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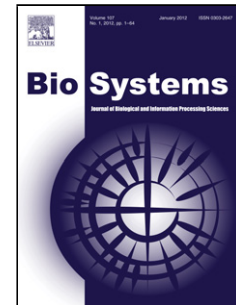
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Ecoacoustic Codes and Ecological Complexity

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Abstract

Multi-layer communication and sensing network assures the exchange of relevant information between animals and their umwelten, imparting complexity to the ecological systems.

Individual soniferous species, the acoustic community, and soundscape are the three main operational levels that comprise this multi-layer network. Acoustic adaptation and acoustic niche are two more important mechanisms that regulate the acoustic performances at the first level while the acoustic community model explains the complexity of the interspecific acoustic network at the second level. Acoustic habitat and ecoacoustic events are two of the most relevant mechanisms that operate at the third level.

The exchange of ecoacoustic information on each of these levels is assured by ecoacoustic codes. At the level of individual soniferous species, a dyadic intraspecific exchange of information is established between an emitter and a receiver. Ecoacoustic codes discriminate, identify, and label specific signals that pertain to the theme, variation, motif repetition, and intensity of signals.

At the acoustic community level, a voluntarily or involuntarily communication is established between networks of interspecific emitters and receivers. Ecoacoustic codes at this level transmit information (e.g., recognition of predators, location of food sources, availability and location of refuges) between one species and the acoustically interacting community and impart cohesion to interspecific assemblages.

At the soundscape level, acoustic information is transferred from a mosaic of geophonies, biophonies, and technophonies to different species that discriminate meaningful ecoacoustic events and their temporal dynamics during habitat selection processes. Ecoacoustic codes at this level operate on a limited set of signals from the environmental acoustic dynamic that are heterogeneous in time and space, and these codes are interpreted differently according to the species during habitat selection and the completion of phenological cycles.

The process of ecoacoustic coding can be interpreted according to the eco-field theory, which describes the procedures utilized by a receiver to intercept and optimize acoustic information.

The acoustic codes may be detected and identified using mathematical models that simulate their performances. The Acoustic Complexity Indices are an appropriate tool to investigate the acoustic codes in action on all three levels.

Ecoacoustic codes are powerful agencies used by sound-adapted species to cope with environmental novelties, and their efficiency may represent an important divide between whether a species perpetuates or becomes extinct.

Key words: Ecological complexity, Soundscape, Ecoacoustic codes, Eco-fields, Acoustic Complexity Index

Introduction

Complexity is a debated concept in the physical, biological, and ecological sciences (Allen and Starr 1982, Davies, 2003, Waldrop 1992). Ecological complexity, specifically, which is produced through interactions of biological diversity with the environment, is the result of a plethora of relationships among organisms and between organisms and the environment (Li 2004) and is assumed to impart stability to the systems (Holt 2006). These relationships are based on complex food-webs regulated by the availability of resources, the intrinsic fluctuation of populations, the richness and turnover of communities and their geographical displacement (Paine 1966, Pimm et al. 1991, Lewin 1992), and by behavioral mechanisms (Mayr 1974). Among the different behavioral processes that are the basis of life, environmental sensing through hearing plays a central role in regulating animal communication (Leger and Nelson 1981, Bradbury and Vehrencamp 1998).

Sounds from soniferous species (e.g., song, alarm, or contact call), sounds from physical phenomena (e.g., wind, rain, volcano eruptions, ice breaking and melting), and sounds from anthropogenic activity (e.g., urban noise, car traffic, airplane traffic) participate in this “vocal milieu” or soundscape that plays an important role in the co-evolution of inter and intra-specific relationships (Farina 2014, Krause 2012, Pijanowski et al. 2011, Gage et al. 2004, Napoletano 2004, Kroodsma 1985).

Most knowledge about acoustic communication mechanisms is based on observations of birds (Kroodsma 1996, 2004) and terrestrial and marine mammals (Kroodsma and Miller 1996). However, the bioecological roles of active and passive sounds have also been documented on

invertebrates and fish (Aiken 1985, Desjonqueres et al. 2015, Parks et al. 2014, Au and Landers 2016).

