



Perspectives in ecoacoustics: A contribution to defining a discipline

Perspective article

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Abstract

Ecoacoustics is a new discipline that investigates the ecological role of sounds. Ecoacoustics is a relevant field of research related to long-term monitoring, habitat health, biodiversity assessment, soundscape conservation and ecosystem management. Several life traits of the species, populations, communities, and landscapes/waterscapes may be described by ecoacoustics. Non-invasive programmable recording devices with on-board ecoacoustic metric calculations are efficient and powerful tools to investigate ecological systems.

A set of processes in four [adaptive, behavioural, geographical, ecosemiotic] domains supports and guides the development of ecoacoustics. The first domain includes evolutionary mechanisms that join sound typology with the physical and biological characteristics of the environment and create frequency partitioning among species to reduce competition. The second domain addresses interspecific signals associated with geophysical and anthropogenic sounds that operate to shape temporary acoustic communities and orient species to select suitable acoustic habitats. The third domain pertains to the geography of sound, an entity composed of three subordinate acoustic objects: sonotopes, soundtopes, and sonotones, which are operationally delimited in a geographical and temporal space by the distribution of the ecoacoustic events. The ecoacoustic events allow the classification of complex configurations of acoustic signals and represent the grain of a soundscape mosaic. The fourth domain operates by ecosemiotic mechanisms within the species level according to a function-specific perception of the acoustic information facilitated by encoding processes.

Introduction

Sound is a mechanical vibration transmitted through an elastic medium, and it travels long distances in the air, penetrating dense vegetation and water layers and preserving some parts of the associated information. For these properties, sound is one of the most efficient vehicles by which meaningful biological and ecological information is shared by organisms through a net of inter-individual relationships (McGregor and Dabelsteen, 1996). Biological sounds have plastic characters modified by learned and/or culturally transmitted adaptive processes (Kroodsma, 2004; Derryberry et al., 2016; Sebastian-Gonzalez and Hart, 2017) and have been proven to be honest signals that reflect food availability or the health conditions of individuals (Buchanan et al., 1999, 2002).

When actively broadcast, biological sounds represent an ecosemiotic tool that species use to communicate (Kroodsma and Miller, 1996; Bradbury and Vehrencamp, 1998; Laiolo and Tella, 2005; Laiolo,

2008), to evaluate habitat suitability (Mullet et al., 2017), to locate food sources (Ward and Zahavi, 1973) and to navigate the environment (Griffin and Hopkins, 1974; Griffin, 1976). Sound may be a byproduct of animal activity (e.g., digging, friction with dense vegetation) and can be produced by predators to localize prey. For instance, foot-paddling or foot-trembling are two techniques utilized by the gull (Tinbergen, 1962) and the ringed plover (Osborne, 1982) to attract surface worms, a behaviour copied by people to capture *Diplocardia* earthworm for bait (Catania, 2008). In addition, geophonies (e.g., blowing wind, falling rain, flowing waters) or technophonies (urban noise, traffic congestion, etc.) are used by organisms as sources of information for habitat selection (Mullet et al., 2017).

Sound production requires energy investment by an emitter (Prestwich, 1994; Oberweger and Goller, 2001), and for this reason, several adaptive strategies are used by species to save energy and to assure a metabolic balance (Gillooly and Ophir, 2010). For instance, during adverse weather conditions or when noise is too high and masks acoustic signals, acoustic communication is stopped and important activities including mating selection, territory patrolling, predator avoidance, or search for food are reduced or inhibited (Lengagne and Slater, 2002; Slabbekoorn and Ripmeester, 2015).

The growing severity and spatial extension of human-induced changes in ecosystems associated to the increase of noisy environments like metropolitan and industrial areas, transportation infrastructures, ship routes, and air corridors, affect the geographical distribution of species and produce disruptive effects on community networks also generating new acoustic habits (Joo et al., 2011; Sih et al., 2011). This may have consequences for sound phenology (Buxton et al., 2016), with unpredictable consequences for species and their aggregations (Krause and Farina, 2016).

The necessity to investigate the complex relationship between sounds and the ecological processes has recently resulted in the foundation of a new ecological discipline: the ecoacoustics. Ecoacoustics is a conceptual and methodological approach developed to face the challenge of interpreting the ecological world from an acoustic perspective and offers new sensors and metrics to be applied both in natural and human-dominated environments (Towsey et al., 2014a; Sueur and Farina, 2015; Farina and Gage, 2017). The aim of this paper is to introduce the discipline, describe its competences, and explain some theoretical foundations.

Ecoacoustic footprints and competence

Ecoacoustics as an independent discipline is the result of a long process of scientific development during which ecologists have investigated the acoustic characters of the environments (e.g., Eyring, 1946; Johnson et al., 1947; Ingard, 1953; Embleton, 1963; Aylor, 1972), documented the relationship between biological sounds and the environments (e.g., Armstrong, 1963; Davis, 1964; Morton, 1970; Chappuis, 1971), and demonstrated the misuse of chemicals in the environment using an acoustic approach (e.g., Carson, 1962; Rossi et al., 2016).

Ecoacoustics was formally proposed during an international meeting of ecologists, acousticians, bio-acousticians, sound recordists, and musicians in Paris in 2014 (Sueur and Farina, 2015; Farina and Gage, 2017). Its name stemmed from the need to avoid potential confusion with "Acoustic ecology" which was used in "The study of sounds in relation to life and society" (Schafer, 1994, p. 205).

