needs to be controlled?
Soundscapes as information resources (6.4)	How do animals use biophony and geophony to navigate through a landscape? What types of sounds are used to identify spatial distribution of resources? How do organisms use sound with visual cues to locate these resources?	How does noise impact the ability of animals to find food, shelter, etc.? Are landscapes where animals use sound exclusively to navigate through the landscape being damaged by anthrophony?

stridulations from crickets are composed of pulses and chirps, which are produced at very short intervals. Crickets are well known for having chirp rates

that are strongly influenced by temperature (Walker 1962). Many insects call during the day (cicadas), at night (crickets), or both (some cicadas) and so exhibit

diurnal patterns. Cycles can be seasonal; the timing of species occurrence during the year relates to the life cycle of an insect (e.g., Williams and Simon 1995).

Anurans can be very dominant participants in many soundscapes as well. Vocalizations in frogs and toads are performed by males who are attracting females (Gerhardt 1994). The calling schedules of many anurans are well known (De Sollar et al. 2006). In the Midwestern USA, some species start mating calls as early as February of each year while other species do not start until late summer.

The life history of organisms that produce sound throughout the year exhibit several distinct temporal patterns and these have been referred to as “rhythms of nature” (Pijanowski et al. 2011). Diurnal patterns (Fig. 4a), such as the “dawn chorus” (Gwinner and Brandstätter 2001), which is characteristic of the increased intensity of bird songs in the morning, and the “dusk chorus” where anurans, insects and other nocturnal organisms sing, are common. Seasonal

patterns (Fig. 4b) are likely to occur as well (Truax 1978), reflected in life history patterns such as breeding and territoriality in many vertebrates (Gwinner and Brandstätter 2001). We also extend the conceptual model to include long-term dynamics across several years. As local climate patterns alter temperature, shifts in the timing of these life history events may occur and several responses are possible. Parmesan (2006) reviewed numerous reports of phenological shifts that have occurred over the last several decades as a result of global warming, and concluded that many organisms, especially amphibians, were highly impacted by increased temperature. Gibbs and Briesch (2001) reported a two week advance on calling phenology from the 1–2.3°C increase in temperature during the chorusing months. Advances in breeding of birds have also been reported (Brown et al. 1999; Collins and Storfer 2003). Thus, climate change can alter soundscapes positively (increasing), or negatively (decreasing).

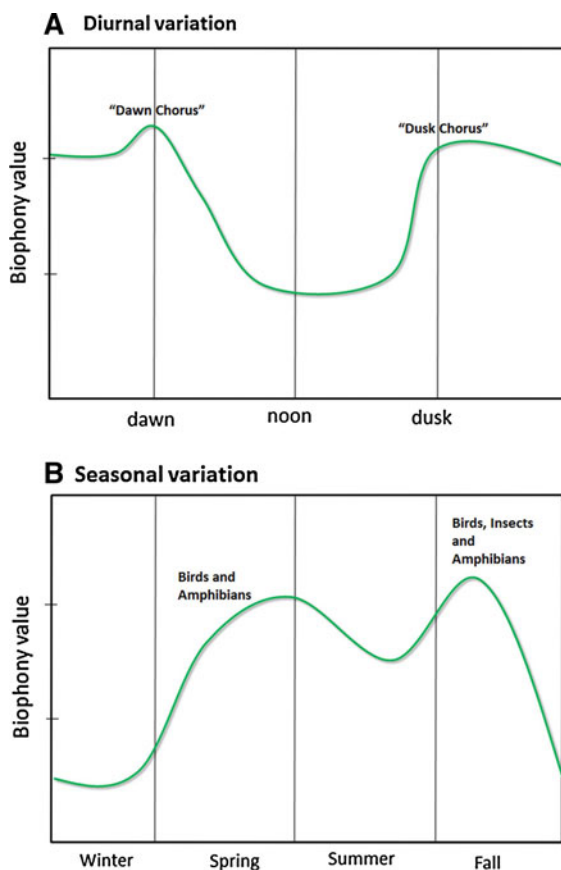


Fig. 4 Conceptual models of how biophony varies over different temporal scales (stylized after Truax 1978)

