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Farina, A and James, P

http://dx.doi.org/10.1016/j.biosystems.2016.05.011

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The acoustic communities: Definition, description and ecological role

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Abstract

An acoustic community is defined as an aggregation of species that produces sound by using internal or extra-body sound-producing tools. Such communities occur in aquatic (freshwater and marine) and terrestrial environments. An acoustic community is the biophonic component of a soundtope and is characterized by its acoustic signature, which results from the distribution of sonic information associated with signal amplitude and frequency. Distinct acoustic communities can be described according to habitat, the frequency range of the acoustic signals, and the time of day or the season. Near and far fields can be identified empirically, thus the acoustic community can be used as a proxy for biodiversity richness.

The importance of ecoacoustic research is rapidly growing due to the increasing awareness of the intrusion of anthropogenic sounds (technophonies) into natural and human-modified ecosystems and the urgent need to adopt more efficient predictive tools to compensate for the effects of climate change. The concept of an acoustic community provides an operational scale for a non-intrusive biodiversity survey and analysis that can be carried out using new passive audio recording technology, coupled with methods of vast data processing and storage.

Key words: acoustic community, acoustic signature, ecoacoustics, sonotope, soundscape, soundtope

Introduction

In the past few years, there has been growing interest in the use of environmental sounds to investigate ecological complexity. Some empirical evidence suggests that biological and non-biological sounds can be used to examine and interpret various dynamic ecological processes (Towsey et al. 2014a) and, as a result, new perspectives in theoretical and applied ecology have
been advanced. One such advance is the emerging discipline of ecoacoustics, which is the ecological investigation and interpretation of environmental sounds (Sueur and Farina 2015), and the associated central concept of the acoustic community.

The term “acoustic community” can be found in the literature of many disciplines: art, sound technology and sociology, as well as biology (bioacoustics), ecology and, in particular, ecoacoustics. The composer, writer, music educator and environmentalist, R. Murray Schafer, who coined the word “soundscape”, argued that an acoustic community can be defined “as a political, geographical, religious or social entity” in which the human voice is used as the primary tool to define the community’s limits (Schafer 1977: 215). Another composer, Barry Truax (1984: 58), defined an acoustic community as:

[A]ny sound-scape in which acoustic information plays a pervasive role in the lives of the inhabitants (no matter how the commonality of such people is understood). Therefore, the boundary of the community is arbitrary and may be as small as a room of people, a home or building, or as large as an urban community, a broadcast area, or any other system of electroacoustic communication. In short, it is any system within which acoustic information is exchanged.

The emphasis of these two definitions is firmly located within the human realm, but the last sentence in Truax’s definition is interesting in that it refers to the exchange of information between members of a community. Outside this human focus, there is a socio-ecological perspective that combines people and wildlife (e.g. Ritts et al. 2016). Here acoustic community is most frequently used as a description of groups of organisms interacting acoustically with each other in a specific habitat (e.g. woodland, urban park, crop field, seabed or reef) (e.g. Drewry and Rand 1983; Price 1984; Sueur et al. 2008b; Luther 2009; Gasc et al. 2013a; Lellouch et al. 2014). However, Truax (1984) took the concept further and used the term to describe patterns and processes related to the ecological role of the sounds: an idea that takes the term beyond descriptive.

Hence, the aims of this article are: (1) to define, with an ecological perspective, an acoustic community and describe its main characteristics; (2) to set out its importance as an aggregative structure in which species operate; and (3) to explore the relationships and the implications of acoustic communities with other key concepts in ecoacoustics, such as the acoustic adaptation
hypothesis (AAH) (Morton 1975), the acoustic niche hypothesis (ANH) (Krause 1993), and more recent concepts, such as the sonotope, the soundtope and the sonotones (Farina 2014), which have emerged from soundscape ecology theory (Pijanowski et al. 2011a, 2011b). Table 1 presents the definitions of some of the terms and concepts used in this article, belonging to the ecoacoustics field.

Table 1 presents the definitions of some of the terms and concepts used in this article, belonging to the ecoacoustics field.

**The acoustic community: definition and description**

The most commonly explored acoustic communities and associated acoustic patterns are terrestrial communities, with the majority of studies focused on avian and amphibian species. Descriptions of freshwater acoustic communities do exist but they are limited to a few habitats (Desjonquères et al. 2015). Studies of marine acoustic communities, although of great interest, are limited due to species identification difficulties and the cost of the research, especially in deep oceans (Hastings and Sirovic 2015). Across all habitats, to date, there have been only a few studies offering information on the structure and dynamics of acoustic communities (e.g. Malavasi and Farina 2013) but even these have not provided details of the ecological processes that create, maintain and shape such aggregations.