Important motivations that justify ecoacoustics as a distinct ecological discipline are connected to the growing recognition of the importance of sounds in the ecology of species, populations, communities, ecosystems, and landscapes. Furthermore, the scientific interest in ecoacoustic research and applications is supported by a consolidated knowledge in bioacoustics (e.g., Hopp et al., 1998). Table 1 shows some examples of research topics and applications in ecoacoustics.

The complexity of sound ecology means that ecoacoustics has interdisciplinary characteristics, attracting scholars from different disciplines such acoustics, ecology, ethology, geography, agro-forestry engineering, architecture, music, etc. Moreover, it shows the relationships of ecoacoustics with acoustics applied to human issues including anthropology (Feld and Brenneis, 2004), planning and managing recreational spaces, and therapeutic soundscapes (Cerwén et al., 2016). Ecoacoustics is also intended to investigate the effects of the growing impact of anthropogenic sounds (noise) on biogeography, biology and ecology of species living in terrestrial and marine human-modified and untouched systems (Lomolino et al., 2015). In fact, the plasticity of some acoustic life traits can be used as proxies to assess environmental and climate change. Since sound of biological origin is one the first life traits to change as a consequence of environmental novelties (Kroodsma, 2004), a change in sound patterns can be used as a sentinel and forerunner of the alteration of the biology and ecology of a species (Risch and Parks, 2017). Evidence that acoustic information can be the first signal of an environmental crisis represents a unique opportunity for decision-makers to act before irreversible change occurs (Rossi et al., 2016). This anticipatory diagnosis, when associated with good practices, could alleviate the loss of biodiversity and

Table 1. Main research topics and applications for Ecoacoustics.

Functional scale	Soniferous species	1. Distribution across habitats
		2. Daily and seasonal change in acoustic activity
		3. Intraspecific acoustic interactions
		4. Interspecific acoustic interactions
		 Acoustic variation across different landscape/waterscape configurations
		6. Acoustic biogeography
		7. Population density estimation
		8. Population seasonal fluctuations
	Acoustic	1. Composition across habitats and landscapes/waterscapes
	community	2. Seasonal turnover
		3. Climate change and composition shift
		4. Human intrusion
	Soundscape	 Geographical and ecological gradients of the acoustic signatures
		2. Acoustic signatures and human intrusion
		3. Acoustic signatures and climate change
Ecological	1. Choruses	
processes	2. Intraspecific communication	
	3. Interspecific communication	
	4. Noise impact	
	5. Interspecific acoustic partitioning	
	6. Invasion and habitat shift	
Applications	1. Long term acoustic monitoring in landscapes/waterscapes	
	2. Biodiversity assessment	
	3. Habitat health assessment	
	4. Soundscape management	
	5. Cultural heritage conservation	
	6. Citizen science and education	
	7. Environmental sound arts	
	8. Technological advancement and standardization of methodologies	

could reduce annoyance and discomfort in human societies as well (Farina, 2014, pp. 107–142; Farina and Pieretti, 2017).

Soniferous and non-soniferous species may suffer biological and ecological consequences when exposed to a noisy environment. Many investigations (for a review, see Farina, 2017, pp. 95–107) have demonstrated the negative effect of noise, especially of anthropogenic origin, on individual species and communities of terrestrial, freshwater, and marine systems. Because of the high transmission speed of sound in the aquatic medium, noise is particularly deleterious for marine mammals, interfering with their navigation systems (f.i., Bailey et al., 2010). To reduce the effect of noise, soniferous species may adopt different strategies like changing signal amplitude (Potash, 1972; Cynx et al., 1998; Brumm and Todt, 2003; Holt et al., 2008), changing frequency (Narins et al., 2004), increasing signal redundancy (Potash, 1972; Brumm and Slater, 2006; Diaz et al., 2011), and changing behavior (Rabin et al., 2006; McLaughlin and Kunc, 2012) or habits (Dominoni et al., 2016). Awareness of the universality of acoustic phenomena like choruses observed in several soniferous species, from snapping shrimps (Johnson et al., 1947) to birds (Burt and Vehrencamp, 2005), and the few understood ecological implications that these phenomena have, represent a promising field for further ecoacoustic investigation (Farina and Ceraulo, 2017).

The recent availability of automated passive recording technologies allows researchers to collect large sets of data that offer new tools for environmental surveys and large-scale monitoring projects (Andreassen et al., 2014; Frommolt and Tauchert, 2014; Eldridge et al., 2016; Gage et al., 2017a). This is facilitated

by the non-invasiveness and relatively low costs of acoustic technologies (Figure 1), often integrated by remote sensing and GIS facilities (Gage et al., 2004, 2017b; Butler et al., 2006; Gage and Axel, 2013; Sueur et al., 2014; Farina et al., 2018). Because of these new technologies, it is now possible to investigate physical and ecological phenomena in habitats where other sensors are less efficient, like in deep oceans (Chapman and Price, 2011; Wall et al., 2014) or in environments where human presence is challenging and the bioacoustic signals prevail, like the forests of tropical and equatorial regions (Burivalova et al., 2017).

The introduction of ecoacoustic analysis, especially in freshwater and marine systems (Au and Landers, 2016), has been a fundamental advance in the exploration of these inaccessible systems (f.i., Parks et al., 2014; Desjonquères et al., 2015; Filiciotto and Buscaino, 2017).

Important progress has been made by the availability of several metrics that can describe and evaluate the majority of emergent acoustic patterns (for a review, see Gage et al., 2017a). These metrics contribute to identifying the focal species phenology, population, and community dynamics and can be integrated in procedures to quickly process large amounts of data and biodiversity issues (Sueur et al., 2008).