Spatial dimensions of soundscapes

We anticipate that biophony, geophony, and anthrophony will vary spatially and will co-vary predictably with certain ecological and human disturbance gradients. Some researchers suggest that there are only a few broad-scale factors that influence biodiversity patterns globally (Gaston 2000; Wiens and Donoghue 2004). We review several that are common to ecological studies, including human land use/habitat structure, altitudinal, flow, edge-to-core patch, and latitudinal gradients. We briefly examine the ecological and acoustic literature that support biodiversity and life history patterns that would give rise to certain soundscape patterns and provide simple conceptual models for how these might vary over the gradient.

Human disturbance gradients

Land use change is a significant stressor on ecosystems (Lambin and Giest 2006), especially as these changes alter biodiversity (Chapin et al. 2000). Land transformations are significant. Globally, over 40% of the land surface is now used for agriculture or urban (Foley et al. 2005). There is considerable evidence to suggest that vegetation structure influences species richness which we expect will also be manifested in its influence on biophony. MacArthur and MacArthur

(1961) and MacArthur (1964) posited that faunal diversity increases with increasing vertical stratification of vegetation in an area, the simplest being canopy height, and demonstrated that the vegetation structure in the vertical dimension correlated well with avian diversity in several areas of the world. Many studies on birds corroborate MacArthur's observation (e.g., Karr and Roth 1971; Rotenberry and Wiens 1980; James and Wamer 1982; Blake and Blake 1992). Siemann et al. (1998) conducted an experimental study and found that insect species diversity increased with increasing diversity of plant species. Across different land uses, vegetation structure is more complex in temperate and tropical forests, followed next by wetlands and then urban areas (Fig. 5) and thus biophony is likely to decrease with increasing human use of the landscape.

Anthrophony is likely to vary across land uses (Fig. 5). In human dominated environments, such as urban areas, anthropogenic sounds will dominate the soundscape (Matsinos et al. 2008). We also assume that as human activities increase so will anthrophony. Overall, anthrophony in urban environments will be composed of sound from vehicles (motors and road noise), another machines associated with structures (e.g., air conditioners). Areas with many land uses (e.g., forests, agriculture) are likely to contain a mixture of sound sources.

Geophony is also likely to vary across different land use classes (Fig. 5). For example, wind rustling through vegetation will be different in forests compared to that in wetlands or farmland with crops or pasture. Rain sounds

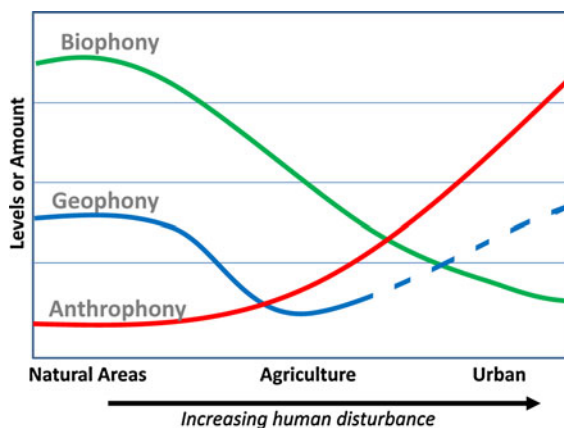


Fig. 5 Conceptual model of variations in soundscape elements across a human disturbance intensity gradient. *Dashed line* represents one possible pattern that could exist

