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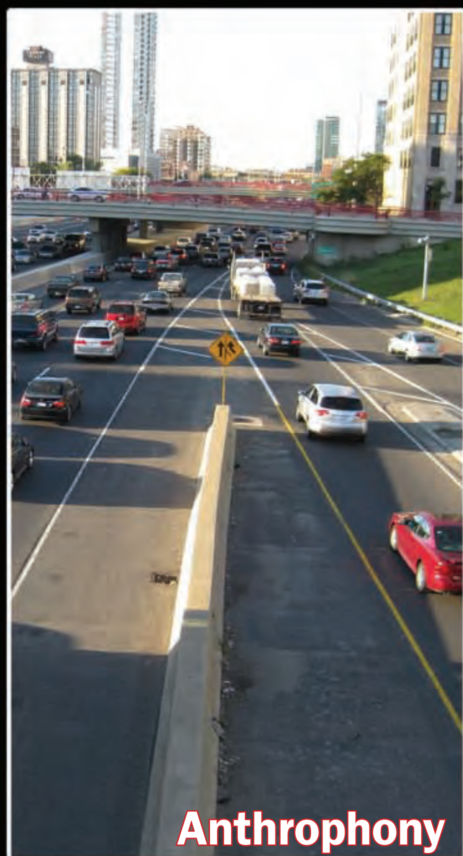

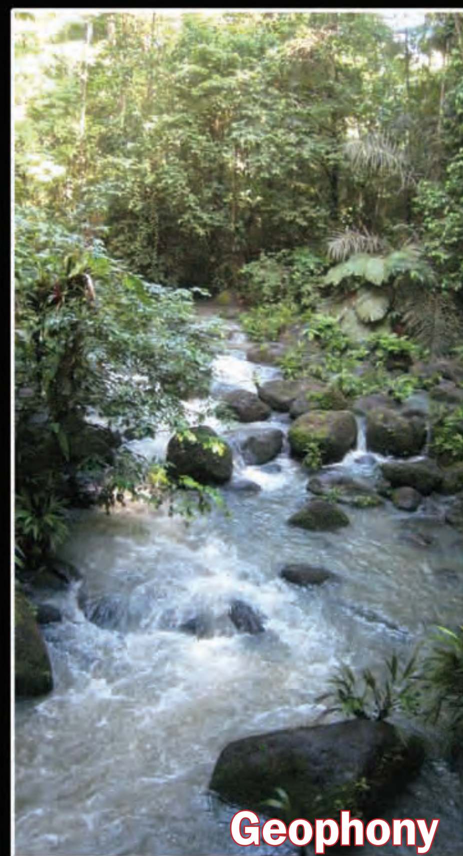

Soundscape Ecology

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Soundscape Ecology: The Science of Sound in the Landscape

BRYAN C. PIJANOWSKI, LUIS J. VILLANUEVA-RIVERA, SARAH L. DUMYAHN, ALMO FARINA, BERNIE L. KRAUSE, BRIAN M. NAPOLETANO, STUART H. GAGE, AND NADIA PIERETTI

This article presents a unifying theory of soundscape ecology, which brings the idea of the soundscape—the collection of sounds that emanate from landscapes—into a research and application focus. Our conceptual framework of soundscape ecology is based on the causes and consequences of biological (biophony), geophysical (geophony), and human-produced (anthrophony) sounds. We argue that soundscape ecology shares many parallels with landscape ecology, and it should therefore be considered a branch of this maturing field. We propose a research agenda for soundscape ecology that includes six areas: (1) measurement and analytical challenges, (2) spatial-temporal dynamics, (3) soundscape linkage to environmental covariates, (4) human impacts on the soundscape, (5) soundscape impacts on humans, and (6) soundscape impacts on ecosystems. We present case studies that illustrate different approaches to understanding soundscape dynamics. Because soundscapes are our auditory link to nature, we also argue for their protection, using the knowledge of how sounds are produced by the environment and humans.

Keywords: soundscapes, bioacoustics, biophony, nature deficit disorder, dawn and dusk chorus

Sounds are a perpetual and dynamic property of all landscapes. The sounds of vocalizing and stridulating animals and the non-biological sounds of running water and rustling wind emanate from natural landscapes. Urban landscapes, in contrast, are dominated by human-produced sounds radiating from a variety of sources, such as machines, sirens, and the friction of tires rotating on pavement (Barber et al. 2010). Since Rachel Carson's seminal work, *Silent Spring* (1962), nature's sounds have been inextricably linked to environmental quality. Because sound is a fundamental property of nature and because it can be drastically affected by a variety of human activities, it is indeed surprising that sound has not become a more universally appreciated measure of a coupled natural–human system (Liu et al. 2007). To date, no coherent theory regarding the ecological significance of all sounds emanating from a landscape exists. Fortunately, new technologies such as automated recording devices (e.g., Acevedo and Villanueva-Rivera 2006), the existence of inexpensive storage capabilities, developments in acoustic data processing (e.g., Sueur et al. 2008, Trifa et al 2008), and theories of related ecological disciplines such as landscape ecology (Forman and Godron 1981, Urban et al. 1987, Turner 1989, Turner et al. 2001, Farina 2006) have advanced sufficiently to allow research on the ecological significance of sounds in landscapes to progress.

This article contains sound files that may be accessed by reading the full-text version of this article online at *dx.doi.org/10.1525/bio.2011.61.3.6.*

The purpose of this article is to present a new field of study called soundscape ecology, emphasizing the ecological characteristics of sounds and their spatial-temporal patterns as they emerge from landscapes. We believe that soundscape ecology shares considerable parallels with landscape ecology (Forman and Godron 1981, Urban et al. 1987, Turner 1989, Turner et al. 2001, Farina 2006), because processes occurring within landscapes can be tightly linked to and reflected in patterns of sounds in landscapes.

To illustrate the main themes of this relatively unexplored field, we introduce new terms and a conceptual framework for soundscape ecology, summarize what is known about sounds in the environment, and present overviews of four case studies that quantify soundscape dynamics. We conclude with an argument for the need to conserve natural soundscapes. This article also represents an innovation in presentation; we introduce sound recordings as an integral component of the article. All acoustic recordings used in this article as single demonstrations and many others used in our analyses may be accessed online in two places: (1) by reading the full-text version of this article online (*dx.doi.org/10.1525/bio.2011.61.3.6*); and (2) at our own self-hosted site (*www.purdue.edu/soundscapes/bioscience*), which features additional Web tools for learning.

What is soundscape ecology?

The term "soundscape" has been used by a variety of disciplines to describe the relationship between a landscape and the composition of its sound. The work of Southworth (1969) exemplifies one of the first uses of the term in the literature. Southworth was interested in urban soundscapes;

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in particular, his work addressed how the sounds of the built environment enhanced people's perception of space and their relationship to the activities occurring within cities. As a result, the first mention of soundscapes appears in urban planning literature. Nearly a decade later, Schafer (1977) recognized that sounds are ecological properties of landscapes, referring to soundscapes as "the acoustical characteristics of an area that reflect natural processes." His primary interest was in characterizing natural sounds that could be used to compose music. Krause (1987) later attempted to describe the complex arrangement of biological sounds and other ambient sounds occurring at a site, and introduced the terms "biophony" to describe the composition of sounds created by organisms and "geophony" to describe nonbiological ambient sounds of wind, rain, thunder, and so on. We extend this taxonomy of sounds to include "anthrophony"—those caused by humans. Soundscape ecology thus can be described by our working definition as all sounds, those of biophony, geophony, and anthrophony, emanating from a given landscape to create unique acoustical patterns across a variety of spatial and temporal scales.

> *"Over increasingly large areas of the United States, spring now comes unheralded by the return of the birds, and the early mornings are strangely silent where once they were filled with the beauty of bird song."*
>
> *— Rachel Carson,* Silent Spring *(1962)*

At the onset, we wish to separate other acoustic studies from what we believe is a unique field of acoustics presented here. To our knowledge, soundscape ecology has not been used in the literature to describe a field of ecology. Acoustic ecology, as introduced by Schafer (1977) and Truax (1999), is seen as complementary to traditional ecological concepts rather than situated within them. Broadly interdisciplinary, acoustic ecology studies the relationships and interactions among humans and sounds in an environment, including musical orchestrations, aural awareness, and acoustic design (Schafer 1977, Truax 1999). Acoustic ecology largely emphasizes human-centered inquiry rather than the larger socioecological systems approach taken here.

Bioacoustics (Fletcher 2007) is another related research area that we distinguish from soundscape ecology. The study of animal communication is a rich and mature field, spanning behavior, life-history theory, and the physics of sound production by animals. However, a majority of these studies focus on a single species or a comparison of species. Our presentation of soundscape ecology focuses mostly on macro or community acoustics. We are interested in the composition of all sounds heard at a location that are biological, geological, or anthropogenic. Another rich area of acoustics research has focused on noise in the environment. Primarily in the field of engineering, significant research has addressed the physics of sound (e.g., Hartmann 1997), and new methods have been employed to calculate noise produced from planes and automobiles across large regions (Miller 2008).