Ecoacoustic methodologies may be applied to satisfy the growing demand of quiet areas for human recreation in urban areas and in the wild (Votsi et al., 2012), the necessity of their assessment and management (Pilcher et al., 2009), and to introduce citizen science to acoustics, identifying and monitoring focal species and contributing to preserve biodiversity (Ritts et al., 2016; Pavan, 2017).

The relationship between plants and animals recently found to be mediated by sounds (Jackson and Grace, 1996), the relationship between plants and sound (Gagliano et al., 2012), and the possibility of applying ecoacoustic research in agro-forestry (Mankin et al., 2011; Quintanilla-Tornel, 2017) seem to be promising fields. The growing interest of musicians and composers to incorporate natural sounds in their composition makes ecoacoustics an interesting way to improve the link between sciences and humanities (Monacchi and Krause, 2017).



Figure 1. The Soundscape Explorer engineered by Lunilettronik (www.lunilettronik.it) is a terrestrial (SE[T]) and aquatic (SE[A]) automatic sound recording (Farina et al., 2016, 2018).

This device has unique characteristics because it is the only machine that records acoustic files and processes such files in real time using the ACI metrics (Acif_t and ACIt_f. The Soundscape Explorer is equipped with two microphones (one for low frequencies (up to 48 kHz) and one for higher frequencies (up to 192 kHz)), environmental sensors (humidity, temperature, light, and atmospheric pressure), and two SD card slots that allow for storage of up to 64 GB of acoustic and climatic data. Its enclosure has been designed to withstand the most severe weather conditions. Further information on SET is available from http://www.iinsteco.org/soundscape_explorer/.

A contribution to an epistemology for ecoacoustics

Ecoacoustics investigates processes that belong to adaptive, behavioral, geographical and ecosemiotic domains ranging from individual species to populations, communities, ecosystems, and landscapes. In Figure 2, the relations between the different domains and their competences are summarized.

Acoustic adaptive domain

This domain pertains to adaptation processes that shape sound expression in vocal animals under the constraint of the geophysics environment and vegetation structure (acoustic adaptation to the environment) and of the interspecific acoustic competition (acoustic partitioning).

Acoustic adaptation to the environment

Every environment has an "acoustic climate" produced by the interference (e.g., reverberation, signal attenuation, scattering) of vegetation with sound sources (Embleton, 1963; Linskens et al., 1976; Martens, 1981; Huisman and Attenborough, 1991). The acoustic adaptation to the environment assumes that soniferous species tune their acoustic emissions according to the environmental characteristics to increase the efficiency of acoustic signal transmission and to reduce energy expenditure.

The structure of vegetation, song post height, and the frequency emitted play an important role in sound transmission with attenuation effects (Eyring, 1946; Aylor, 1972; Price et al., 1988). The Acoustic Adaptation hypothesis was tested on soniferous animals (Morton, 1975; Marten and Marler, 1977; Lemon et al., 1981; Brown and Handford, 2000), but this has been challenged (Daniel and Blumstein, 1998; Blumstein and Turner, 2005; Burns, 2007). Based on playback experiments, Graham et al. (2017) proved the different environmental adaptations of sound emission between sexes of rufous-and-white wren (*Thryophilus rufalbus*). The song of the male was maximized for long-range transmission, but for females, the song seems more adapted to be

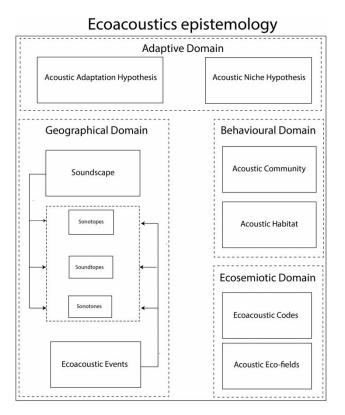


Figure 2. An epistemological framework for ecoacoustics.

Four domains can be distinguished. In the first domain, adaption is operating on sound typology and on frequency partitioning among species. In the second domain, interspecific communication and associated geophysical and anthropogenic sounds operate to shape acoustic communities, including mechanisms that species use to select the most suitable habitat. The third domain pertains to geographic competencies: soundscape and the nested acoustic entities: sonotopes, soundtopes, and sonotones. The fourth domain has ecosemiotic competencies and considers ecoacoustic codes and the acoustic eco-field that operates within the individual species level according to a function-specific perception of meaningful information.

transmitted in dense vegetation. Environmental modification by human manipulation or as a consequence of climate change may create challenging ecological novelties for several species (Kueffer, 2015).

Acoustic partitioning mechanism

Spectrograms, characterized by high soniferous species diversity like in tropical areas, show frequency and temporal partitioning of the sounds of insects, frogs, birds, and mammals (Figure 3). It appears that each species tries to avoid the acoustic overlap with other species, a strategy to prevent or reduce acoustic competition (Lemon et al., 1981; Monacchi, 2013, 2017). Bernie Krause has interpreted this evident and widespread phenomenon as a demonstration of the existence of acoustic niches (Krause, 1993, 2012).

Frequency partitioning is particularly evident in insects where the species-specific acoustic signatures occur in a narrow frequency band (Aide et al., 2017). For instance, Sueur (2002) has described the frequency partitioning in cicadas from Mexico.