Following Gasc et al. (2013b) and Lellouch et al. (2014), we propose to define an acoustic community as an aggregation of species that produce sound by using internal or extra-body sound-producing tools. Such communities occur in both terrestrial and aquatic environments.

There are three broad types of acoustic communities: (1) infrasonic (e.g. whales (Cetacea) <20 Hz); (2) “ordinary” (the majority of vertebrates 20–20000 Hz, humans included); and (3) ultrasonic >20000 Hz (e.g. bats (Chiroptera), dolphins (Cetacea) and some insects). It is reasonable to assume there are evolutionary mechanisms for frequency partitioning that reduce acoustic niche overlap and interspecific competition for frequencies in which communication takes place. Each community, therefore, has a distinctive acoustic signature which describes the frequencies and amplitude of the sonic signals produced by its members (see also Bormpoudakis et al. 2013). An acoustic signature is defined as the fingerprint that emerges from the distribution of frequency categories of sounds emitted by the species comprising an acoustic community. This signature can be considered equivalent to a biological code (Barbieri 2015) and is species- and community-specific (Farina and Pieretti 2014a; Malavasi et al. 2014).
Figure 1 presents examples of acoustic signatures of fish, snapping shrimp, frogs, tropical birds and insects from Borneo, and bats, obtained by adopting the Acoustic Complexity Index (Pieretti et al. 2011). The acoustic signature of each species can be used to measure the acoustic niche overlap and breadth of the entire community (e.g. Sinsch et al. 2012). The niche overlap measures the degree of potential competition between two or more species. Niche breadth can be used as a proxy for species richness in an acoustic community and allows a comparison of the different acoustic communities, as the more species that contribute to an acoustic community, the wider the resultant niche breadth. The specific acoustic signature of an acoustic community changes temporally because it is connected to the species-specific variability of the sound produced throughout a day, a season or a year. As reported in the example in Figure 2, the same location shows different acoustic signatures between 0400 a.m. to 0800 a.m. At every hourly interval different species interact acoustically, confirming the dynamic character of an acoustic community.

At the seasonal scale, the arrival and departure of migratory species can be tracked by the changes in the acoustic signature as the arrival or departure of one or more species adds or reduces the complexity of the signature (e.g. Farina et al. 2013).

Frequencies within an acoustic community are not random but are the result of adaptations that operate to reduce interspecific competition (Planqué and Slabbekoorn 2008). From empirical observations it is known that species can limit acoustic overlap in both frequency and time (Malavasi and Farina 2013). This frequency/time partitioning is conceptualized by the acoustic niche hypothesis (ANH). The ANH, an extension of the niche theory of Hutchinson (1957), is an important concept which was described by Bernie Krause (1993). Although some authors consider the ANH to be a controversial assumption (Planqué and Slabbekoorn 2008; Tobias et al. 2014), the ANH is the result of empirical observations that demonstrate that species that vocalize at the same time in the same location do not overlap acoustically, thus producing a partitioned acoustic space (Sueur 2002; Sinsch et al. 2012; Malavasi and Farina 2013).

Spatial aspects of an acoustic community
The spatial delimitation of a community is central to research in community ecology and biogeography (MacArthur and Wilson 1967). Communities are frequently defined according to different modalities of aggregations based on the physiological traits (functions) of their components, including “foraging communities”, “habitat communities”, or by environmental fundamentals as “patch communities”. For instance, Forman and Godron (1981: 734) define a “patch community” as “communities or species assemblages surrounded by a matrix with a dissimilar community structure or composition”. A patch community exists within a wider species assemblage and is determined by the degree of interaction between these species. An acoustic community is an appropriate way to consider the temporal and spatial associations between species. For example, there may be least twelve species of birds living on a Mediterranean farm habitat: three species sing from the rooftop (house sparrow (Passer domesticus), black redstart (Phoenicurus ochruros), and starling (Sturnus vulgaris)), five species sing in the hedgerows (blackcap (Sylvia atricapilla), European goldfinch (Carduelis carduelis), serin (Serinus serinus), great tit (Parus major), and blackbird (Turdus merula)), and four in ecotonal woodland (European robin (Erithacus rubecula), blue tit (Cyanistes caeruleus), wryneck (Jynx torquilla), and chaffinch (Fringilla coelebs)). Rarely do these different groups of species coincide in acoustic activity. Depending on the weather conditions, at different times of the day and in the different seasons these species create acoustic communities that are independent according to the sub-habitat in which the species live (Malavasi and Farina 2013; Farina et al. 2014b).