Conceptual framework for soundscape ecology

Since its conception, landscape ecology has focused on the interaction of pattern and ecological processes across large spatial regions (Urban et al. 1987, Turner 1989, Turner et al. 2001, Farina 2006). Many of the basic principles of soundscape ecology are common to those of landscape ecology. These include the assignment of a soundscape to a geographic context, the identification of anthropogenic and biological processes and spectral and temporal patterns in the soundscape, how disturbance alters patterns and processes across scales, the emphasis on interactions between biological and anthropogenic factors, how organisms perceive spatial configuration in landscapes, and the need to develop tools to quantify pattern.

Our general conceptual framework (figure 1) bases soundscape ecology on the same foundations as landscape ecology and draws from areas of coupled natural–human systems (Liu et al. 2007), with natural and human systems interacting to form spatial-temporal patterning of sound in landscapes. Humans transform landscapes (Lambin and Geist 2006) through land-use and land-cover change (figure 1, arrow 1), and these human modifications of the land interact with a variety of biophysical features (e.g., terrain, soils) to produce heterogeneity in spatial structure across

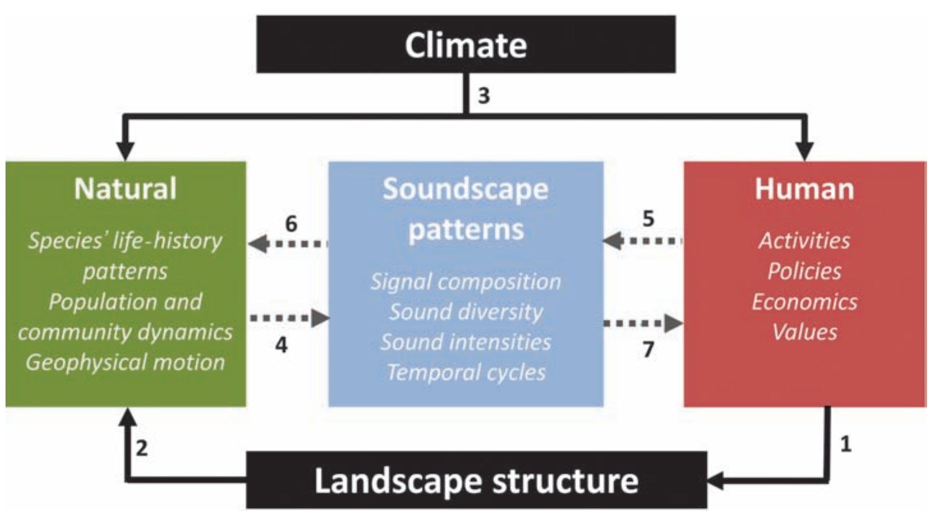

Figure 1. Conceptual framework for soundscape ecology.

the landscape (Farina 2006). Landscape structure in turn (figure 1, arrow 2) influences the distribution and abundance of species and their interactions at multiple spatial and temporal scales (MacArthur and MacArthur 1961). Landforms (e.g., valleys, rivers) also provide for types of geophysical motion patterns, especially those that make frequent sounds such as water and wind. Furthermore, climate (figure 1, arrow 3) controls the distribution of species (Currie 1991) in conjunction with the timing of specific life-history events (e.g., breeding or the emergence of noisy insects; e.g., Brown et al. 1999, Beebee 2002, Ahola et al. 2004). Climate (arrow 3) also influences geophonic sounds. The natural components of biophony and geophony (both as arrow 4) at any given location and time contribute to the observed soundscape. Human activities produce sounds (anthrophony) as well (arrow 5). Biophony, geophony, and anthrophony (arrows 4 and 5) integrate to create the complete soundscape. What occurs in the soundscape can feed back to natural processes (arrow 6); for example, animal vocalizations masked by human-generated noise may alter population or community dynamics such as predator-prey relationships (Barber et al. 2009).

Our conceptual framework for soundscapes also emphasizes two unidirectional components between humans and soundscapes (figure 1, arrows 5 and 7); such feedbacks characterize coupled natural–human systems (Liu et al. 2007). In the direction of humans to soundscapes (arrow 5), anthropogenic sounds often permeate natural landscapes. Unwanted sound, or noise, is a common issue in cities globally, and the problem has spread to more rural and remote areas with the expansion of motorized transportation networks (Wrightson 2000). As such, many policies have been enacted to control noise. For example, the importance of sounds in national parks was identified early on with the increasing volume of motorized recreation (National Parks Overflight Act of 1987). The National Park Service (NPS) formally recognizes soundscapes as a park resource, and that the organization should "restore to the natural condition wherever possible those park soundscapes that have become degraded by unnatural sounds (noise), and will protect natural soundscapes from unacceptable impacts" (NPS 2006, p. 56).

In the opposing direction, soundscapes can influence human well-being (figure 1, arrow 7). As with other natural resources, natural and unique soundscapes have many associated human ideals, such as cultural, sense of place, recreational, therapeutic, educational, research, artistic, and aesthetic values. Many of these values foster a conservation ethic by directly influencing people's ability to connect with the natural world (Rolston 1988). Indeed, the NPS recognizes the importance of healthy soundscapes for positive park visitor experiences (Miller 2008). Natural sounds engage one of our senses and provide information about our surroundings. Wilson (1999) suggested that the natural world is the most information-rich environment that humans can experience, and we believe that some of the important information conveyed is through sound. In contrast, urban soundscapes are described as containing little acoustic information (Schafer 1977), reinforcing a growing disconnect between humans and nature (Louv 2008). Therefore, the sounds of an environment should not be something that we try to block out, but rather something that we value.

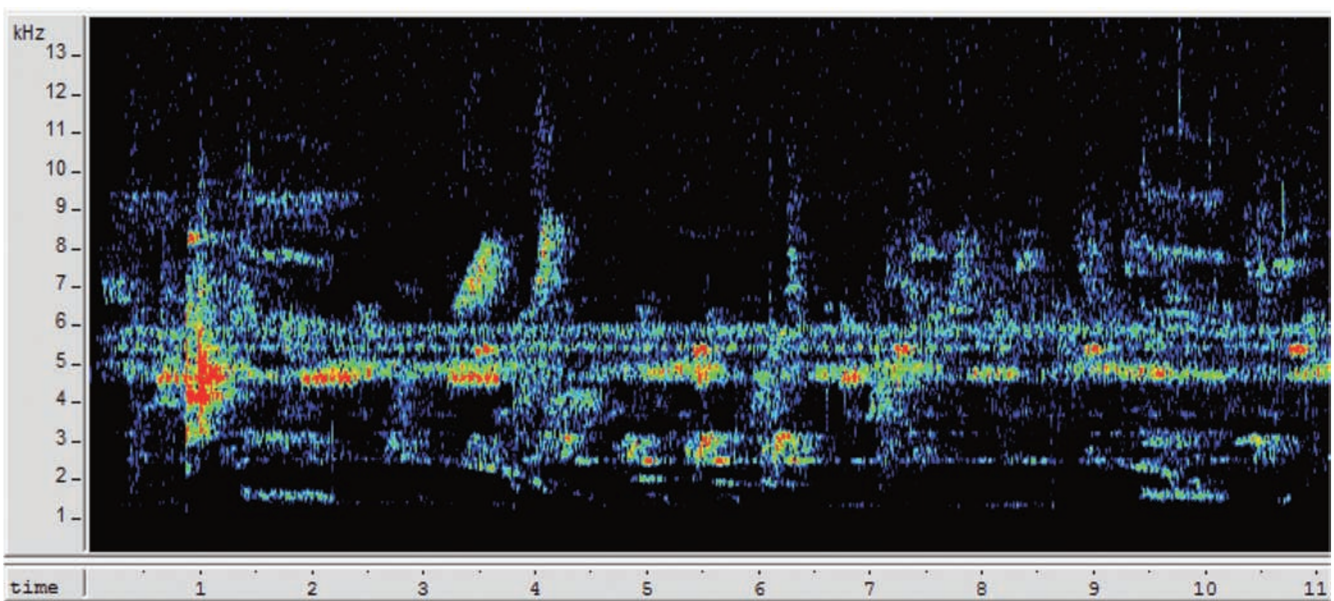

Figure 2. Spectrogram of an 11-second recording of the dawn chorus at the La Selva Biological Station, Costa Rica. Birds and insects are creating a variety of sounds from 1 kilohertz (kHz) to some even above 12 kHz. There is considerable biophonic activity between 4 and 6 kHz, with the loudest sounds occurring 1 second into this recording. Crickets are stridulating at 4.7, 5.3, and 6.0 kHz. Note that raindrops falling from the tropical canopy can be heard (sounds below 2 kHz), an example of geophony.

Sound in the environment

There are many ways to quantify sounds in the environment.