The potential interspecific acoustic overlap is further reduced by a temporal segregation. For instance, Hart et al. (2015) found that cicada sounds were avoided by a tropical forest bird community that interrupts singing at the onset of cicada acoustic signals. Further evidence of temporal partitioning has been described by Stanley et al. (2016) on Barro Colorado Island (Panama) where some species of birds with high-vocalization frequencies started to sing at dawn after the orthopteran insects emitting sounds in the same frequency are on pause. Playback experiments using emerald cicadas (*Zammara smaragdina*) conducted by the same authors confirmed inhibitor effects of birds that were singing in the same frequencies of cicadas.

However, Schmidt et al. (2016) did not find evidence of acoustic partitioning in a cosignaling multispecies assemblage of tropical crickets, and acoustic partitioning was not fully demonstrated by Planqué and Slabbekoorn (2008) in birds of a tropical rainforest, although they found less overlap than expected in the most used frequencies.

A high level of acoustic overlap may indicate a recent species assemblage, assuming that communities more stable in time have a more organized acoustic partitioning than new communities (Malavasi and Farina, 2013). This hypothesis offers the possibility to verify the impact caused by climate and land use change on acoustic communities and to assess the capacity of these communities to adjust to new acoustic conditions.

Behavioral acoustic domain

The behavioral acoustic domain pertains to the processes that create acoustic aggregation of vocal species (the acoustic community) and influence the habitat selection based on the sonic ambient (the acoustic habitat).

Acoustic community

Soniferous species create a temporary net of acoustic signals. This functional aggregation has been defined by Farina and James (2016) as an acoustic community. Such functional temporary aggregations have been described

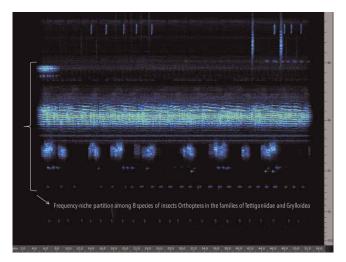


Figure 3. An example of acoustic partition in frequency of Tettigoniidae and Grylloidea.

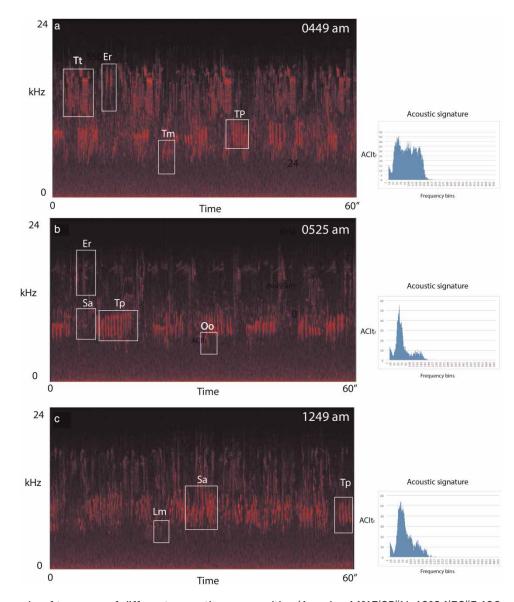
The sound environment was recorded in Dipterocarp primary forest at Ulu Temburong, Borneo, for the project "Fragments of Extinction" by David Monacchi in 2012. Spectrogram analysis courtesy of David Monacchi.

in terrestrial (Drewry and Rand, 1983; Luther, 2009; Gasc et al., 2013; Lellouch et al., 2014), freshwater (e.g., Desjonquères et al., 2015), and marine systems (Hasting and Sirovic, 2015).

Several physical and biological factors concur to structure this community. An acoustic community changes according to the lunar phases (McCauley, 2012; Staaterman et al., 2014) and along the daily light cycle (Leopold and Eynon, 1961), but geoclimatic factors can also be important to determine the composition of the acoustic communities. For instance, Campos-Cerqueira and Aide (2017) have found that elevational gradients drive the acoustic space in tropical communities. The acoustic space created by an acoustic community plays an important role in interspecific communication and environmental exploration.

Taking part in an acoustic community may represent important advantages for the members, like the optimization of defense from common predators when some sentinel species inform of predator arrival. For instance, red-breasted nuthatches (*Sitta canadensis*) interpret the mobbing call of black-capped chickadees (*Poecile atricapillus*) as a signal of danger and thus avoid a possible impending predator attack (Templeton and Greene, 2007).

An acoustic community is characterized by the amount and recurrence of sounds from the most soniferous species at that time of day or season according to the phenological species-specific dynamics. Figure 4 shows spectrograms and acoustic signatures of three different acoustic communities, recorded in the same locality during a day, as an example of the species turnover inside an acoustic community. The great variability in the





Acoustic data were collected using SET (Lunilettronik, It) on May 9, 2016, and spectrograms are displayed by Adobe Audition®. The acoustic signature is obtained by ACIt_f metric. Dominant birds: Tt (*Troglodytes troglodytes*), Er (*Erithacus rubecula*), Tm (*Turdus merula*), Tp (*Turdus philomelos*), Sa (*Sylvia atricapilla*), Oo (*Oriolus oriolus*), Lm (*Luscinia megarhynchos*).

composition of an acoustic community, the variability of the daily time at which species are acoustically active, reflects a short-term behavioral unpredictability, challenging efficient interpretative models.