The perception of an acoustic community is dependent on the position of the listener in exactly the same way that the visual appreciation of a landscape can change depending on the location of the viewer. If there is more than one listener in a location, that is, either by there being more than one person or more than one audio recorder (for example, an array of microphones), then it is possible to produce a spatial map of the acoustic community. Like a patch of land or seabed mosaic, a core area may be distinguished from a marginal area for each acoustic community (e.g., Catchpole and Slater 2008).

To overcome the spatial issues associated with acoustic communities, a filter can be applied on the amplitude of the signal to empirically distinguish the “far field” (signals at low amplitude) from the “near field” (signals at high amplitude) at which individuals operate within an acoustic community (Farina 2014). This procedure is based on the assumption that species that are part of the same guild emit sounds with similar amplitude and that the amplitude of signals has a low variability due to different physiological conditions of species. This assumption must be
considered with some caution because minor differences in amplitude have been found between individuals of the same species (Brumm 2009). For example, sub-song (an unstructured, often rambling vocalization of low volume emitted by young birds and by adults of some species at the start of the breeding season) is a temporary phenomenon. The variation is not voluntary but depends on the physiological status of the individual. Nonetheless, variation in the amplitude of the sound from more than one individual within such a guild means that these individuals are at different distances from a biological listener or microphone. In this way, an acoustic habitat where there is a high occurrence of high amplitude signals (near field) is expected to be richer in individual species than a habitat with a high occurrence of low amplitude signals (far field).

In marine environments, where sound propagates much faster and further, it is challenging to apply the far-near field model, at least using the terrestrial-scaled distance.

Temporal aspects of an acoustic community

Acoustic communities vary throughout the day, according to lunar phases, as recently described in marine communities (McCauley 2012, Staaterman et al. 2014) and over a year. On a daily scale, there are daylight and crepuscular communities (e.g. songbirds, insects) and nocturnal communities (e.g. insects, frogs, bats, fish, snapping shrimps) (Figure 3). An acoustic community that has a daylight cycle generally reaches its acoustic maxima twice, at dawn and dusk (e.g. Leopold and Heynon 1961). In passerine birds, dawn and dusk are the two periods during which, especially during the breeding season, all the species vocalize together. This phenomenon, though recognized for a long time and well investigated, has not been unequivocally explained in terms of its role (e.g. Staicer et al. 1996; Berg et al. 2006). In songbirds, during the breeding season, the acoustic activity prevalent in the morning is divided into three periods of equal length: the dawn chorus, the post-dawn chorus 1 and the post-dawn chorus 2 (Farina et al. 2015). The dawn chorus has been calculated empirically as the time lag between the first song and sunrise. A lull at sunrise separates the dawn chorus from the post-dawn choruses 1 and 2 and is explained by a simple model that postulates that singing is an energy-demanding behaviour and that such energy spent singing continuously before sunrise should be recovered by subsequent intensification of foraging activity and a reduction of the singing behaviour during the post-dawn chorus 1 and a successive increase of singing activity after this recovery during the post-dawn chorus 2 (Farina et al. 2015).
Other animals have acoustic activity peaks outside these two periods, for example, male cicadas ‘sing’ when the ambient temperature is at its maximum (Sueur and Sanborn 2003), thus illustrating differences in acoustic communities. Cato (1969) and Wyllie (1971) reported on a fish chorus occurring at night. This behaviour has been confirmed in fishes of the Terapontidae family where the choruses, associated with reproduction, occur nightly from November to May (McCauley 2012). A night-time peak of humpback whale (Megaptera novaeangliae) song activity has been observed in the waters off western Maui (Hawaii Islands) by Au et al. (2000). On an annual scale, variation within an acoustic community, especially in terrestrial habitats, depends largely on the latitude at which an acoustic community is situated. In the tropics, variation in acoustic activity changes little during a year, but once one moves to higher latitudes (> 70° north or south), seasonality becomes important, with the maximum in June–July and the minimum in winter (Pijanowski et al. 2011b). For instance, at temperate latitudes, acoustic communities of birds have a secondary peak in autumn during migration (e.g. Farina et al. 2013).