Measuring sound. Soundscapes can be measured using automated digital recording systems. Digital acoustic recorders store the timing and intensity (or power) of the sounds detected by microphones, which allows signal processors to reconstruct the frequency distribution of signal intensity over time. Intensity is most commonly recorded as dB (decibels), although digital recorders store amplitude in dBFS (or decibels full scale); the peak is assigned a value of dBFS = 0, and all other values scale on the basis of the bit value of the recording. Humans tend to interpret frequency as pitch (although the relationship is not one to one) and ideally can detect signals with frequencies ranging from 20 hertz (Hz) to 20 kilohertz (kHz). Many digital sound recorders sample at 44.1 kHz with a 16-bit depth, which is CD quality, and store the data as uncompressed WAVE (or WAV) files.

Figure 2 shows a visual representation, called a spectrogram, of a 10-second recording from the La Selva Biological Reserve in Costa Rica (for reference, listen to sound file 1). This spectrogram contains three dimensions of sound: (1) time, along the x axis; (2) frequency, represented along the y axis; and (3) energy, also called amplitude, normally color coded or plotted on the z axis. Reading a spectrogram, also called a sonogram, is done in the same way that one reads sheet music: Notes are arranged linearly through time with higher frequencies (or pitch) at the top of the musical staff.

Biophysical models of sound transmission. Biologists have invested significant effort into understanding animal communication, and their findings offer insight into the soundscape's role in ecological communities. Much of the research into animal acoustic communication (e.g., Marten et al. 1977) has utilized the Sender-Propagation-Receiver (SPR) model to describe the three primary elements of information propagation: (1) the sender's biophysical characteristics and the intent of its message, (2) the role of the physical environment in shaping the signal, and (3) the perception and interpretation of the signal by its recipient (figure 3a). The sender encodes a string of information into a sound signal that is composed of certain physical factors, including the signal's (a) frequency, (b) energy or amplitude, (c) directionality, and (d) the point (or points, if the sender is in motion) of origin. The propagation of the signal depends both on the medium through which it passes (air, water, solid media, etc.) and on the arrangement of reflective and absorptive surfaces of that medium (e.g., vegetation, buildings, and water bodies). Finally, the signal the receiver interprets will be further influenced by that receiver's hearing range and its ability to translate the signal back into information (Forrest 1994). Although most organisms cannot actively control which sound signals they receive, selection pressures can adjust the configuration of their auditory organs to optimize their ability to detect conspecific signals (Dooling et al. 1992).

A multisource model is illustrated in figure 3b. Note that sounds from birds and amphibians may be interfered with by wind, rushing water, or potentially noise created by humans (Ryan and Brenowitz 1985). The integration of all these signals, natural and human, makes up the soundscape. Note also that an acoustic sensor array could be employed to record sounds at multiple locations; sound waves could then be conceptualized as an acoustic field that changes with time.

Relevant ecological hypotheses. Two complementary hypotheses, the morphological adaptation hypothesis (MAH) and the acoustic adaptation hypothesis (AAH), describe how ecological feedback mechanisms give rise to changes in animal signals, whereas the acoustic niche hypothesis (ANH) describes how these feedback mechanisms lead to the complex arrangement of signals in the soundscape. The MAH focuses on the sender, and posits that an organism's physical attributes, such as its body size, the length of its trachea, and the structure of its beak, influence what sorts of sound signals an organism can produce (e.g., Bennet-Clark 1998). A larger bird with a longer trachea, such as a heron or a goose, will usually produce sounds at lower frequencies than a smaller bird with a shorter trachea, such as a thrush or a finch.

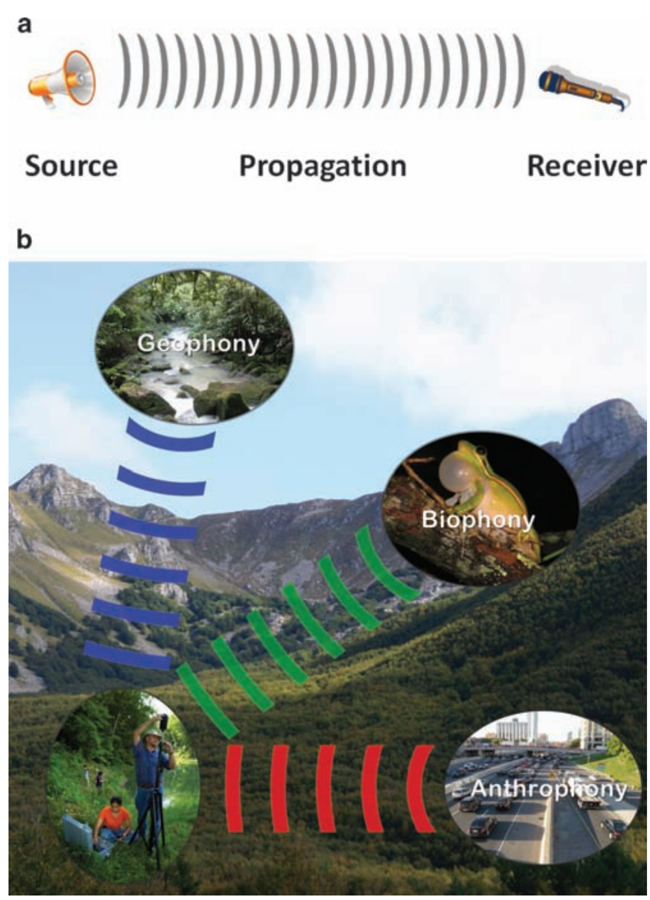

Figure 3. Sound transmission models for (a) single and (b) multiple sources of sound.

The AAH (e.g., Daniel and Blumstein 1998) focuses on interactions between the sender and the medium, and proposes that certain groups of organisms will adjust the attributes of their sounds to maximize their propagation (Morton 1975). Support for the AAH has been mixed; some researchers found no correlation between signal composition and habitat (Daniel and Blumstein 1998), whereas others (e.g., Brown et al. 1995) found evidence that the acoustic properties of an environment can influence the evolution of vocalizations.

In his formulation of the ANH, Krause (1987) pointed out that both the morphological and the behavioral adaptations described by the MAH and the AAH can also be triggered by interspecific interference when organisms' calls contain similar frequency and timing features. After repeatedly observing complex arrangements of nonoverlapping signals in his recordings of soundscapes in multiple habitat types, Krause (1987) postulated that such interspecific competition for auditory space would prompt organisms to adjust their signals to exploit vacant niches in the auditory spectrum to minimize spectral or temporal overlaps in interspecific vocalizations. Ficken and colleagues (1974), for instance, observed that least flycatchers (*Empidonax minimus*) at Lake Itasca, Minnesota, would insert their shorter songs between the longer songs of red-eyed vireos (*Vireo olivaceus*) when the two species shared the same habitat. An important prediction that follows from this hypothesis is that less-disturbed habitats with unaltered species assemblages will exhibit higher levels of coordination between interspecific vocalizations than more heavily disturbed habitats, in which species assemblages were recently altered. Likewise, invasive species could create biophonic disturbances, thereby altering natural acoustic partitioning (figure 4, sound files 2–4). Finally, Farina and Belgrano's (2006) eco-field hypothesis can be used to describe the soundscape from the receiver's perspective as a carrier of meaning. This hypothesis proposes that an organism uses the signs it identifies in