In the autoecological domain, biophonic sounds are specific tools to communicate a direct or indirect message (Burt and Vehrencamp 2005). Individuals inform other individuals about their physiological and cognitive status and anticipate the actions necessary to survive and reproduce (e.g., Catchpole and Slater 2008). These display mechanisms are important strategies that could facilitate adaptation during periods of change in niche availability (Crutzen and Stoermer 2000), where the prompt occupation of a new niche is the difference between perpetuation and extinction (Wong & Candolin 2015).

In the sinecological domain, sounds from individuals, groups, and assemblages create an acoustic mosaic and a communication network available to interacting and/or eavesdropping individuals (McGregor and Dabelsteen 1996).

Every species as “observer” of the environment (Levin 1992) must have precise knowledge of the external world, the *umwelt* (von Uexküll 1982, 1992), to survive and maintain its autopoiesis (Wake 2008). For this, perception by the senses through semiotic processes (Barbieri 2008) is a requirement of every living being. Moreover, due to the scarcity and heterogeneous distribution of resources, semiotic mechanisms are necessary to economize energy during their research.

To complete this narrative, the eco-field theory seems a more efficient semiotic tool to explain the complexity of the communication issue (Farina and Belgrano, 2004, 2006). The eco-field is defined as a spatial configuration carrier-of-meaning utilized by organisms to intercept resources. This theory considers obtaining resources (material and/or immaterial) a common goal for every organism (Farina 2012). Cognitive templates that are resource specific are requested to transfer resources from the external world into an organism system. For instance, the combination of different sounds from an acoustic assemblage of species may be an eco-field to detect local resources. A high level of an anthropogenic sound may be perceived by a noise-intolerant species as a breeding eco-field of low quality.

To maintain adaptive strategies against the risk of biological extinction, organisms recognize a multitude of signals, which requires an unambiguous interpretation obtained by processes of signal discrimination and identification (Marler 1982, Nelson and Marler 1989, Horn and Falls 1996, Baugh et al. 2008) that Barbieri considers bioecological codes. Later, these codes, used to discriminate and identify acoustic displays with an ecological impact, were called “ecoacoustic codes” by Farina and Pieretti (2014).

Recently, communication processes have been examined from an ecological perspective by Sueur and Farina (2015), who proposed ecoacoustics as a new ecological approach to study the

acoustic output of abiotic and biotic agents. The ecoacoustic processes exhibit heterogeneity and patchiness according to the scale of resolution, a fundamental characteristic common to population dynamics, community organization, and nutrient cycles (Levin 1992).

Ecoacoustics offers theoretical, methodological, and application tools to investigate the effect of sound emissions on the biology and ecology of species, populations, and communities. For instance, the Acoustic Complexity Indices (Pieretti et al. 2011, Farina et al. 2013, 2016) are examples of new ecoacoustic metrics to analyze the frequency distribution and structural properties of acoustic emissions.

The aim of this paper is to describe the properties and the mechanisms of the ecoacoustic communication and to discuss the types, characters, and roles of the ecoacoustic codes used by species to transform the environmental and intra- and interspecific signals into meaningful information.

Ecoacoustic communication and the related encoding-decoding process are approached according to three ecoacoustic levels that focus on (1) individual soniferous species, (2) acoustic communities, and (3) soundscapes. For each level, the properties and the role of the acoustic components, the main characters of the ecoacoustic codes, and their contribution to ecological complexity are described and discussed.

The tradeoff mechanisms utilized by species to navigate the complex scenario of dyadic and collective intra- and interspecific communication are discussed using the narrative associated with eco-field theory (Farina and Belgrano 2004, 2006). Finally, the ecoacoustic codes are discussed according to the mathematical formalization of the Acoustic Complexity Indices.