It has been demonstrated that climate change is influencing species’ range expansion and contraction (Hughes 2000; McCarty 2001; Walther et al. 2002). Hence, knowledge of the temporal patterns that emerge from the study of communities located at different latitudes assumes a central importance when tracking the effects of global climate change (IPCC 2007). The design of a global scale inventory that characterizes acoustic communities in focal habitats or biomes may represent a reasonable goal to better understand what is happening in the climatic scenario, and consequently to devise the best policies to reduce the negative effects of such a worrying emerging phenomenon.

In fact, animal sounds are life traits characterized by high plasticity, and hence enhance a species’ ability to cope with variations in environmental fundamentals, such as vegetation cover, land mosaic structure, temperature, humidity and pH (for aquatic medium) (Krause and Farina 2016). Pairing acoustic data sets with efficient models produced for vegetation processes, such as the global vegetation models (DGVMs) (Pearson and Dawson 2003), should be further explored to address the challenge of climate change.

**Physical aspects of an acoustic community**

When monitoring a habitat using passive acoustic procedures (Merchant et al. 2015), recording the spatial limits of an acoustic community is vital. For instance, in terrestrial habitats, it is important to know the spatial boundaries of sounds emitted by species in order to optimize the
locations of the monitoring equipment in the correct position. However, this is not an easy task as the behaviour of acoustic energy is affected by the physical structure of the environment. Sound is transmitted in different ways, according to the relief of the landscape and the character of the vegetation. For instance, in mountainous areas, sounds are transmitted differently from those of flat regions (Hunter 1989). Hence, the geographical character of a region represents an important element that affects sound transmission. The acoustic adaptation hypothesis (AAH) elaborates on this fact (Morton 1975). According to the AAH, in order to maximize the efficiency of communication, acoustic species should adapt to the quality of the sounds. For example, species have modified their acoustic performances to adapt to their environment (Patten et al. 2004). Hence, for each typology of environment, it can be expected that sounds emitted by different animals will have similar characteristics. This has important effects on the patterns emerging from an acoustic community because the dynamics of the acoustic communities are affected by the sonic context in which such communities are embedded.

A new challenge is facing the AAH in the modern world where new environmental constraints are emerging. As the technological world has spread, technophonies have been increasing in amplitude. Such technophonies are classified as noise. From a human perspective, noise is unwanted sound that can interfere with the transmission of signals (Truax 1999). It is reasonable to assume that the acoustic noise also represents a problem for animal communication.

Sound quality level may be expressed as high fidelity (Hi-Fi), where the ratio signal-to-noise is greater than 1, or low fidelity (Lo-Fi), when the signal-to-noise ratio is less than 1 (Rumsey and McCormick 2009: 583). This concept, which was first used with respect to humans (Schafer 1977), is now being extended and applied to ecoacoustic investigations of animals (Farina 2014). In a Hi-Fi environment, acoustic information is transmitted fully to the listener without significant losses. A sonic environment is defined as Lo-Fi when a noise reduces the possibility of fully decoding the acoustic information from the surroundings. For instance, the urban soundscape is usually Lo-Fi, but a wild remote area far from technophonies and in the absence of geophonies is expected to have a Hi-Fi soundscape. An acoustic community can be active in both Lo-Fi and Hi-Fi environments but the adaptive strategies of species differ accordingly (Brumm 2004), as a consequence of the effect of the sonic environment quality on the acoustic community (Francis et al. 2011). In Lo-Fi environments, species may change the amplitude of their signals and shift frequencies in order to communicate successfully. Species that do not have such an adaptive
capacity can experience a dramatic decrease in abundance or even become locally extinct (Baynes et al. 2008).

**Behavioural aspects of an acoustic community**

Sounds used by acoustic animals have several functions: mate attraction, mate stimulation and guarding, territorial defence, male disputes or foraging, especially during the breeding season (Catchpole and Slater 2008; Laiolo 2010) and sound signals are considered an honest signal (Gil and Gahr 2002), that is to say that their quality is a proxy for the individual’s health. These animals may have a dyadic relationship – a signaller and a receiver – but when several individuals are signalling and receiving at the same time, there is a network of signallers-to-receivers that creates an acoustic community (McGregor and Dabelsteen 1996).