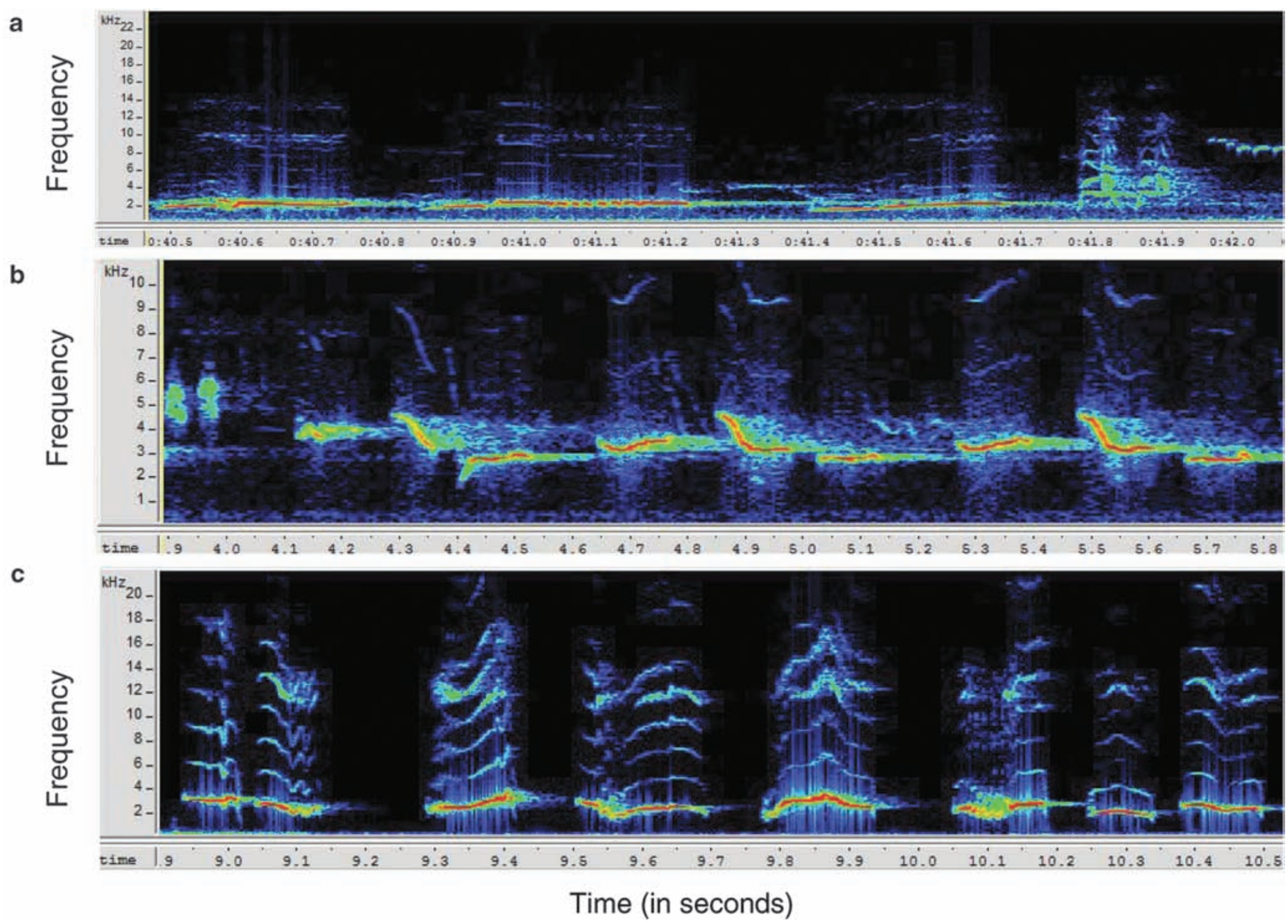

Figure 4. Spectrograms of two endemic birds, **Turdus merula** *(a) and* **Sylvia atricapilla** *(b), and the nonendemic, invasive* **Leiothrix lutea** *(c). Note that* **L. lutea** *and* **T. merula** *have overlapping frequencies in their songs, especially around 2 kilohertz (kHz), which are the loudest parts of their calls.* **Sylvia atricapilla** *sings at higher frequencies that are potentially masked by* **L. lutea**, *which has many parts of its song in high frequencies (> 6 kHz) and with clear modulation patterns.* **Leiothrix lutea** *has more behavioral overlap with* **S. atricapilla** *than it does with* **T. merula.**

the soundscape to construct a cognitive template that it then uses to match particular spatial configurations with life functions such as food, water, and shelter.

What produces sound? The urban environment generally contains sounds with considerably different spectral and temporal properties from those produced by living organisms. Urban landscapes are saturated with signals that carry little or no intentional information and are regarded as unwanted noise by many people. These signals emanate from vehicles (e.g., motors and road noise) and stationary machines (e.g., air conditioners; sound file 5). Most of these sounds occur at low acoustic frequencies (less than 4 kHz).

The geophysical environment produces a variety of *in situ*, contextual ambient sounds. Familiar such sounds are wind, rain, and running water, the frequencies of which occur between 100 Hz and 1 kHz with little rain, or between 100 Hz to 8 kHz during windy or moderate to heavy rain. Geophony varies seasonally and diurnally.

Among terrestrial organisms, vertebrates and certain groups of insects produce the most sound. The most audible insects are crickets, katydids, grasshoppers, and cicadas. Insects produce sounds most strongly around 3 to 4 kHz and 6 to 8 kHz, either through stridulation (crickets and katydids) or by vibrating a rigid membrane (cicadas). Stridulation is created by insects by rubbing body parts together. Insects call during the day (cicadas), at night (crickets), or both (some cicadas). Additionally, songs from many insects possess a certain periodicity. For example, sounds from crickets are composed of pulses and chirps produced at precise intervals, and crickets are well known for having chirp rates that are strongly influenced by temperature (Walker 1962). Other cyclical patterns of sound production in insects throughout the year relate to the phenological life cycle of the species. Annual cicadas (*Tibicen* spp.), for instance, will sing during hot days, late in the summer after they emerge from the ground, with the timing of emergence being a function of accumulated heating degree days (Williams and Simon 1995). Sounds produced from wing beats from flies, bees, and wasps could contribute significantly to the soundscapes if these insects are present in large numbers.

Amphibians such as frogs and toads rely primarily on vocalizations to attract mates (Gerhardt 1994). In the northern temperate regions of eastern North America, spring peepers (*Pseudacris crucifer*) are common singers at night in wetlands and ponds. Calls are intense during the breeding seasons, which extend from late winter (February) to early spring (May) in the northern United States and from late fall (October) to early spring (March) in more southern locations. Frequencies of frog and toad choruses range from 2 to 5 kHz.

Almost all birds use sound to attract mates, defend territories, sound alarms, and communicate other types of information. Many of the passerines are especially known for producing elaborate songs (Kroodsma 2005). Most songs and calls produced by birds occur in the 2 to 6 kHz range. The acoustic frequency of a bird's song relates to its body size (large-bodied birds produce sounds as low as 1 kHz) and habitat type and structure; for example, some tropical birds use protracted pure tones in environments with persistent geophonic sounds of wind and rain, and some vocalizations reach frequencies in the 10 to 12 kHz range (Kerry Rabenold, Department of Biological Sciences, Purdue University, West Lafayette, Indiana, personal communication, 5 October 2010).

A variety of terrestrial mammals also produce sounds (McComb and Reby 2005). Groups that are frequent contributors of sound produced in landscapes include primates (e.g., monkeys, baboons), elephants, canines (e.g., wolves and coyotes), rodents (e.g., squirrels, chipmunks), and felines (e.g., lions), among others. Bats generally produce two types of sound; the first, referred to as "echolocation," is emitted as ultrasonic frequencies (above human hearing ability) and is used to locate prey. The second, communication calls, are more readily audible to humans and are used to identify individuals.

Recently, considerable evidence has emerged showing that anthrophony can influence animal communication in a variety of ways. For example, American robins (*Turdus migratorius*) shift the timing of their singing in urban environments to the night (Fuller et al. 2007). In song sparrows (*Melospiza melodia*), the lowest-frequency notes were higher in environments with high ambient noise (Wood and Yezerinac 2006). Brumm (2004) found that free-ranging nightingales (*Luscinia megarhynchos*) in noisier environments sing more loudly than those in quieter environments, and Slabbekoorn and Peet (2003) determined that the great tit (*Parus major*) sings at higher pitches in urban noise conditions.

Rhythms of nature. The sounds of nature contain numerous rhythms or cycles. Many recognized temporal cycles of communication occur in terrestrial animals, the most well studied being those of birds, amphibians, and insects. Collectively, we refer to these periodic acoustic patterns as "the rhythms of nature." Most songbirds are known to begin singing at the same time each year (Saunders 1947), and these birds sing most intensely early in the morning (Kacelnik and Krebs 1982) and late evening (referred to as the dawn and dusk chorus, respectively). Dawn chorus in birds is thought to occur when individuals, arriving back to their territory, use songs to advertise their presence (Staicer et al. 1996). This circadian pattern of singing in birds, the timing of which is largely affected by weather and climatic conditions, strongly correlates with sunrise and sunset and becomes more pronounced with the onset of breeding and migration.

A research agenda for soundscape ecology

We believe that we are now well poised to place soundscape ecology into a more research and application focus. Research is needed in several new areas, organized around the following main themes: measurement and quantification, spatial-temporal dynamics, environmental covariates, human impacts on soundscapes, soundscape impacts on humans, and soundscape impacts on wildlife.

Theme 1: Improve the measurement and quantification of sounds. Acoustic sensors are needed that can automate the recording of sounds, that are inexpensive, and that can be placed in large networks in hostile environments. Research is required that can automatically differentiate all sounds emanating from landscapes. For example, researchers need tools that can classify biological, geophysical, and anthropogenic sources of sounds. Scientists also need a better understanding of how these sources of sounds differ in their composition. How do anthrophonic sounds differ in composition (acoustic frequency, time interval) from biophonic sounds? Is the presence of certain kinds of sounds indicative of a healthy or deteriorating landscape? *In situ* measurements of biodiversity need to be compared with soundscape measures to determine how well vocal organisms provide a proxy for biodiversity in general. Research in this area can also advance our ability to use soundscape measures for natural resource management and biological conservation.