Fundamentals of ecoacoustic communication

The individual soniferous species level

The acoustic evolution in soniferous species assumes that acoustic characters are fixed in the animal genome with the same modalities of other morphological or behavioral characters, although in many cases these acoustic characters require or are completed by learning processes and cultural transmission (e.g., Kroodsma 1985, Fitch et al. 2016) (Fig. 1a).

The body size of soniferous species seems to be an important constraint for the intensity and frequency of sound emissions. This hypothesis, based on allometric rules (West et al. 1997), has been proven in birds and mammals (Wallschläger 1980, Fletcher 2004, 2007). Larger animals use low frequencies and smaller animals use high frequencies, like the sonic performances of musical instruments.

Individual species communicate with conspecifics by using sophisticated acoustic displays (Marler 1960, Lemon et al. 1981, Horn and Falls 1996) that have major effects on the regulation of population dynamics and on inter-individual recognition (Galeotti and Pavan 1991, Galeotti et al. 1993). These acoustic cues release several types of information that may be utilized for different purposes (e.g., territory defense, mate attraction and stimulation, pair bond maintenance, antipredatory strategies) (Naguib and Riebel 2014). The acoustic repertoire, under the effects of environmental constraints, may be modified by creating regional acoustic variations or dialects (Baker and Cunningham 1985, Laiolo and Tella 2005, Laiolo 2008). The appearance of dialects proves the great plasticity of the acoustic signals and confirms the strategy to cope with environmental change (Krause and Farina 2016). The character and modalities of acoustic displays of individual species are the result of habitat adaptation and acoustic partitioning, explained by the Acoustic Adaptation Hypothesis and the Acoustic Niche Hypothesis.

The Acoustic Adaptation Hypothesis (AAH): According to the AAH, dominant frequencies and long-distance calls are the result of the evolution of interaction mechanisms between acoustic emissions with the physical environment to optimize the transmission of signals by the species. Low frequencies dominate acoustic signals in densely vegetated habitats, and high frequencies are more common in open habitats.

This hypothesis, tested with playback experiments by Morton (1975), has been confirmed by Marten and Marler (1977) in temperate habitats by measuring the effect of the height (from the soil) of the signals and frequency used to transmit sound. Later, Lemon et al. (1981) found differences in song emission depending on the singing height of 19 species of warblers (Family *Parulidae*).

The AAH has been debated for a long time and has received many criticisms (Daniel & Blumstein 1998, Blumstein & Turner 2005, Burns 2007), but this hypothesis also has supporters (Tubaro and Segura 1994, Brown and Handford 1996, Patten et al. 2004, Ziegler et al. 2011). The disparity of evaluations of AAH is probably related to the complexity of the environment that produces no linear reactions to the acoustic signals. The unknown level of impedance of trees, rocks, grasses, and water masses may represent additional limits of an experimental test of this hypothesis.

The Acoustic Niche Hypothesis (ANH): Species-specific acoustic repertoire operate as the foundation of adaptive partitions within a potential audible spectrum that prevents or reduces acoustic competition among species (Lemon et al. 1981). The acoustic signals of one species often

do not overlap with the acoustic signals of other species, and this has been interpreted by Krause (1993, 2012) as an acoustic niche.

The Acoustic Niche Hypothesis seems to be influenced by the history of communities, so it is considered consistent in communities that have been stable for a long time, like tropical communities where an invertebrate's richness is bounded in distinct species-specific frequencies (Sueur 2002).

However, communities located in areas where changes of environments and anthropogenic conditions are frequent, may not have time to adopt a co-evolutionary acoustic partitioning (Malavasi and Farina 2013). Without rejecting the ANH, it is reasonable to admit that predictions of this hypothesis are confirmed in some contexts, while in others the ANH does not seem to be validated.

The acoustic community level

Animals do not live in isolation but dwell in complex communities that may change in composition and abundance across space and time (Allen and Hoekstra 1992), and where complex communication networks are in action (McGregor 2005) (Fig. 1b). Every community is structured by environmental heterogeneity and resource scarcity (Allen and Hoekstra 1992, Farina 2012). If biophonies are considered “behavioral resources,” their distribution reflects either the landscape complexity or the spatial distribution and phenological activity of soniferous species assemblage.