There is a high probability that a high amplitude of sound emitted corresponds to the presence of a signaller close to the recorder, and low amplitude is the result of individuals that are emitting a sound far from the recorder (Figure 4). This acoustic fading, strictly connected with the physics of sounds, is perceived by species to be a degraded form (e.g. Naguib 1996). If a signal is degraded too much, the risk is that it will be wrongly decoded, with associated unfortunate consequences for the quality and efficiency of intra- and inter-specific communication.

Unexpected effects on the entire acoustic community that are attributable to noise have been observed in urban areas (Joo et al. 2011). Francis et al. (2009) have argued that noise disrupts prey–predator interaction because predators seem more sensitive to the noise level and avoid areas in which this noise is high, that is to say, they avoid Lo-Fi environments. In this case, noise represents an advantage for some species of birds but, in the majority of cases, noise affects the acoustic habitat of species (Barber et al. 2009), masking signals that could prevent an efficient transmission or successful reception of the acoustic information.

**The relationship between acoustics communities and the soundscape narrative**

Recent advances in soundscape ecology (Pijanowski et al. 2011a, 2011b) have enabled a better understanding of the structure and dynamics of the sonic environment. The relationship between the soundscape and acoustic communities is both epistemological and hierarchical. In this section, to reduce the semantic confusion that is typical of every young discipline, such as soundscape...
ecology and ecoacoustics (Sueur and Farina, 2015), we clarify the relationship between the
episodic objects used to describe the patterns and the process of a soundscape (Farina 2014), and
the acoustic community paradigm is described.

The soundscape, or sonic environment, has been defined as the entire range of geophonic,
biophonic and technophonic sounds produced in a region (Schafer 1977; Truax 1984; Porteous
and Mastin 1985; Krause 1993; Qi et al. 2008; Pijanowski et al. 2011b; Farina 2014). Geophonies
are the sounds produced by geophysical sources such as a waterfall, thunder, the wind, an
earthquake, etc. Biophonies are the sounds produced by biological activity and are mainly related
to intra- and inter-specific communication (e.g. songs, contact calls, alarm calls, and
vocalizations). Technophonies are the sounds produced by machinery. A soundscape approach
takes into account all the components of the sonic environment and analyses the sonic patterns
that emerge from the relations between sound sources and land or seabed cover typologies
(Tucker et al. 2014; Fuller et al. 2015), and temporal dynamics (Gage and Axel 2014).

The soundscape, like the geobotanical landscape, is heterogeneous in space and time, and is
composed of acoustic patches or sonotopes (Farina 2014) that result from the spatial combination
of three acoustic sources: geophonies, biophonies and technophonies. Sonotopes (Farina 2014:
17), or acoustic habitats, as recently argued by Merchant et al. (2015), are the result of natural and
man-made processes, and differ according to the location, creating specific acoustic identities.

Moreover, the three components of a sonotope may be present, each with a different importance,
inside a single sonotope. For instance, in urban landscapes, technophonies (often also called
anthrophonies) will likely contribute more than 90% of the sound energy (Joo et al. 2011), but in
native forests, the prevailing sounds will be biophonies, and along a mountain stream, geophonies
are the dominant component (Krause et al. 2011). A sonotope is an important ingredient in the
habitat quality of acoustic communities and its assessment represents a good proxy for predicting
and explaining the distribution of species in space and time.

In each sonotope the biophonic activity of the animals changes as different individuals move
through the habitat, and aggregations of species change, thus creating a unique sonic environment:
the soundtope (Farina 2014: 19). The concept of a soundtope, a pattern exposed to ephemeral
behavioural processes, is linked to the acoustic activity of each species along with any
technophonies and geophonies, and may vary according to the abundance of individuals that are
singing at a precise time in a season and in a day. The soundtope model is equivalent to the
acoustic community concept but the soundtope model incorporates environmental conditions not considered by the acoustic community model used to describe only biophonic processes (Figure 5). For instance, the soundtope is the context within which birds are counted by aural census work (Bibby et al. 1992). Counting animals using aural methodology results in an aleatory approach that requires highly trained operators and the investment of a lot of human energy in the field. Inevitable biases are introduced that are due to inter-individual variability in the evaluation of species abundance and due to the disturbance caused by the physical intrusion of the operator in the investigated habitats.