Acoustic habitat

According to Mullet et al. (2017) an acoustic habitat is defined as a space selected by a species according to a unique emergent sonic ambient character perceived as favorable by a species. Evidence from field observations has proven that species utilize the acoustic information of the environment to select places in which to establish a territory or to stay to forage (e.g., Blumenrath and Dabelsteen, 2004; Derryberry, 2009; Both and Grant, 2012). Experimental evidence has demonstrated how some species like the black-throated blue warbler (*Dendroica caerulescens*) avoid favorable habitats to prefer low-quality habitats in which conspecific calls were playbacked (Betts et al., 2008). In the same way, Mönkkönen et al. (1990) observed how chaffinches (*Fringilla coelebs*) and willow warblers (*Phylloscopus trochilus*) were distributed with a higher abundance associated with a high density of resident tits (*Parus* sp.).

The acoustic quality of habitat is an important factor because habitat selection is a matter of survival or the cause of local extinction for several species. Some species are very sensitive to noise intrusion of anthropogenic origin changing their acoustic habitats (Gil et al., 2015), but others result in tolerance, and the establishment in a noise environment represents an advantage because of less competition with noise-sensitive species (Francis et al., 2009).

The quality of an acoustic habitat represents an important factor of species adaptation, and when such conditions are degraded by human generated noise (Shannon et al., 2014) or by intrusion of alien species (Farina et al., 2013), severe consequences are expected on the fitness of individual species.

The geographical domain of sounds

The geographical domain of sounds represents an important issue, especially in human ecogeography and landscape ecology (Hedfords and Berg, 2003). Sounds penetrate for some extension inside vegetation cover, respond to soil morphology and water bodies with complex diffusive processes that transform, reduce, and degrade the acoustic waves according to the frequencies considered. Sounds of different origin, intensity, and frequency may mingle, creating complex acoustic mosaics or soundscapes that can be interpreted differently by animals according to the species and their "culture" and by humans as well.

The soundscape paradigm

Soundscape is the result of a combination of geophonic, biophonic, and technophonic sources that concur to compose an acoustic mosaic relevant to individual species and their aggregations (Qi et al., 2008). In a seminal paper, Pijanowski et al. (2011) considered the soundscape as the reference entity that represents the acoustic character of a landscape/waterscape and provides the acoustic signature of a locality.

The soundscape paradigm is based on the presumption that animals, including humans, may extract information from the overall acoustic signals that emerge from a landscape. In particular, from a human perspective, the sensitivity of the listener, mediated by cultural background and by the activity being done, may change the meaning of the perceived sonic information (Jennings and Cain, 2013).

Because of the inherent heterogeneity of the landscape/waterscape, soundscapes are not homogeneous in space and time (Rodriguez et al., 2014). This spatial heterogeneity creates sonic patches or sonotopes (Farina, 2014, p. 18). The delimitation and interpretation of sonotopes as suitable or hostile sonic patches depends on the hearing and listening capacity of individual species and by what functions that species is performing.

When only biophonies are considered within a sonotope, a sub-set of sonic entities, called "soundtopes," are distinguished (Farina, 2014, p. 19). As in the landscape narrative, ecotones are areas where different patches are in contact (Clements, 1905; Odum, 1971; di Castri et al., 1988), in the same way, sonic edges or sonotones are the locations where different soundtopes meet each other. In sonotones, many sounds coming from different soundtopes are blended, and conflicting or confused acoustic configurations could be perceived by species. Habitat fragmentation increases the number of acoustic edges and their extension and may have relevant effects of birdsong meme diversity (Sebastian-Gonzalez and Hart, 2017).

The acoustic heterogeneity of the landscape/waterscape is higher than the visual dimension and therefore the soundscape is a better proxy of the complexity of a landscape than geographical or vegetation-based descriptors (Farina, 2014, p. 21).

Often, soundscapes of terrestrial environments are related to human land use and are strongly affected by landscape fragmentation, shape and dimension of composing patches and human disturbance regimes (Tucker et al., 2014; Fuller et al., 2015).

Soundscape is a particularly popular topic in marine research where the identification of soniferous species of invertebrates and vertebrates is restricted to a few groups and where geophonic sounds (water flow, wind, rain) and submerged vegetation have a great impact on the soundscape (Lillis et al., 2014; Ceraulo et al., 2018). In addition, an increased noise intrusion caused by human activity and ocean acidification are of growing concern, and seems especially important for marine soniferous species (Hildebrand, 2009; Radford et al., 2014; Rossi et al., 2016; Haver et al., 2017; Risch and Parks, 2017).

Ecoacoustic event model

A soundscape is not homogeneous in time and space and its heterogeneity is formally composed of a mosaic of sonotopes (and/or by a sub-set of soundtopes), which may represent an important indicator of the characteristic of the landscape. Searching for acoustic patterns like the acoustic sequences (Kershenbaum et al., 2016) is an important endeavor in ecoacoustics, but it remains a difficult task to categorize different ecoacoustic events that emerge from a soundscape in which the acoustic dynamics of soniferous species, often associated with background sounds, create patterns hard to be interpreted (Virtanen et al., 2018).

To better address this issue, Farina et al. (2016, 2018) defined ecoacoustic events as "emergent sonic patterns resulting from individual geophonies, biophonies or technophonies including their combination."

According to this definition, an ecoacoustic event may be represented by a unique sound or a combination of sounds that has ecological relevance for a listener along a specific time scale (Payne et al., 2009). Definitively, an ecoacoustic event is a matter of temporal scale. If the scale is too fine-grained, only one part of an acoustic object is considered, but if the scale is too coarse-grained it is not possible to distinguish emergent patterns of interest, and at both these extremes there is a degradation of meaningful information. To reduce the negative effects of this uncertainty, the temporal scale to detect and identify ecoacoustic events has been tentatively fixed by Farina et al. (2018) to one minute, without excluding other temporal resolutions.