Theme 2: Improve our understanding of spatial-temporal dynamics across different scales. Research is needed on how soundscapes vary with landscape patterns and processes (figure 1, arrows 1 and 2). How do soundscapes differ with land-use patterns? Comparisons of soundscape dynamics should be made of various natural ecosystems around the world but also across areas that differ in the amount of human disturbance within an ecosystem. Vertebrate species richness has been shown to vary with vegetation structure (canopy height, density). Is soundscape diversity greatest where vegetation structure is most complex? More research is needed that attempts to characterize the different types of the temporal patterns of soundscapes. How do soundscapes vary over different time frames (seconds, minutes, hours, diurnally, annually) (figure 1, arrows 4 and 5) in different landscapes? How are the dawn and dusk choruses affected by human activities?

Theme 3: Improve our understanding of how important environmental covariates impact sound. Biophonic and geophonic sounds very likely vary according to many environmental factors, such as weather, plant phenology, and elevation. Specific research is needed on how soundscapes vary by temperature (air, soil, and water), solar radiation, lunar radiation, relative humidity, heating degree days, and moisture budgets (figure 1, arrow 4). Knowledge of these covariates will be necessary as researchers attempt to understand how human activity impacts natural soundscape dynamics. Studies on how geophonic sounds of wind, running water, and rain affect biophonic patterns will help us to understand the plasticity of biological communication as it relates to human-generated sounds.

Theme 4: Assess the impact of soundscapes on wildlife. There is a need for more research on how certain soundscape qualities (e.g., noise, ambient sounds like running water and wind) affect individual wildlife species and populations (figure 1, arrow 6). Research is required on the ways anthrophony affects wildlife behavior, such as breeding, predator-prey relationships, and physiology. As soundscape patterns such as signal composition, sound diversity, and temporal cycles change, what are the impacts to species' life-history patterns?

Theme 5: Assess the impacts of humans on soundscapes. Humans create many objects that produce sounds (figure 1, arrow 5). How do engines, road noises, bells, sirens, and other machines affect soundscape composition? As new technologies emerge, how do these affect the soundscape? What policies are needed to protect soundscapes in various settings such as national parks or our cities and neighborhoods? How can land-use planners and policymakers determine future soundscapes?

Theme 6: Assess soundscape impacts on humans. Humans are surrounded by sounds that emanate from the environment and these sensory connections to nature are from the soundscape (figure 1, arrow 7). Research is needed on how natural sounds influence the development of individuals' sense of place, place attachment, and connection to nature. More specifically, how do human demographic variables such as culture, place of residence, or age affect the strength of human values associated with soundscapes? What factors affect human (in)tolerance of soundscape changes, especially where those changes increase noise?

Soundscape ecology case studies

We present four case studies that illustrate various aspects of soundscape ecology. These studies also exemplify the kinds of research that can be conducted across the six research themes posed above. The first case study, which is not a separate study in itself as are the three others, represents selected recordings from the massive Krause 40-year-old soundscape archive. Krause, a musician and recording engineer, has recorded natural sounds for use in the entertainment industry. The second focuses on characterizing the "rhythms of nature" in midlatitude landscapes that vary across a human disturbance gradient. A third study, conducted in Sequoia National Park in the United States, attempts to determine whether organisms are partitioning their sounds and the extent to which geophonic sounds, such as rivers and wind, interfere with animal communication. The final study, conducted in montane forests in Tuscany, Italy, centers on mapping dynamic soundscapes.

Krause ambient sounds soundscape archive. We use several field recordings that are part of the massive Krause soundscape archive to illustrate how sounds reflect certain characteristics of landscapes and the organisms that live within them. A 1-minute-28-second recording of a tropical forest in Madagascar in 1996 (sound file 6) represents an excellent example of the ANH, exemplifying that sounds produced by animals are separated in space, time, and frequency. Here, dozens of birds vocalize with little frequency or temporal overlap. One bird (probably a sickle-billed vanga, *Falculea palliata*) produces four rapid calls followed by a brief pause at 1 kHz, much below the frequency of other bird vocalizations. This recording most likely represents some of the greatest acoustic niche separation in the world.

The nighttime recording of organisms producing sounds in a bai in the Central African Republic (sound file 7) illustrates how unique landscapes can create unique soundscapes. Here, the normal synchronous production of nighttime sounds by insects and frogs is interwoven with the loud trumpeting, bellowing, and grunting of forest elephants (*Loxodonta cyclotis*). A bai is a special landscape where forest elephants go (areas have been cleared by elephants) because of the high salt content of the mud surrounding ponds created by groundwater upwelling; thus, landscape structure and the specific animals occupying these areas can create a unique soundscape.

A recording (sound file 8) of the dawn chorus in Zimbabwe illustrates not only the complexity of sounds produced in the morning but also animals' use of special landforms to propagate calls. The first minute contains a typical chorusing of about 30 different species of birds (see supplementary online materials at *www.jstor.org/stable/10.1525/bio.2011.61.3.6*). At 1:13 into this recording, however, baboons (*Papio cynocephalus*) begin to bark. Note how the echo decay of the baboons (> 4 seconds) differs from the echo decay of the birds (approximately one-third of a second), such as the black-eyed bulbul (*Pycnonotus barbatus*) in the dry forest. The landform is thus exploited by these animals to propagate their voices. Many animals, such as African lions (*Panthera leo*), forest and plains elephants, and hyenas, choose the time and place to make their voices echo.

Wiens and Milne (1989), among others, have emphasized the need to understand landscapes from the perspective of the size of an organism; they found that from a beetle's point of view, the very fine structure of a landscape influences movement patterns. Additionally, many insects produce sounds that aid in breeding or communication that may not be audible to humans or to other organisms in the landscape. Ant stridulations (sound file 9) are not audible to the human ear but are known to occur continuously in ant colonies. Recent research (Hickling and Brown 2000) has also shown that only sounds produced in a near field on the order of 100 millimeters or less are detected by ants, and ambient sounds produced farther away are ignored.

Sounds produced by many organisms may also reflect the animals complex social structure. The recording (sound file 10) of gray wolves (*Canis lupus*) in Canada's Algonquin Provincial Park in 2008 captures the vocalizations of wolves as the normal foreground biophony progresses. This recording may also elicit a strong sense of wildness, triggering many human senses and values. The entire context of wolves howling among the tapestry of boreal sounds can be a memorable experience (*sensu* Fisher 1998), emphasizing the importance of our auditory connection with nature.

Tippecanoe Rhythms of Nature study. Several of this article's authors (LJV, BCP, and BMN) conducted a yearlong study to measure near-continuous sounds in a variety of landscapes in northwestern Tippecanoe County, Indiana (see online supplementary material at *www.jstor.org/stable/10.1525/bio.2011.61.3.6*), in order to characterize different rhythms of nature and the impacts of humans on them. We deployed automated Wildlife Acoustics Songmeters in eight locations that varied in land-use characteristics, spanning old growth forest to agricultural fields (figure 5). The proportion of

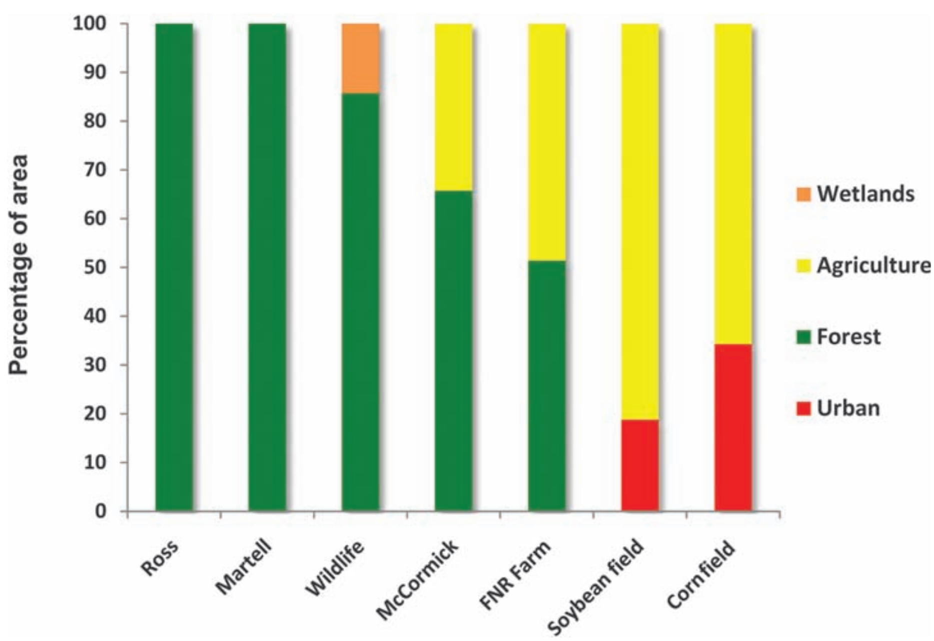

Figure 5. Land-use and land-cover composition within 100 meters of each acoustic recorder. Land-use and -cover data were from the 30-meter 2001 National Land Cover Database, classified into major land-use and -cover types. Martell Forest is a secondary forest owned by Purdue University, the Wildlife Area is a wetland surrounded by 10- to 15-year-old trees, Ross Reserve is an old growth forest also owned by Purdue University. FNR Farm and McCormick Woods are two mixed use sites; the former is an abandoned orchard and McCormick Woods is a small (40-hectare) forest stand surrounded by residential urban development.

urban and agriculture within 100 meters of the recorder was used as a measure of human disturbance. We collected and analyzed more than 34,000 15-minute recordings. We were also interested in applying metrics traditionally used by ecologists, such as diversity, evenness, richness, and dominance. To accomplish this, we discretized the spectrogram into 10 frequency bands and calculated the amount of sound occurring in each band. We used these values to calculate (a) diversity (using Shannon's index) and (b) evenness (using the Gini coefficient). We also determined the most dominant frequency band occurring in each 15-minute recording. The total amount of acoustic activity in each recording was used as a surrogate for sound sources, which in some cases will be correlated to species richness. These metrics were examined across landscapes and over two time periods.