The adjacency of two or more soundtopes creates a sonotone (Farina 2014: 19). This is a process analogous to the creation of an ecotone in landscape ecology (Forman and Godron 1986; Hansen et al. 1988). The acoustic space in a sonotone may be mixed, creating a diffuse area of interference for acoustics communities. It is not easy to measure the effects of sonotones on individual species but it is reasonable to expect that the acoustic habitat (*sensu* Merchant et al. 2015) present at the margins of soundtopes may be more difficult to interpret by acoustic animals because individuals are at the same time exposed to more signals from a higher variety of species than individuals living in core areas. This excess of information may have consequences on territory delimitation, prey–predator interference, reproductive success, and represents an important area for further investigation (McGregor and Dabelsteen 1996: 410).

**Advances in hardware and analytical approaches to describe acoustic communities**

Today, as a result of advances in hardware (e.g. digital recorders, Farina et al. 2014a) and software (Sueur et al. 2008b; Pieretti et al. 2011; Kasten et al. 2012; Villanueva-Rivera and Pijanowski 2012, Towsey et al. 2014c; Merchant et al. 2015), it is possible to describe the acoustic composition of an acoustic community on a large scale (Towsey et al. 2014b), to explore and map the partitioning of acoustic space (both temporal and spatial) by the community members (Sinsch et al. 2012), to assess the acoustic diversity (Depraetere et al. 2012; Gasc et al. 2013b), and to measure the acoustic interactions within and between species in a community (Farina and Pieretti 2014b). This opens up new potential to apply the acoustic community paradigm to environmental assessment and nature conservation in terrestrial (Laiolo 2010) and marine systems (Cato et al. 2006; Hastings and Sirovic 2015; Harris et al. 2016). In fact, the composition of an acoustic community is a good proxy for a broad appraisal of the biodiversity at a location. This
approach, like the other acoustic assessment techniques, is possible only when animals are acoustically active. New automated sound recording techniques are available to improve such an approach (Brandes 2008). Recently Sueur et al. (2008b) have applied the concept of alpha and beta diversity to 540 simulated acoustic communities, demonstrating for the first time that an indicator of biological diversity can be obtained in a non-invasive way. These authors applied the Shannon index of entropy (H) to measure the value of diversity in artificial choruses, demonstrating that high values of H correspond to a high number of species. Some bias can be introduced by wind, running water, and human activity, but Sueur et al. (2008a) argued that applying a cut-off frequency for values below 200 Hz is a precaution sufficient to eliminate the saturation of the H index.

Other metrics have been used to evaluate the richness of acoustic communities as a proxy for overall biodiversity (Pieretti et al. 2011; Depraetere et al. 2012; Staaterman et al. 2014; Towsey et al. 2014c; Fuller et al. 2015) but, when passive recording is utilized, the evaluation of species richness still requires a vast computational effort. To reduce the time required, Wimmer et al. (2013) suggested selecting 120 1-minute samples from the three hours after dawn. With this strategy these authors were able to detect using an aural approach 62% of the species actually present. In another case study, Pieretti et al. (2015) proved that the passive recording of 1 minute in every 5 is a good compromise in a tropical ecosystem. However, comparison of automatic passive recordings with aural identification remains an obligatory step, when possible, for an accurate biodiversity assessment (Farina et al. 2013).

**Discussion**

Ecoacoustic research in terrestrial and in aquatic (freshwater and marine) environments is flourishing on a global scale as an important new tool to monitor human-dominated wild ecosystems (Truax and Barrett 2011; Towsey et al. 2014c, Mullet et al. 2016) and otherwise inaccessible aquatic systems (Hastings and Sirovic 2015). In June 2014 terrestrial and marine sound ecologists gathered in Paris for the first ecoacoustics meeting. At this meeting the International Society of Ecoacoustics (ISE) (https://sites.google.com/site/ecoacousticssociety) was launched. This interest is, in part, a direct consequence world-wide of the intrusion of anthropogenic noise which is having a major effect on the functioning of animal populations and communities (e.g. Slabbekoorn and Ripmeester 2008) and in appreciation of the huge potential of ecoacoustics methods to describe environmental complexity (Sueur and Farina 2015; Farina et al. 2016).
Most of the research in ecoacoustics that has appeared recently in the scientific literature has been at the acoustic community level. Definition and the major properties (such as spatial characters and adaptive processes) operating at the level of acoustic communities are important components of this narrative. For this reason it was necessary to clarify the terminologies and standardize the methods in order to conduct homogeneous and comparable studies of the acoustic communities and the sonic environment in which they are embedded.