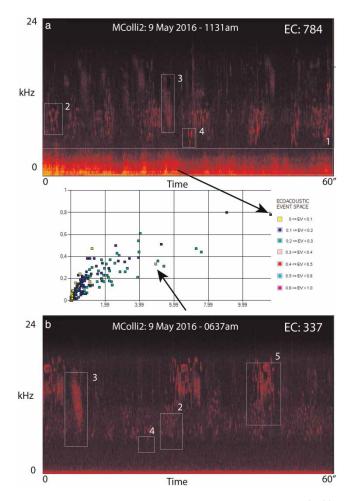
A specific procedure (Ecoacoustic Event Detection and Identification, EEDI) has recently been developed based on the behavior of three metrics (Acoustic Complexity Indices: $ACIf_t$, $ACIf_t$ evenness, and $ACIt_f$ evenness) (Farina et al. 2016, 2018). Every metric is expressed by a number from 0 to 9 and then associated to create a three-digit code where the hundreds represent categories of $ACIf_t$, the tens represent $ACIf_t$ evenness, and units represent $ACIt_f$ evenness. The codes obtained by the EEDI procedure indicate the amount of acoustic information ($ACIf_t$), how it is distributed along a temporal step ($ACIf_t$ evenness), and how $ACIt_f$ is distributed across frequencies ($ACIt_f$ evenness). The total information obtained by this code may be labelled and conveniently aggregated and georeferenced.

If a fast Fourier transform (FFT) window of 1,024 points is applied to one-minute acoustic files, 512 frequency bins are obtained, and 2,812 temporal intervals are scanned. The $ACIf_{t \text{ evenness}}$ is calculated on 2,812 temporal intervals of 0.0022 seconds each, and $ACIt_{f \text{ evenness}}$ on 512 frequency bins. The EEDI procedure can detect and identify hundreds of potential ecoacoustic events.

Figure 5 shows the distribution of 240 one-minute ecoacoustic events in a 24-hour period during the breeding season of an acoustic community from a Mediterranean biome. Only a few of the detected events are unambiguous, and the comparison with a library of classified events is requested for their definitive identification.

The EEDI procedure can be utilized not only to investigate the dynamics of acoustic communities in a single location but also to map a soundscape using an array of calibrated and synchronized autonomous recorders. The ecoacoustic event approach is a useful tool to discover recurrent patterns across a soundscape and to establish geographic delimitation of the sonotope/soundtope mosaic.

In the same way, it is possible to establish acoustic borders of sonotones between sets of different ecoacoustic events. This delimitation may have a great impact in landscape management at every level of human intrusion. The delimitation of sonotopes, soundtopes, and sonotones in a landscape is an important exercise to describe the level of acoustic patchiness. The ecoacoustic event has the great advantage to produce information about sonic patterns generated in a soundscape without the bias of human perception and interpretation. This approach allows the addition of acoustic descriptors of the complexity of landscapes and freshwater and marine waterscapes and can be applied to evaluate the level of noisy intrusion or the level of human manipulation of natural systems and to assess their quality.





For more details on the methodology, see Farina et al. (2018). The Ecoacoustic Event Space is the ordination of each minute according to the EEDI procedure (X axis = $AClf_t$, Y axis = $AClf_t$ evenness, color = $AClt_{f evenness}$). At the temporal scale of one minute, two ecoacoustic codes, EC784 and EC337, with their spectrographic representation, have been selected from the 240 identified and are shown as an example. Components of these events resulted in a technophony (1: Low altitude airplane) and four types of biophonies (2: Sylvia atricapilla; 3: Fringilla coelebs; 4: Turdus merula; and 5: Troglodytes troglodytes songs).

Ecosemiotic domain

This domain pertains to ecoacoustic codes used to transmit acoustic intra- and interspecific information between individuals, populations, and communities, and the acoustic mechanisms (the acoustic eco-field) utilized by individual species to track resources (food supply, nesting place, refuges, etc.).

The ecoacoustic codes

Despite their insufficient consideration in ecological literature (Mislan et al., 2016), there is a lot of evidence on the presence of ecological codes that assures the exchange of information between organisms, their aggregations, and the environment (Barbieri, 2003, 2013). According to the communication theory (Shannon and Weaver, 1949), there is an emitter and a receiver connected by an operational channel through which information passes after a process of encoding and decoding.

The ecological codes have been defined by Farina and Pieretti (2014) "as mechanisms that establish an arbitrary set of connections between two or more components (organisms and/or their aggregations) of a complex system". At the same time, it is reasonable to assume a role of codes in the flow of meaningful information during acoustic communication between species and during the use of sounds to perform some biological functions (Farina, 2018).

The ecoacoustic codes are operating from an individual species (the receiver) and acoustic sources that may be individual species, acoustic communities, or soundscapes. A dyadic intraspecific exchange of information operates

between an emitter and a receiver at an individual level, where the acoustic signals are discriminated, identified, and labelled, transferring information that considers theme, variation, motif, repetition, and intensity of signals.

At the level of acoustic community, ecoacoustic codes transfer information coming from voluntary or unintentional heterospecific emitters to a receiver. The decoding process provides information on habitat suitability, the presence of predators, location of food sources, and availability and location of refuges.