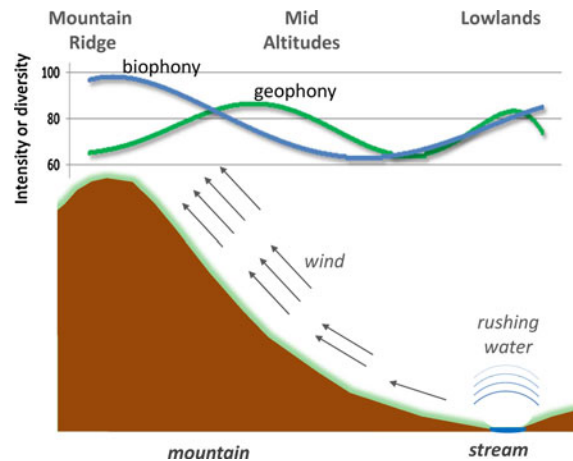


Fig. 6 Altitudinal gradients with patterns of biophony and geophony

different in areas that have a canopy (i.e., forests) compared to areas lacking vegetation, such as urban areas where rain sound is amplified by hitting concrete and other human made structures.

Altitudinal

Biogeographers (cf. Lomolino et al. 2004) have studied biodiversity patterns along elevational gradients for decades in order to determine how biophysical gradients influence biodiversity patterns. We anticipate that the composition of the soundscape would vary naturally across altitudinal gradients, similar to those observed of biodiversity patterns (Fig. 6). Most studies have shown that species richness is greatest at mid-altitudes (for a review, see Lomolino 2001; Brown 2001; although see Terborgh 1977); however, species richness in the lowlands could also be high as streams provide ample habitat and food for animals (Heaney 2001). Atmospheric scientists have identified patterns of wind (and in some cases precipitation, Garcia-Martino et al. 1996) that occur along altitudinal gradients as well showing that wind increases with increasing elevation. Indeed, studying biophony and anthrophony patterns along mountain sides could help elucidate important ecosystem factors impacted by climate change.

Flow gradients

Rivers are dynamic systems that channel water across landscapes. When rivers contain considerable

volumes of water, after a heavy rain event, the sounds from these rivers can be substantial (Amoser and Ladich 2010). Ficken et al. (1974) report that whistles are more common among birds that sing along streams; whistles can penetrate noise created by rivers more effectively than buzzes or trills. At low flow, sounds from the river may not mask sound production by animals; however, as flows increase, the level of ambient noise from the rivers also increases eventually masking any biophony that is produced by animals. As local and regional climates change however, the soundscape flow gradients could change as well, thus potentially having a negative effect on fragile life history behaviors like mate attraction and breeding performance of certain species.

Habitat interior-edge gradients

Leopold (1933), McIntyre (1995), and other ecologists, have long studied how animal species are distributed across gradients related to the distance from the edge of a natural habitat. Ries et al. (2004) reviewed the abundant literature on edge ecology and found that some animals are attracted to forest edges, leading to greater abundance of some species such as birds and mammals, and greater species richness of birds, mammals and plants in some cases. On the other hand, some studies (e.g., on reptiles and amphibians) reported a decrease in abundance of individuals of a species or decreased species richness (a negative effect). Thus, the edge of a natural habitat is likely to be composed of different vocalizing animals, possibly harbouring more vocal species. The biophony along edges is likely to be different than that at the core of the habitat. Lovejoy et al. (1986), Miller et al. (1991), Laurance (2004), Laurance et al. (2007) and others have studied forest-climate interactions along forest edges and have found that edges contain increased wind speed, turbulence and vorticity compared to forest interiors and that undisturbed forest interiors have little wind. Therefore, geophony along an edge should differ from the core. As land use change continues to fragment the landscape and create more edges, and climate change alters surface wind patterns, the impacts of geophony along edges of habitats and in turn, on biophony, could be considerable.

Latitudinal gradients

Variation of species richness and species distribution patterns at a global scale has been observed since von Humboldt. Latitude, through annual temperature and radiation budgets, is likely to control both biodiversity and life history schedules which will in turn influence soundscape patterns as one moves from the poles to the higher latitudes (Hillebrand 2004). The number of frost free days and diel radiation patterns differ substantially from the equator to the poles. Thus the timing of the dawn and dusk chorus along with the timing of all life history events (e.g., breeding) varies as one moves from the equator toward the poles.