In this article, we have addressed some hitherto unresolved issues, specifically the difficulty in spatially and temporally delimiting such a community and estimating the biodiversity richness of a community using its acoustic signature. Moreover, the difficulties in measuring the habitat in which an acoustic community is located ought not to be underestimated (Gage et al. 2004). From the seminal work of MacArthur and MacArthur (1961), which demonstrated the strict relationship between the complexity of vegetation and bird diversity, it is clear that efficient methods to measure vegetation patterns are necessary to interpret data gathered from passive acoustics (Tucker et al. 2014). Such a combined approach requires a considerable effort and the lack of vegetation monitoring standards discourages this research (Farina and Pieretti 2014b). The space-delimitation issue is important when a comparison between the structure of the environment and the distribution of the acoustic activity of animals is required. To overcome this constraint we suggest using an amplitude threshold based on empirical data. To date, there are few systems that automatically pair sound with individual species for an entire acoustic community (e.g. Sueur et al. 2008a) and calculate the relevant animal density (Marques et al. 2012), though good examples limited to individual species identification (Acevedo et al. 2009) or groups of animals (Anderson et al. 1996; Oswald et al. 2003; Brandes 2008; Tricas and Boyle 2009; Walters et al. 2012) have been presented.

**Conclusion**

In concluding, we suggest six key areas of investigation are required that will place acoustics habitat assessment and ecoacoustics at the centre of both applied and theoretical science. These six areas are:

1. Define the spatial dimension of an acoustic community.
2. Evaluate the level of affordability of the relationship between acoustic diversity and biodiversity.
3. Improve the efficiency in the monitoring of land and seabed mosaic structures using acoustic communities.

4. Improve the capacity of acoustic communities to operate as a tool in a long-term monitoring scheme.

5. Transfer the scientific knowledge of acoustic communities to assist in land and aquatic conservation, nature design and planning.

6. Educate society to listen to sounds from the environment.

Acknowledgements

We are grateful to Giuseppa Buscaino, Raphael Marquez, Jamie McWilliam, and David Monacchi for providing the acoustic files of the animal communities which we have used as examples. We would also like to thank Susan Dunsmore for editing.

References


Luther, D., 2009. The influence of the acoustic community on songs of birds in a neotropical rain


**Figure captions**

Figure 1. Examples of acoustic signatures: (a) Fish acoustic community dominated by Banded grunter (*Amnibata percoides*), Australia, sampling rate: 48 kHz, ACI set at 1024 Hz, Hamming window, clumping 1”, noise filter 3000 mV²/Hz. Courtesy of J. McWilliam. (b) Snapping shrimp chorus on the Lampedusa coast, sampling rate: 44.1 kHz, ACI set at 1024 Hz, Hamming window, clumping 1”, noise filter 3000 mV²/Hz. Courtesy of Giuseppa Buscaino. (c) Frog acoustic community (*Ranae perezi* and *Hyla arborea*), Spain, sampling rate: 44.1 kHz, ACI set at 1024 Hz, Hamming window, clumping 1”, noise filter 3000 mV²/Hz. Courtesy of R. Marquez. (d) Terrestrial chorus in a cloud forest of Borneo, sampling rate: 48 kHz, ACI set at 1024 Hz, Hamming window, clumping 1”, noise filter 3000 mV²/Hz. Courtesy of David Monacchi. (e) Bird chorus in Mediterranean maquis, sampling rate: 44.1 kHz, ACI set at 1024 Hz, Hamming window, clumping 1”, noise filter 3000 mV²/Hz. Farina unpublished. (f) Bat community in a Mediterranean farmland, sampling rate: 192 kHz, ACI set at 1024 Hz, Hamming window, clumping 1”, noise filter 3000 mV²/Hz. Farina, unpublished.