Finally, at the soundscape level, a receiver may utilize acoustic encoded information from the three sub-entities that compose a soundscape: sonotopes, soundtopes, and sonotones. This is obtained from an integration of geophonic, technophonic, and biophonic sources that are interpreted as a complex signal carrying meaningful information.

The acoustic eco-field

Sound represents a communication vehicle and also an ecosemiotic tool adopted by species to explore the environment and to track resources. The mechanisms involved in such ecosemiotic processes have been described by Farina (2018) as a process that generates an acoustic eco-field.

An eco-field is a spatial configuration (of objects) that carries meaning through a cognitive template, when a specific function is activated to satisfy a physiological need (Farina and Belgrano, 2004, 2006). For instance, a recently plowed field is recognized as a foraging eco-field for black redstarts (*Phoenichurus ochruros*), and a kaki tree with ripe fruits is a foraging eco-field for different species of frugivorous passerines like blackcaps (*Sylvia atricapilla*) or log-tail tits (*Aegithalos caudatus*). A meadow margin in a forest landscape is recognized as a foraging eco-field (f.i., searching ground insects and earthworm) for blackbirds (*Turdus merula*) and European robins (*Erithacus rubecula*).

Supported by the General Theory of Resources (Farina, 2012), the eco-field theory considers some sounds to be carriers of meaning for functions like food searching, refuge location, or predator avoidance. Like the dance of honey bees is a visual representation of nectar and pollen sources (von Frisch, 1967) associated with the release of chemical compounds with semio-chemical functions (Thom et al., 2007), the intensity of calls and their persistence in time of some birds like blackcaps (Figure 6) at a foraging site generate an acoustic eco-field that actively informs other conspecifics or accidentally eavesdropping species about the quality and quantity of the source of food.

The eco-field hypothesis requires a preliminary assumption that soniferous species recognize in some way the biophonies of other resident species and give it a precise meaning.

The interpretation of heterospecific sound has been supposed to be present in many communities and favors the suitability of habitats. From the literature, there is evidence that species utilize interspecific visual, olfactive, or acoustic information extensively to create heterospecific assemblages (Goodale et al., 2010; Suzuki and Kutsukake, 2017). Some bird assemblages have been considered information centers for finding food (Ward and Zahavi, 1973; Waltz, 1982; Brown, 1988).

That some species are able to interpret the acoustic signals of other species is increasingly evident (Alatalo et al., 1985; Magrath et al., 2007; Fallow and Magrath, 2010; Dorado-Correa et al., 2013; Wheatcroft and Price, 2015). This evidence supports the theory of the acoustic eco-field as an ecosemiotic information structure that is used by every individual of every species that is an emitter (creates the acoustic eco-field for other species) and a listener (utilizes the acoustic eco-field as a result of the acoustic activity of other species).

Discussion

Sounds play such a broad role in the environment that exploring their ecology represents a great opportunity and an important way to better understand adaptation mechanisms and evolutionary radiation of species under environmental change. Ecoacoustics can approach these issues in a qualitative and quantitative manner across a broad range of functional scales from individuals, populations, communities, ecosystems, and landscapes and according to interconnected epistemological domains.

Inside the acoustic adaptation domain, the main factors responsible for the adaptation of acoustic emission of sonifeorus species to the environmental variability that occurs over a long period of time are described. The time of adaptation probably depends on the adaptive capacity of species to a specific life trait, and this process requires a long stability of the systems in a way that evolutionary changes may operate.

Conversely, the acoustic partitioning should be a process operating to a relatively lower evolutionary time because the control factors (species) have a short life span and the entire process is relatively short. Both processes are active at the same time on the same subjects driven by a convergent tradeoff.

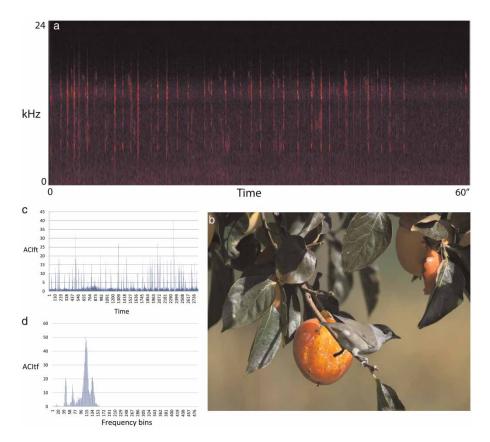


Figure 6. Example of acoustic eco-field produced by calls (a) of blackcaps (*Sylvia atricapilla*); (b) at a foraging site (a plant of kaki (*Diospyros sp.*)).

In (c), temporal distribution along one minute of recording of $ACIf_t$. In (d), the acoustic signature of the calls produced after the application of $ACIt_f$ algorithm. This acoustic eco-field may attract the attention of other species of frugivorous birds like blackbirds (*Turdus merula*), great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), and chaffinches (*Fringilla coelebs*).

The behavioral acoustic domain is active during a very short period of time, and acoustic communities are really a temporary aggregation of acoustic expressions that probably affect daily and seasonal functions. A large overlap between acoustic community and acoustic habitat can be recognized. The acoustic community is more dominated by behavioral responses and the acoustic habitat process is midway between environmental adaptation and acoustic community function. Both processes consider the individual perception of the surrounding acoustic space.