The Acoustic Community Hypothesis: Farina and James (2016) have defined an acoustic community as a temporary acoustically-interacting species. An acoustic community is an ecological phenomenon that emerges in a restricted temporal interval that is variable in space and time and that comprises a changing number of interacting species (Fig. 1b). This hypothesis assumes that soniferous species have temporary acoustic interactions that generate an emergent biophonic network that has important consequences on the individual behavior and adaptation mechanisms (Farina & James 2016). The interspecific communication likely has competencies on a limited portion of the entire acoustic repertoire of these assemblages (Caro 2005).

The soundscape level

A soundscape is defined as a combination of geophonies, biophonies, and technophonies produced in a landscape that is perceived without distinction (Pijanowski et al. 2011, Farina 2014, p. 3). A soundscape is a source of information and has effects on the listeners according to

modalities that are supported by two interrelated hypotheses: Acoustic Habitat Hypothesis (Mullet et al. 2017) and Ecoacoustic Event Hypothesis (Farina et al. 2016, Farina et al. 2017) (Fig. 1c).

The Acoustic Habitat Hypothesis (AHH): The AHH explains how the soundscape influences the habitat selection of sound-dependent species (Mullet et al. 2017). An acoustic habitat is a place selected by a species after positively evaluating the acoustic information received. For instance, a windy place or a place close to a fast-flowing stream may be less preferred by songbirds because such geophonic sources may mask acoustic signals of potential interacting species. Similarly, some technophonies may be perceived as hostile by bats due to their masking effects (Voigt and Kingstoon 2016) or by marine mammals like whales (Au and Green 2000) and fish (Radford et al. 2014), while some birds seem more tolerant or may receive benefits from living in noisy habitats (Francis et al. 2009).

The Ecoacoustic Event Hypothesis: Farina et al. (2016, 2017) have defined an ecoacoustic event as an emergent sonic pattern resulting from individual geophonies, biophonies, and technophonies, including that their combinations that have consequences on the acoustic repertoire and communication process of different species, at time.

For instance, a storm or a breeze can be an ecoacoustic event, and sound-dependent species may perceive such acoustic sources as an interference that reduces their capacity to communicate and/or to find resources. Roosting choruses generated by intra- and interspecific flocks of birds can be an important source of information for animal assemblages (Ward and Zahavi 1972). Frog choruses have been proven to be a source of spatial information for birds during their nocturnal migration (Griffin and Hopkins 1974, Griffon 1976).

Ecoacoustic codes

Biological codes are responsible for the maintenance of autopoietic mechanisms (*sensu*) (Matura and Varela 1980) in mono and multicellular organisms. However, other (ecological) codes (Barbieri 2003, <http://www.codebiology.org/ecologicalcodes.html>) make possible the relationships between organisms, their assemblages, and the environment and *de facto* control (facilitate or prevent) the adaptation processes under a regime of environmental novelties and behavioral plasticity (Wong and Candolin 2015).

The distinction between biological and ecological codes is not based on inherent mechanisms but on the scale of the application and on the effects produced. The transition from biological to ecological codes is a matter of semiotic competencies: the biological codes initiate a

process of intra- and interspecific communication, and the ecological codes extend such communication mechanisms to the environment, creating a flow of continuous semiotic feedback between organisms and their habitats.

Ecoacoustics codes are artifacts (*sensu* Barbieri 2006, Farina and Pieretti 2014) based on unequivocal mechanisms used by organisms to establish communication channels within populations and communities and to interpret and process information from the physical environment. According to the three levels of ecoacoustic complexity at which the sound is considered, there are specific codes that change in terms of complexity, frequency of occurrence, diversity, and capacity to interact at a multispecies level.