The high amount of biodiversity at the equator is likely to contribute toward greater soundscape diversity there than compared to higher latitudes (cf. Gaston 2000; Rickelms 2004). This suggests that acoustic niche partitioning should be greatest at the equator. Also, more species should occupy higher acoustic frequencies in the tropics than in the higher latitudes; higher acoustic frequencies are likely to be occupied last because these frequencies require more energy to produce in species (most vertebrates) that use a vocalization organ to produce sounds; these sounds also travel shorter distances than lower frequency sounds.

As the planet continues to warm, one may surmise that the dynamics of soundscapes may also change across this latitudinal gradient. Birds breeding earlier (Both and Visser 2001; Ahola et al. 2004; Parmesan 2006) and amphibians chorusing earlier (Blaustein et al. 2001; Gibbs and Breisch 2001; Beebe 2002; Parmesan 2007) have been documented by examining historical records of the timing of life history events. Thus soundscapes may be altered by climate change through changes in circadian rhythms.

Phonic interactions

There are many possible interactions between biophony, geophony and anthrophony, which we broadly call phonic interactions (Fig. 7). Adjustments can be made by most organisms, either through the modifications of amplitude (Brumm 2004), frequency and/or timing by the signaller. Many aspects of geophony are known to affect biophony (label #1). Frogs, birds and insects often stop producing sound when it is windy or raining heavily (Feng and Schul 2006). The

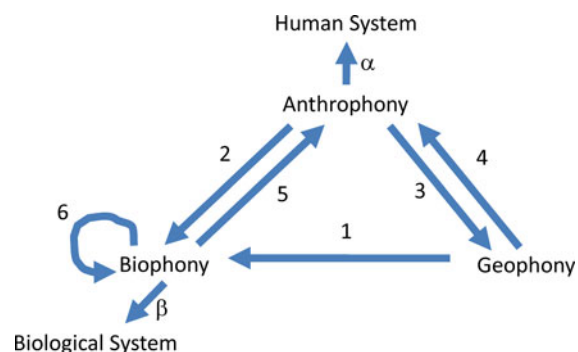


Fig. 7 Interactions between anthrophony, biophony and geophony and how they ultimately impact the biological and human system. See text for complete description of the types of interactions

frequencies of many animal vocalizations, are adapted to be above the background frequencies of low to moderate levels of wind (Greenfield 1994). The timing of chorusing has also been argued to be during times of the day (e.g., dawn and dusk) when wind speeds are the lowest (although see Cuthill and Macdonald 1990; Hutchinson 2002; Berg et al. 2006; Hardouin et al. 2008). All of these responses are active, in that the timing, acoustic frequency and amplitude of calls and vocalizations are adjusted by the signallers (i.e., animals) to increase the propagation of biophonic sounds in the environment.

How human produced sounds affect biophony (label # 2) has recently been well studied (see Warren et al. 2006 for an excellent summary). Some birds adjust the timing of their calls and sing more often at night in urban environments (Katti and Warren 2003; Fuller et al. 2007). Slabbekoorn and Peet (2003), Wood and Yezerinac (2006), Parris and Schneider (2009), among others, have shown that some birds sing at higher frequencies in urban environments. Persi and Pescador (2004) studied population levels of several species of birds in high traffic and low-traffic noise conditions and concluded that 15% of the species were affected by traffic noise. Patricelli and Blickley (2006) and Slabbekoorn and Ripmeester (2008) argue that the increased levels of noise in urban environments selects for songbirds that have more behavioural plasticity, demonstrated by the ability to adjust their calls; thus human-created noise may create micro-evolutionary selection pressures on urban avian communities. Noise from traffic and airplanes has been demonstrated to alter predator–prey relationships where sound is used

by the predator to cue into prey (Barber et al. 2010). Anthrophony has been shown to impact other vertebrates as well. Wollerman (1999) showed that moderate levels of background noise disrupted frogs from finding mates. Anthrophony frequently masks geophony in a landscape (label #3). Many sounds produced by humans are below 1 kHz, the same frequency that low level wind and rain sounds occur. The amount of energy in human-produced sounds is often great and could mask geophonic sounds such as heavy down-pours. Anthrophony is more common during the daylight hours, and thus interference of the soundscape is less likely at night.