Activity, diversity, and evenness were greatest for the natural landscapes (forests and wetlands), and all values decreased as human disturbance increased (figure 6). A plot of mean monthly Shannon's diversity index values by site (figure 7a) shows that a peak in entropy occurs during the late summer. Late summer soundscapes are composed of birds and insects (mostly cicadas and crickets). Comparing these same sites across time of day (figure 7b) aggregated from May through September, a 7:00 a.m. (i.e., dawn chorus) and 10:00 p.m. peak (i.e., dusk chorus) are evident in all but the agricultural sites. Nighttime entropy values are twice that of midday values in all sites except the cornfield site. Sound files 11–34 contain a full day of recording from our wetland site. In May, all sites were dominated by low-frequency sounds (figure 8), but by late summer (August and September) bands 3 through 8 became prominent, especially in natural landscapes.

Sequoia National Park acoustic niche hypothesis study. Four relatively pristine habitats located in the Sequoia National Park were selected by BK and SHG (see figure 9) for a yearlong study to determine whether (a) sounds from animals occurred with any acoustic niche separation, and (b) geophony affected biophony patterns. A forest riparian zone (near a relatively noisy stream), an oak savanna, a dry savanna chaparral (with high winds), and an old-growth forest site were monitored daily at dawn, midday, dusk, and midnight (for 60 minutes during the period of September 2001 through October 2002) using digital acoustic recorders (see supplementary online materials for details). Randomly selected 11.5-second segments were analyzed by

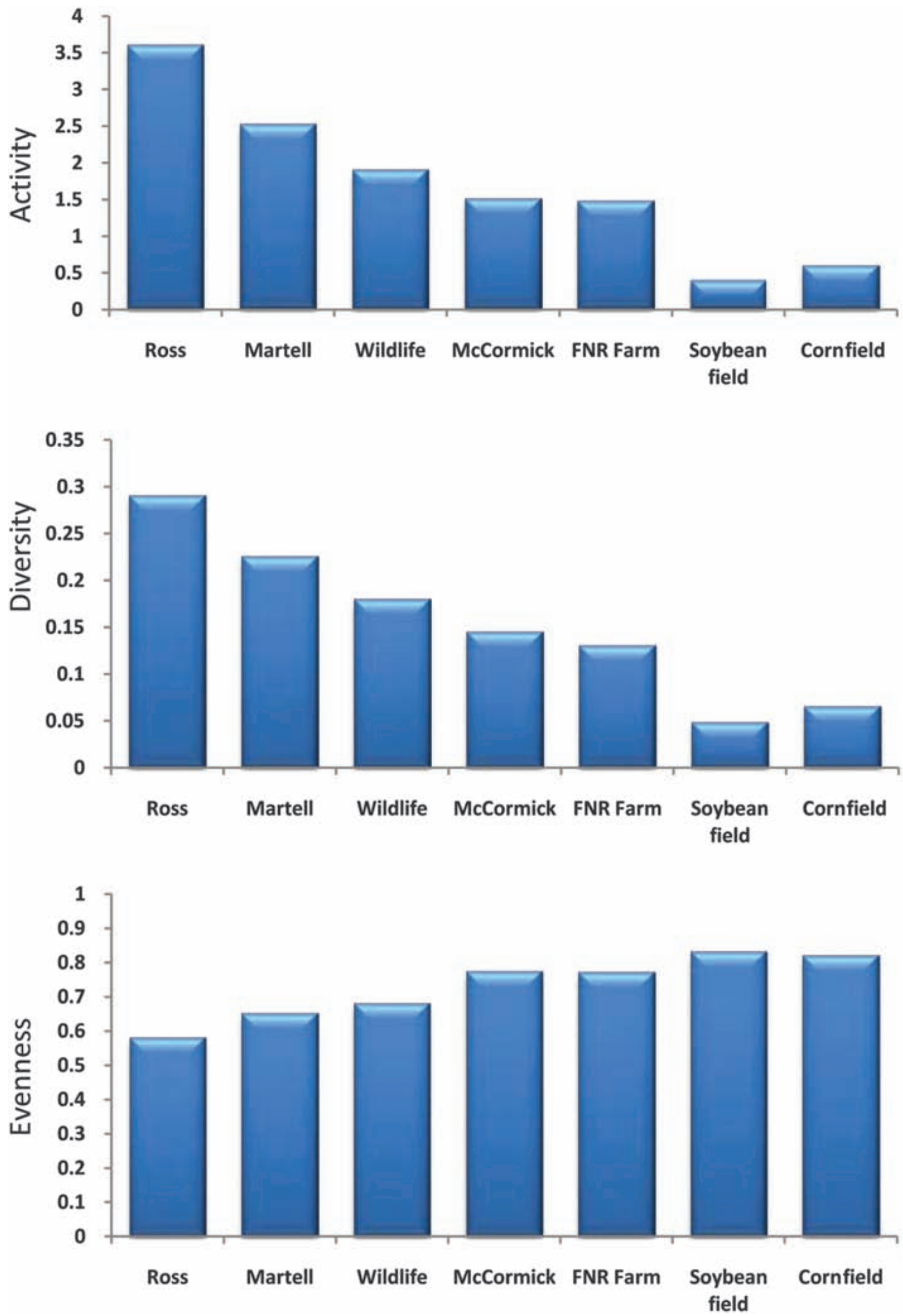

Figure 6. Annual average values for (a) total activity, (b) frequency band diversity, and (c) frequency band evenness in the Tippecanoe Rhythms of Nature Study.

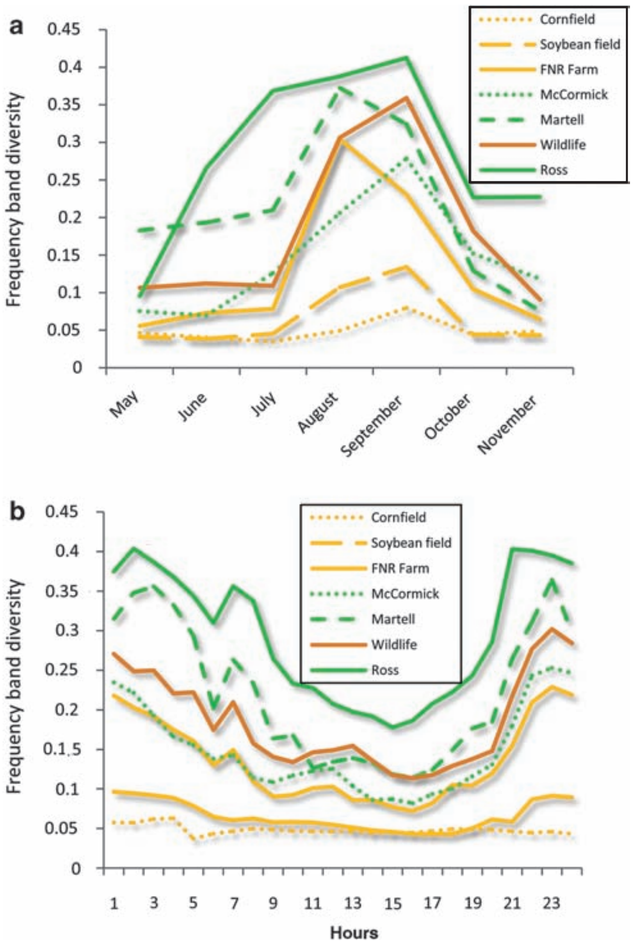

Figure 7. Temporal cycles of frequency band diversity plotted by (a) month and (b) hour. (a) Monthly average frequency band diversity (Shannon's) as it differs between sites and (b) hourly average frequency band diversity (Shannon's) as it differs between sites.

examining spectrograms and listening to the recordings. A total of 190 spectrograms were produced, and the vocal niches in these spectrograms were analyzed (a) qualitatively, by describing biophonic and geophonic patterns; and (b) quantitatively, by calculating the acoustic activity occurring at each site.