Figure 2. The dynamics of an acoustic community using the Acoustic Complexity Index (Pieretti et al. 2011) during four hours of passive recording from 4.00 to 8.00 a.m. on 13 May 2015 in Madonna dei Colli location (44°12'37.85"N, 10°03'27.12"E, 217 m a.s.l.) using the Sound Explorer [Terrestrial] SET (International Institute of Ecoacoustics and Lunilettronik Inc.) at a sampling frequency of 48 kHz. (A) Distribution of ACIτ over the period. (B) The acoustic signature was calculated by adopting an FFT of 1024Hz, Hamming window, clumping 60”, noise
filter 3000 mV^2/Hz. The first 100 Hz were not included in the evaluation. The acoustic niche breadth was calculated adopting the Evenness index \( J' = H'/H_{\text{max}} \) (Hill 1973) where \( H' \) is the Shannon diversity (Shannon and Weaver 1949) index and \( H_{\text{max}} = \ln S \), where \( S = 512 \) frequency bins. The acoustic signature undergoes important changes over the period with a lull around sunrise. At dawn, the acoustic community is composed of more species (higher \( J' \)) than after sunrise. Farina, unpublished.

Figure 3. Models of acoustic communities based on the temporal distribution of the activity.
Nocturnal community: A; Twilight community: B+B'; Diel community: B+B'+C+C'; Full light community: C+C'.
Note: B = sunrise hours; B' = sunset hours; C = morning hours; C' = afternoon hours.

Figure 4. Spatial repartition of an acoustic community on the basis of a near field/far field model empirically estimated on the amplitude of the signals
Note: A–E amplitude of broadcasted signals, a’–e’ amplitude of perceived signals.

Figure 5. The hierarchical organization of the landscape/soundscape narrative and its relationship to the acoustic community

Table 1 Ecoacoustics terms and their definitions

<table>
<thead>
<tr>
<th>Ecoacoustics term</th>
<th>Definition</th>
<th>Reference</th>
</tr>
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<tbody>
<tr>
<td><strong>Acoustic Complexity Index</strong></td>
<td>A measure of acoustic information based on the difference between successive pitches along frequencies and time</td>
<td>Pieretti et al. 2011</td>
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<td><strong>Acoustic habitat</strong></td>
<td>The sonic context in which species are living</td>
<td>Merchant et al. 2015</td>
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<td><strong>Acoustic niche</strong></td>
<td>Frequency partitioning to reduce interspecific competition</td>
<td>Krause 1993</td>
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<tr>
<td><strong>Acoustic niche breadth</strong></td>
<td>The range of frequencies used by a species</td>
<td>*</td>
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<tr>
<td><strong>Acoustic niche overlap</strong></td>
<td>Level of frequency overlap between two or more species</td>
<td>*</td>
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<tr>
<td><strong>Acoustic signature</strong></td>
<td>Species-specific repartition of frequencies</td>
<td>*</td>
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<td><strong>Adaptation Acoustic Hypothesis</strong></td>
<td>The adaptation of species-specific biophonies to the environment</td>
<td>Morton 1975</td>
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<tr>
<td><strong>Ecoacoustics</strong></td>
<td>The science that investigates the ecological role of natural and anthropogenic sounds</td>
<td>Sueur and Farina 2015</td>
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<td><strong>Noise</strong></td>
<td>An unwanted sound, any disturbance in a communication system</td>
<td>Truax 1999</td>
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<td><strong>Ratio-to-signal-noise</strong></td>
<td>A measure of the impact of noise on the</td>
<td>*</td>
</tr>
<tr>
<td>Term</td>
<td>Definition</td>
<td>Author(s)</td>
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<tr>
<td>Sonotone</td>
<td>The acoustic pattern created at the edge between sonotopes</td>
<td>Farina 2014</td>
</tr>
<tr>
<td>Sonotope</td>
<td>The acoustic mosaic created by the overlap of geophonies, biophonies and technophonies</td>
<td>Farina 2014</td>
</tr>
<tr>
<td>Soundscape</td>
<td>The sonic context created by the physical interactions between geophonies, biophonies and technophonies</td>
<td>Qi et al. 2008, Pijanowski et al. 2011b</td>
</tr>
<tr>
<td>Soundtope</td>
<td>The acoustic pattern created by the distribution of biophonies</td>
<td>Farina 2014</td>
</tr>
<tr>
<td>Technophony</td>
<td>Sounds produced by machineries</td>
<td>Fuller et al. 2015</td>
</tr>
</tbody>
</table>

Note: * different authors.
Figure 1
Figure 4

Perceived amplitude

Near field

Far field

Selected threshold

a

b

c

d

e

a'

b'

c'

d'

e'

Broadcasted amplitude
Landscape

Soundscape

Sonotope  (Geophonies+Biophonies+Technophonies)

Soundtope  (Biophonies)

Sonotones

Acoustic communities  (Interacting biophonies)