The acoustic processes in the geographic domain are related to the species-specific perception of the subjective acoustic surrounding or "acoustic Umwelt" (sensu von Uexküll, 1982, 1992). Soundscape is the overall sounds that are perceived by a listener as a carrier of meaning. The capacity of a listener to distinguish acoustic patterns and to assign a meaning is a matter of individual perceptive and cognitive competence (Truax, 2001, pp. 15–32). The soundscape conceptualization arouses great interest in human sciences because people, although they have similar age-dependent hearing capacity, listen differently according to their cultural background (Truax, 2001, p. 11): soundscape diversity reflects the culturally-driven perception of local human populations.

The extension of the soundscape concept to perception and cognition of animals represents a true challenge because little is known about the listening and interpretive capacity of soniferous species. To overcome such difficulties, the acoustic event model is proposed as a statistical method to assign a specific code algorithmically to an aggregate sequence of sounds. This procedure may be powered by the application of a further fractal analysis (Hsü, 1993; Bigerelle and Iost, 2000; González et al., 2012) to better illustrate the complexity of the acoustic system.

The ecosemiotic domain may be considered conceptually well separated from the other domains discussed. The ecosemiotic paradigms investigate the sign relationship utilized by organisms to perceive, categorize, and use environmental objects (Maran and Kull, 2014). The importance of semiotic processes in the ecological realm is often considered subordinate to other processes, ignoring that semiotic mechanisms are at the basis of every relationship from cell resolution to ecosystems, and that the semiotic process is itself life (Barbieri, 2015). Acoustic

encoding is a fascinating topic with great implications in the intra- and interspecific relationships. Unfortunately, little knowledge about acoustic cognition in non-human animals reduces the possibility for a comparative analysis and the separation of confounding effects (Hoeschele and Fitch, 2016). There is evidence that some species recognize heterospecific signals especially as alarm calls that have a direct effect on the survivorship of emitters and eavesdroppers (Magrath et al., 2014). The results discussed by Ridley et al. (2013) on the benefits for a solitary bird (the scimitarbill (*Rhinopomastus cyanomelas*)) to utilize the sentinel calls of a social species (pied babbler (*Turdoides bicolor*)), reducing 60% of the vigilance in the presence of pied babblers that have a more advanced system of social helping, are very convincing.

All this evidence of heterospecific acoustic reconnaissance can be explained by the presence of acoustic codes that transfer important information from species-specific acoustic Umwelt to another translating a perceptivecognitive language into another language. Experimentation and acoustic engineering could help discover the acoustic codes involved.

The acoustic eco-field operates inside the ecosemiotic paradigm where individual species use acoustic signs as carrier of meaning to track some resources. Several implications support this approach, such as species that lose the capacity to recognize an acoustic pattern linked to a specific resource may suffer from an ecological debt (sensu Tilman, 1994). The disappearance of some acoustic configurations, due to climate change or human intrusion, may weaken the capacity to find specific resources.

Concluding remarks

Sound is a powerful, universal vehicle of meaningful information, mandatory for several species to establish fundamental relationships with the surrounding world, and ecoacoustics has been demonstrated to have several ecological, behavioral, ecosemiotic, and geographic competencies to face environmental sonification.

A rich set of principles, paradigms, and hypotheses creates a robust theoretical framework for ecoacoustics, but a few spaces, like in "classic" ecology (Scheiner et al., 1993), are still devoted in the literature to the epistemological aspects and their implications: a few models and experimental tests have sprung up from these theoretical bases. The majority of research in ecocoustics is focused on heterogeneous epistemological thematics like the distribution of soniferous species in relation to habitat, landscape, and biome characters, noise effects, chorus patterns, biodiversity assessment, and acoustic phenology under climate and/or anthropogenic change, confirming the distance that in ecology apparently exists between theory and emergent topics, as recently outlined by Scheiner and Willig (2008).

Due to an intrinsic variability and a strong correlation with climate events and human disturbance regimes, a large set of data from which to identify emergent properties and to avoid confounding effects is requested. But a large time series requires shortcuts during data mining to save time to detect and classify species and acoustic sequences (Kasten et al., 2010). A trade-off between a detailed aural survey that requires a great amount of time, specific biological competencies, and too synthetics indices is represented by the spectrogram pattern analysis obtained, for instance, by visual comparison (Towsey et al., 2014b,c, 2015, 2016) or by numerical encoding using the EEDI procedure (Farina et al., 2018). Both approaches can be used as intermediaries to distinguish common events from exceptional or rare events.

Often for an efficient application to a species, a survey and biodiversity assessment is necessary to filter biophonies from geophonies and technophonies. This procedure requires metrics of denoising based, for instance, on a wavelet transform (Graps, 1995; Priyadarshani et al., 2016).

As happens for other scientific disciplines, ecoacoustics investigates entities like soundscapes or acoustic communities that require temporal and spatial reference systems that often are not available, and data collected may be difficult to use, especially for a comparative analysis. A lack of standardized protocols in data collection and processing in some cases makes the ecoacoustic approach challenging, although these difficulties will likely be overcome in the near future when researchers have access to innovative technologies, affordable metrics, and robust statistical procedures. For instance, when and how long to deploy field autonomous recorders, their positioning and density, microphonic input gain, temporal interval between a recorder episode and the next, or a background noise filter threshold are some technical ways to standardize surveys and calibrate devices. Seasonality of field surveys may have a great impact on the extension of the results to a comparative analysis.

Despite these limits, ecoacoustics is successfully practiced in several biomes under different landscape/ waterscape configurations, confirming its great potentiality to describe distribution, abundance, and acoustic dynamics of soniferous species and to improve the knowledge of the role of sounds in natural history across a broad range of ecological scales, offering new proxies to better understand environmental functions.

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