The vocalizations of American robins and the American dippers (*Cinclus mexicanus*) in the riparian zone (Buckeye Flats) location were evident, with frequencies of songs occurring in a manner that avoided masking by the nearby noisy stream. Insects produced sounds that were higher in pitch than birds, demonstrating niche partitioning. Only 57% of the spectrograms contained sounds. Within the oak savanna site (Sycamore Creek), vocalizations by birds ranged from 500 Hz (mourning dove, *Zenaida macroura*) to more than 20 kHz (unidentified bird); approximately 94% of the spectrogram was occupied by at least one vocal organism. The dry savanna chaparral (Shepard's Saddle) site possessed the greatest diversity of sounds, from flies (200 Hz) to birds (8.7 kHz from one unidentified bird). Finally, in the old-growth site (Crescent Meadow), animals produced sounds from 200 Hz (flies) to around 9 kHz (birds); about 82% of the spectrogram was occupied by vocalizations. Frogs chorused between 600 Hz to 2 kHz, just below the acoustic frequency of the robin, which sings in the 2 to 3.3 kHz range. Sound files 35–38 contain sample dawn chorus recordings from this study. The amount of acoustic activity for each site (figure 9a) shows that the Buckeye Flats site contained more than 10 times the amount of acoustic activity, mostly from the geophonic sounds of the stream. Within each site (figure 9b), acoustic activity was highly variable over a season; fall, in half of the cases, was the most acoustically active season (see sample sound files 35–38).

Mapping the soundscapes in the Tuscany study. A two-month study was conducted from June to July of 2008 in a secondary montane beech forest in the Italian Apennine National Park, located along the northern slopes of Mount. La Nuda. The study was conducted to determine how spatially variable soundscapes are in a relatively homogenous forest. Twenty digital recorders (Handy Recorder, H4) were placed in a 5 × 4 grid with 100-meter spacing. Eleven three-hour recordings (0600 to 0900) were collected under ideal meteorological conditions. Approximately 13 species of birds, such as the European robin (*Erithacus rubecula*), the chaffinch (*Fringilla coelebs*), and the blackcap (*Sylvia atricapilla*), vocalize in this forest (sample in sound file 39). An acoustic complexity index (see supplementary online materials) was used to quantify spectral complexity, and interpolation software was used to create soundscape maps.

Data from the acoustic recorders were used to construct soundtopes (Farina 2006)—a three-dimensional map of acoustic complexity (y axis) plotted across the landscape (plotted across the x and z axes). The 11 daily soundscape maps for this landscape (figure 10) indicate that large interseasonal changes of the soundscape occur. We anticipated that the soundscape maps would be similar throughout the year, reflecting static territorial boundaries. The breeding period of every species has a different phenological time and for each time requires specific resources (food, shelter, singing spots, etc.), these resources are spatially and temporally variable as well. The soundtope shifts across the environment consequently.

Summary of case studies. The above case studies illustrate various ways that data can be collected, analyzed, and interpreted. These case studies highlight many of the research themes described above. The Krause archive demonstrates the complex composition of a community of organism vocalizations, the interaction of landscape features and sound propagation, and the importance of an organism's perception of scale in the landscape in which it lives. The Tippecanoe study shows that temporal patterns

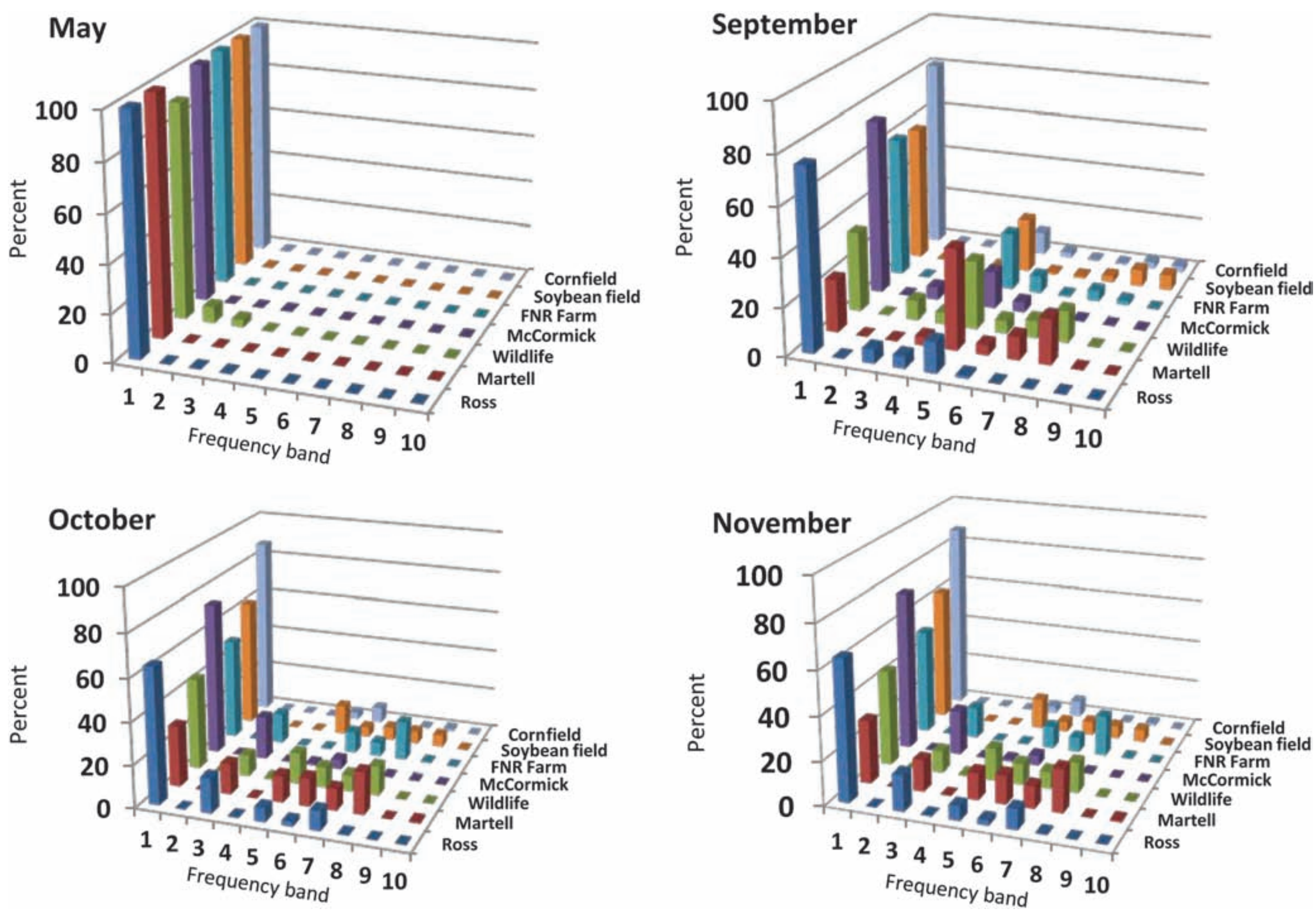

Figure 8. Frequency band dominance summarized for four months of the Tippecanoe study.

of soundscapes exhibit strong dawn and dusk chorus peaks that diminish with increasing human disturbance on the landscape. The Sequoia study attempts to quantify the effects of geophony on biophonic patterns, and shows that animals that communicate in each habitat do so at different frequencies to avoid overlap. Lastly, the Tuscany soundscape mapping study illustrates that soundtopes constructed from acoustic arrays could be used to quantify the spatial dynamics of soundscapes.

The way forward

The study of soundscapes can yield valuable information about the dynamics of a variety of landscapes. Given that technological advances are occurring rapidly and theories about the interplay of patterns and processes occurring within landscapes are maturing, we believe that soundscape ecology can enhance our understanding of how humans affect ecosystems. Indeed, we are at a critical juncture in our history, and there is a need for transformative approaches that help us to more thoroughly elucidate how humans affect our planet (Vitousek et al. 1997, Chapin et al. 2000).

At present, there is a renewed interest in studying ecosystems at large, continental scales. Automated acoustic recordings could provide a means to collect information at fine temporal resolutions (Porter et al. 2005). Initiatives such as the National Science Foundation's NEON (National Ecological Observatory Network) project are being built to study ecosystems at subcontinental scales (Keller et al. 2008). Furthermore, recordings made today will become tomorrow's "acoustic fossils," possibly preserving the only evidence we have of ecosystems that may vanish in the future because of a lack of desire or ability to protect them.

We also argue that society should value natural soundscapes as it does other aspects of nature. Soundscapes represent the heritage of our planet's acoustic biodiversity, and reflect Earth's natural assemblage of organisms—soundscapes are an ecosystem service (MA 2005) that provides cultural and other services. Natural sounds are our auditory link to nature, and the trends toward increasing society's "nature deficient disorder" (Louv 2008) are likely to continue as we replace natural sounds with those made by humans. This research reflects again on Rachel Carson's call made in *Silent Spring*, in which she highlighted the dangers of pesticides and their potential threat to wildlife and the environment. The unintended silencing of organisms by a myriad of human activities provides yet another indication of our impact on the planet's ecosystems.