Geophony and biophony impact anthrophony (labels #4 and #5) in several indirect ways. Schafer (1977) argued that humanities (especially performing arts) have historically acquired its motivation from the sounds of nature. In this way, some sounds that humans make (a type of anthrophony) are a result of humans listening and interpreting these sounds and incorporating them into music (labelled α).

Interspecies biophonic interactions (label #6) can be positive, with endemic species adapting to different acoustic niches, or negative, as invasive species move in and potentially masks the calls of an endemic animal (Pijanowski et al. 2011). Given that the effector invasive species is one of several important global environmental change processes occurring, the potential for new species to produce sounds that disrupt existing endemic acoustic niches is evident. We consider this interaction as biophonic invasions and people can obviously have a direct role in this by transporting organisms from their endemic location to a new location.

Finally, biophony also feeds back (labelled β) on the rest of the biological system (Fig. 7) as vocalizations/stridulations etc. influence important life history events like mate attraction, territoriality and predator–prey interactions. A rich and diverse biophony likely reflects a healthy ecosystem.

Soundscape as information resources for animals

Ecologists know that animals navigate through landscapes using a variety of senses: visual, acoustic and olfactory (Isard and Gage 2001). Indeed, many landscape ecologists have argued that researchers need to consider “organismal perspectives” (Wiens and Milne 1989) to fully understand the relationship between

organisms and their environment. We believe that the soundscape should be considered as an information medium that allows for many organisms to transform signals from their surroundings into useful information to locate resources. **Acoustic signals across a landscape can act as a template by which organisms navigate through a landscape certain signals serve as “signs” (Farina and Napoletano 2010) containing specific information or “meaning” and feedback on important biological functions** (cf. Rothschild 1962). Burt and Vehrencamp (2005) suggest that some individuals can “eavesdrop”, listening to others vocalize about their surroundings and thus learn about where resources might be located. Likewise, organisms can listen for certain geophonic patterns that could be used to locate food, or specific resources that relate to that habitat. **When an individual has a need (e.g., hunger), immediately a specific function (e.g., searching for food) is activated. This function is linked to a cognitive template (e.g., social calling of foraging by a bird flock). The cognitive template is overlapped to the acoustic spatial configuration perceived in that moment.** Such a configuration, also called an eco-field (Farina and Belgrano 2006), is a signal that when coupled to the specific cognitive template, is transformed into a biosemiotic sign of food location. In this example, mapping a conspecific calling of a flock means an area where there are good possibilities to find food. Acoustic signs are probably especially important in densely vegetated environment, like forests and shrub lands, where visual cues cannot be used efficiently.

Soundscape ecology tools

Landscape ecology has flourished as a discipline because spatial analysis tools, such as geographic information systems (GIS), remote sensing software, and spatial metric software have matured and become relatively user friendly (Turner et al. 2001). Bioacoustics software has also become very powerful in recent years with several no-cost versions of sound processing software readily available for multiple computer platforms. Although soundscape ecology will benefit from the use of existing tools within related ecological disciplines, new tools will be needed that enable researchers to analyze acoustic data from soundscapes (Butler et al. 2006).

Challenges to ecological analysis of soundscapes

High resolution sound files are large. For example, one 30 s monaural acoustic signal recorded at 16 bits at 22 kHz is 2.5 MB. Sampling at ½ h intervals yields 120 MB/day and if there are 10 replicates per habitat the data size is 1.2 GB/day or 36 GB/month. Studies that examine temporal patterns of soundscapes will generate many files and increase the need for sophisticated management tools that can query, extract, process, and integrate (e.g., with meteorological data) large numbers of sound files. Several current soundscape studies have generated hundreds of thousands of files, making their management a challenge.

Placing several acoustic sensors across the landscape presents several other challenges. If researchers are interested in the effects of short-term sound events (e.g., clap of thunder on the chorusing patterns of amphibians), synchronizing all sensors would require specialized features to be built into the sensors (Porter et al. 2005; Collins et al. 2006). As the number of acoustic sensors increases in a study, visiting each recorder to swap out data storage cards and batteries can become impractical. Therefore, wireless sensor networks powered by some form of renewable energy may be needed.