Ecoacoustic codes at the individual soniferous species level: Codes operating at the individual soniferous species level are the result of categorical perception, where organisms “compress” some signals and expand others in distinct categories (Harnad 2003), which are assigned a meaning with a label (Nelson and Marler 1989). For instance, Ehret (1992) proved that female house mice can distinguish the pup ultrasounds into two categories according to the duration of the continuous ultrasounds. Categorical perception has also been demonstrated during mating calls in tungara frogs (*Physalaemus pustulosus*), a frog common in South America and in some parts of Central America (Baugh et al. 2008).

Complex codes operate within specific evolutionary forces that shape the genome and require time to spread and establish across populations. At this level, every individual exchanges acoustic information with other members of the same species. For example, it is expected that a song from a chaffinch male may have an effect on a conspecific female but not on a blackbird female, and vice versa. Furthermore, intraspecific communication may be facilitated by other possible encoding-decoding mechanisms according to environmental and behavioral contexts.

Thematic variation, motif repetition, and intensity of the acoustic signals enter into a system that requires further codification (Naguib and Riebel 2014), like a song repertoire of an isolated bird that may be repeated during the day with a lower temporal frequency than a song repertoire in a dense population of the same species. For instance, blackcaps (*Sylvia atricapilla*) that are present at a very low density in the beech forests of the Apennines mountains (Italy) sing only a few times each day. However, denser populations living in the same area but in blackthorn (*Prunus spinosa*) shrublands sing continuously all day (Farina, unpublished data). In some species, alarm calls uttered to inform others about predators may change according to type, size of predator, distance, and behavior (Manser 2009). This capacity is particularly evident in tits (*Paridae*), small birds distributed in the northern hemisphere and in Africa, that live in flocks and are acoustically active

year-round. These species adopt a double mechanism of coding, the first based on behavioral stimuli and the second based on psychological reactions to specific conditions (e.g., Hahn et al. 2017).

Ecoacoustic codes at the acoustic community level: The acoustic community codes are the result of complex interactions among different species in which each individual has the capacity to extract information from a series of acoustic cues. Protection from predators and the presence of food resources may represent the most important “messages” that are decoded at the community level (Krams 2010).

One example is the transfer of alarm between the white-bellied go-away bird (*Corythaixoides leucogaster*) and the Gunther’s dik-dik (*Madoqua guentheri*) (Lea et al. 2008). When these birds emit alarm calls, dik-diks modify their behavior, increasing the rate of head turning and period of vigilance and decreasing foraging activity. However, the idea that an emergent biophonic mixer may inform a species about an environmental status requires further investigation. Presently, we can only admit some degree of influence of the acoustic mosaic perceived by an eavesdropping individual. For instance, mobbing behavior of tits (*Parus*) may discourage predators or intruders by informing heterospecifics as well as conspecifics (Suzuki 2014).

Ecoacoustic codes at the soundscape level: At the soundscape level, where an entire acoustic system is under a variety of physical parameters, there is evidence that acoustic conditions of the environment play a relevant role in several sound-dependent species. Biophonies, geophonies, and technophonies are the components of the acoustic environment in which species may produce an accurate selection to optimize their active acoustic performances. For instance, the intensity of the sound produced by rain or wind or an anthropogenic noise may reduce or interrupt all singing activities of the majority of soniferous birds.

Ecoacoustic events are in turn affected by many environmental variables. For instance, temperature and sky luminosity, although not acoustic phenomena, are factors that elicit acoustic reactions at an individual level and at the ecoacoustic community level as well. Exceptionally hot days frequent during these events have important consequences on the behavior of several soniferous species since high temperatures can interfere with physiological responses, reducing or stopping the singing activity.

Some ecoacoustic events may be recognized, then decoded and interpreted, producing changes in the behavior of the entire assemblage. Other events are ignored by soniferous species because they are not discriminated, identified, and labelled.

Ecoacoustic events are phenomena that have an impact on large areas and, at the same time, on large sets of organisms (Farina et al. 2017). However, decoding acoustic events may be different according to species and environmental conditions. The frequency, intensity, and temporal distribution of ecoacoustic events become, in turn, active components of the coding at this level.