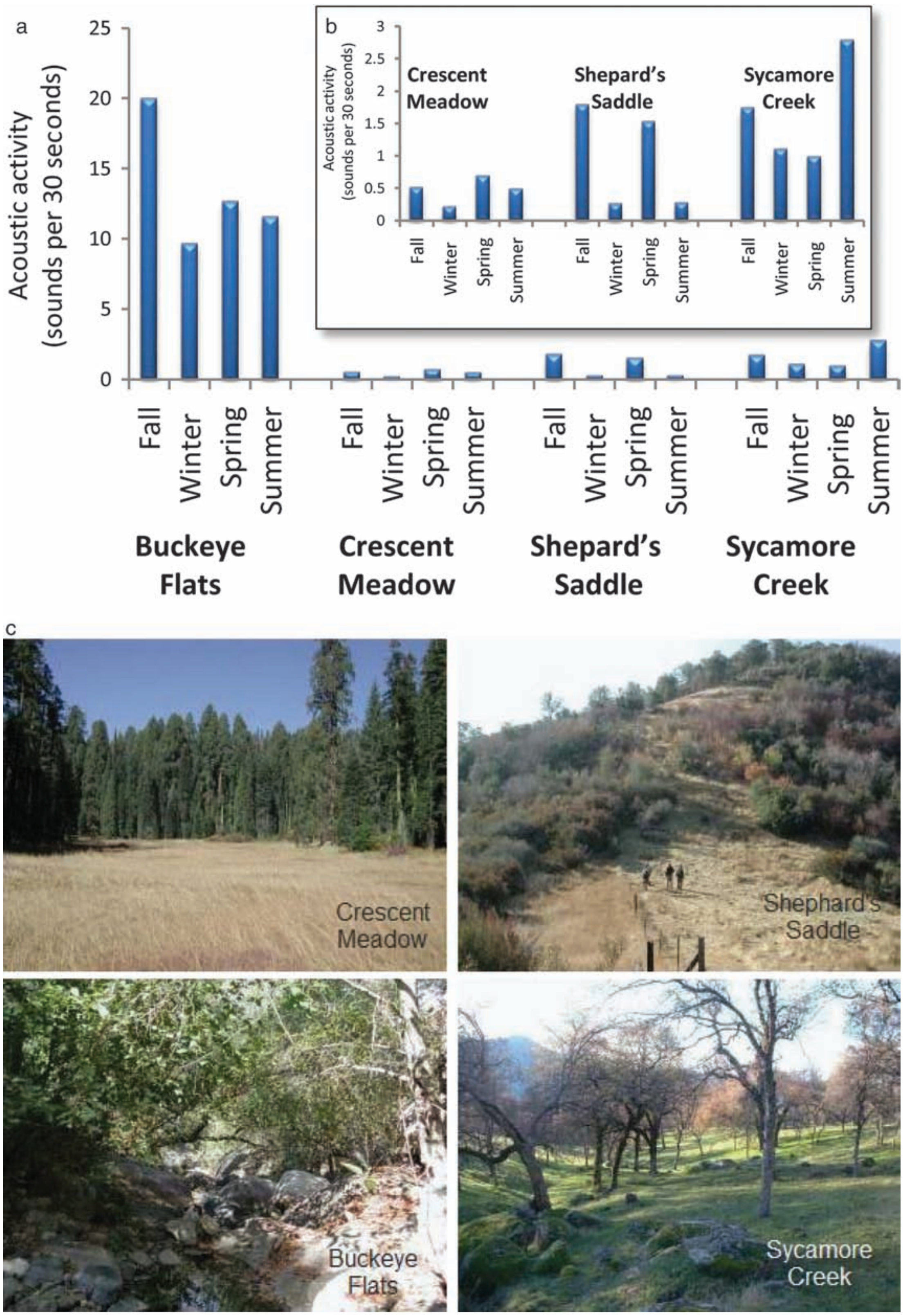

Figure 9. Summary of the Sequoia National Park study. Acoustic activity averages for each site and by season. Note that the Buckeye Flats location (a) contains greater acoustic activity, a result of the nearby rapid flowing stream that produced considerable geophonic sounds. The inset (b) graphs the same data but with Buckeye Flats removed. These values (b) reflect mostly biophony. Sycamore Creek contained the greatest acoustic activity of these three. The fall contains the greatest activity although there was no consistent pattern across sites. Photos of each landscape are provided in (c).

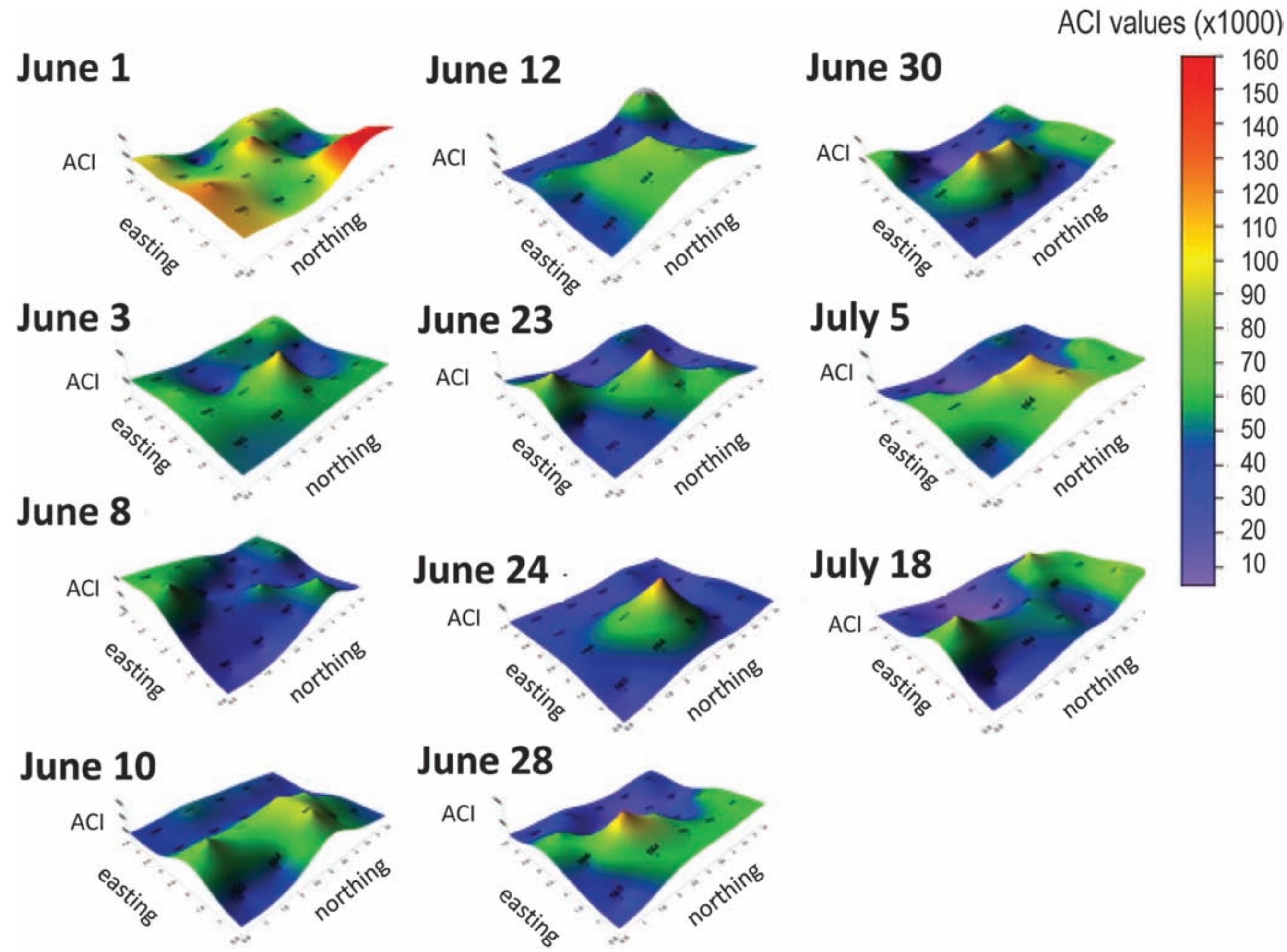

*Figure 10. Soundscape maps for the Tuscany bird acoustic study. Twenty recorders were placed in a 4 × 5 grid with 100-meter spacing and 180 minutes of recordings made. An acoustic complexity index (ACI) was calculated for each point and then interpolation software used to create a surface similar to an ecotope; we call these "soundtopes." See supplementary material online (*dx.doi.org/10.1525/bio.2011.61.3.6*) for details on how to calculate ACI.*

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