Finally, the cost of microphones and data logging equipment has been prohibitive, thus preventing the collection of recordings for long-term studies on soundscapes. This is rapidly changing as low cost, field-ready microphones and data loggers are now available. Indeed, many of these technical challenges (e.g., need for large data storage) are likely to diminish in the near future as the costs of these technologies (e.g., cost of Terabytes of storage) continue to decrease.

Current bioacoustic analysis tools

Several tools have been developed to assist soundscape ecologists to analyze the soundscape and to facilitate the identification of species in the soundscape. For example, Raven, a software program for the acquisition, visualization, measurement, and analysis of sounds developed by the Cornell Laboratory of Ornithology, is available for use on a variety of computer platforms. Another is SEEWAVE (Sueur et al. 2008a, b), a software tool based on R which

performs several dozen analyses of sound files. Wave surfer is a freeware software package that contains a variety of powerful plug-ins, its use is demonstrated in the Farina et al. paper in this issue.

Advances have also been made in the development of automatic identification of animal sounds. Researchers have successfully employed advanced machine learning and non-linear statistical tools to classify different vocalization or stridulating patterns of insects, birds and mammals (McIlraith and Card 1997; Härmä 2003; Chesmore 2004; Trifa et al. 2008; Baker and Logue 2003; Kasten et al. 2010). One software package that uses these approaches, Song Scope, developed by Wildlife Acoustics Inc., uses built-in statistical classifiers that automatically scan field recordings for patterns matching known training recordings.

Despite the power and ease of use of many bioacoustics current software packages, most are not entirely “soundscape-ready”. Because soundscape ecologists will need to analyze a large number of files (e.g., see Pijanowski et al. 2011 who analyzed over 35,000 files) across landscapes and spanning long periods of time, processing of potentially millions of recordings will require advance scripting capabilities, with interfaces to sophisticated pattern matching and database software.

Mapping soundscapes

Advances are needed that can adequately represent a soundscape in a map. Because the soundscape contains many elements, such as loudness, spectral features, qualitative aspects such as human perceptions of sound, using mapping technologies like Geographic Information Systems (GIS) could help to understand the interaction of sound patterns, the biophysical environment and humans. Work in this area is only now emerging (e.g., Klæboe et al. 2006; Papdimitriou et al. 2009; Pijanowski et al. 2011). Integrating information from other sensors (e.g., wildlife movement, rainfall patterns, temperature profiles, and traffic patterns) is likely to require mapping technologies found in a GIS and lead to advances in understanding spatial–temporal dynamics of the soundscape.

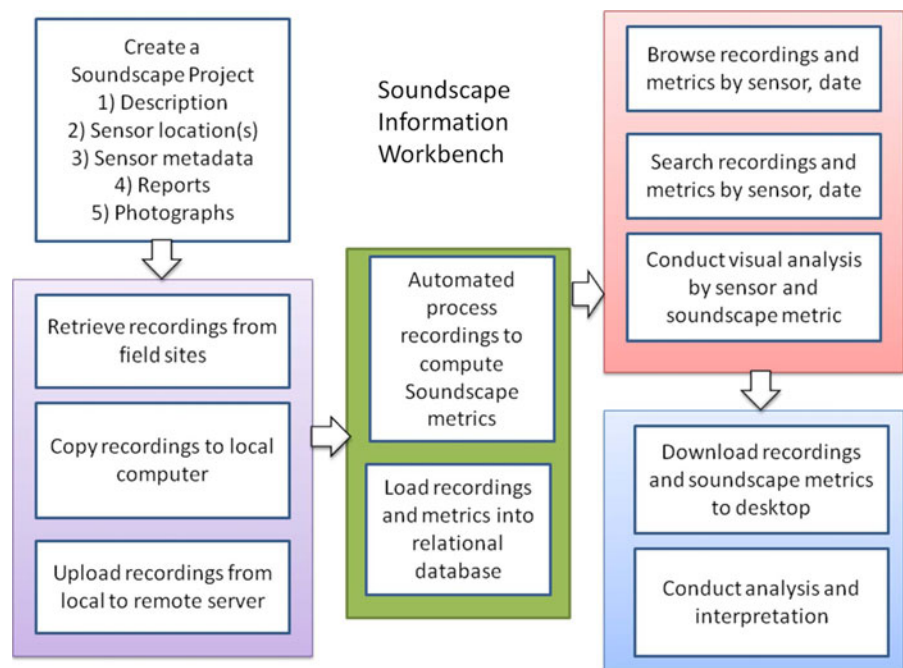
Soundscape information systems

Geographic information systems software has been the hallmark tool of landscape ecologists. GIS helps to manage, integrate, and process spatial data. Soundscape ecologists require a similar set of tools integrated into a Soundscape Information Systems (SIS) (Gage et al. 2004). The SIS needs to feature an end-to-end design, from input of large sets of acoustic recordings through analysis of the recordings including generation of acoustic metrics and pattern searching algorithms (Kasten et al. 2010). **Ideally, a web-based Soundscape Information System is needed to enable a soundscape ecologist to input, archive, retrieve, visualize, listen to, analyze, manage and access raw and processed information based on large collections of audio recordings from automated sensors (Fig. 8).** Early Soundscape Information Systems include Pumilio, a free and open source PHP/MySQL application (<http://pumilio.sourceforge.net>) developed at Purdue University and REAL (<http://real.msu.edu>) developed at Michigan State University. Both are designed to manage large numbers of sound files and allow researchers to query, analyze and listen to files over the web (see also Mason et al. 2008).

Soundscape conservation

Soundscape ecology undertakes a comprehensive research approach linking human and environmental interactions and outcomes (Fig. 1). In this respect, it is well suited for understanding threats to soundscapes and the benefits that “hi-fi” natural and unique soundscapes provide. Previous efforts have focused on the negative approach of noise regulation, but researchers have noted that noise regulations are neither effectively mitigating noise nor limiting the spread of anthrophony (Berglund and Lindvall 1995; Blomberg et al. 2003; Adams et al. 2006). Thus, a new approach is needed that identifies high quality soundscapes as a resource with both benefits and associated values. Once these benefits and values are understood new, more effective, soundscape conservation strategies can be defined and implemented.

Fig. 8 Soundscape Information Systems “workbench” illustrating the major features of an end-to-end acoustic data collection, management, analysis and presentation system



Soundscapes provide ecosystem services to humans in the form of many life-fulfilling functions (Fisher 1998; Dumyahn and Pijanowski, in review a). An important consideration for soundscape conservation is that from these benefits, numerous values are derived. Schafer (1994) likened soundscapes to the acoustic manifestation of place and emphasized the role sounds play in place attachment (Dumyahn and Pijanowski, in review b). Many soundscapes also have cultural, historical, recreational, aesthetic, and therapeutic values. Unique and natural soundscapes can be subtle or powerful links for humans to their environment (Schafer 1994; Torigoe 2003; O’Connor 2008).

Soundscape conservation has the potential to be more effective than noise mitigation (Dumyahn and Pijanowski, in review b), since it accounts for the integrative nature and multiple values of soundscapes. Expanding transportation systems and habitat conversion are homogenizing many soundscapes (Wrightson 2000; Miller 2008). Human dominated land uses are decreasing biodiversity and have caused species extinctions (Vitousek et al. 1997; Chapin et al. 2000), which are reflected in biophony. In light of the multitude of threats, unique and natural soundscapes have been referred to as an endangered resource. Indeed, the increasing loss of natural sounds could be an indication of humans’ weakening

connection with nature (*sensu* Louv 2008). Schafer (1994) argues that we need to improve our relationship with sound and actively listen to soundscapes to truly appreciate them. Doing so will reunite humans with sounds, and also inspire the appreciation, management, and conservation of the organisms and resources that create them.

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