Temporal dimension of ecoacoustic code ontogenesis: The ecoacoustic codes utilized by species require a long period of adaption and evolution. The ecoacoustic community codes, however, seem to act more quickly to cope with a changing scenario. Soundscape codes are consistent with a limited range of environmental conditions, but their evolutionary history seems the most diluted.

Any change in communication modes is important for the ecoacoustic code theory. A fixed set of acoustic patterns incorporates every possible variation expressed at a superior level of signaling. This last level has a lower complexity because it represents a type of advanced syntax that should face the uncertainty of ecological interactions. The reactions must be as simple as possible to be efficient and to respond to the ecological phenomena that occur in an unpredictable way.

Environmental novelties, human impact, and ecoacoustic codes: Despite evidence that many species have in their allelic asset all the necessary information to adapt to environmental change (Wong & Candolin 2015), some sonic novelties may be really deleterious for species when there are not coding processes to interpret and/or adapt. Species invasion and shifts in biogeographic range are some processes responsible for environmental novelties. The recent invasion of the red-billed leiothrix (*Leiothrix lutea*) in the Mediterranean shrublands is the probable cause of the blackcaps' (*Sylvia atricapilla*) local decline (Farina et al. 2013). Playback experiments have proven that blackcaps remain silent during the song of the red-billed leiothrix and resume singing only when the red-billed leiothrix has completed its song sequence (Farina, unpublished).

From the vast literature on the consequences of human involuntary and voluntary sonic activity on animal behavior emerges evidence that many soniferous species have the capacity to change the frequency, intensity, repertoire, and habitat when an anthropogenic noise enters their habitat (Brumm 2004, Brumm and Slater 2006, Fuller et al. 2007, Duarte et al. 2015, Farina 2017). In many marine mammals, the level of acoustic intrusion due to tourism and ship activity may

create unresolved problems for their complicated system of long-distance communication and echo-location (Hildebrand 2009).

Entire assemblages may have changes in acoustic habits due to soundscape modification. For example, a bird community close to the Madrid airport changed the beginning of the dawn chorus to account for airplane traffic that probably masked the birds' voices (Gil et al. 2015). The cost of this behavior and the consequent modification of the ecoacoustic code should be evaluated in the future.

Ecoacoustic codes and eco-field theory: The acoustic codes, regardless of their operational level, can be incorporated into the eco-field theory (Farina & Belgrano 2004, 2006). All the ecological codes involved in the communication process may be produced by different agents (individuals, populations, communities, soundscapes) but operate within a unique individual receiver.

According to the eco-field theory, every species has an innate or learned capacity to perceive its external world according to its physiological needs (active perception) using function-specific cognitive templates. The sonic environment is scanned using these acoustic templates, and when a specific acoustic eco-field is identified, it is assigned a specific meaning. However, every species is also able to perceive external stimuli that are not solicited by internal mechanisms. This dual capacity probably has a common encoding-decoding process that is largely inborn, although some acoustic signals may be discriminated and categorized after learning/training processes that generate new acoustic cognitive templates.

The resources tracked by the different acoustic eco-fields range from territory defense, mate selection, intra- and interspecific competition avoidance, signal quality maintenance (e.g., avoiding noisy areas), reduction of energy investment in acoustic cues when less efficient, and optimization of the social exchange of information on nesting places, food location, predator avoidance, etc. A tradeoff between the different “needs” creates a complex scenario from which individual fitness is achieved by a “negotiation” of fulfilments. Definitively, the eco-field process operates simultaneously across different ecoacoustic levels, and the causes and effects are constrained by the momentary physiological priority of individuals.

The formalization of the ecoacoustic codes

Today the ecoacoustic methodology allows us to investigate and interpret the alleged structure of the ecoacoustic codes. New metrics like the Acoustic Complexity Indices (ACI: ACI_{t_f} , ACI_{f_i}) have been successfully tested (Pieretti et al. 2011, Farina et al. 2017). ACI_{f_i} is an index calculated for each temporal step along the frequency bins, and $ACI_{f_i \text{ evenness}}$ is its temporal

distribution. ACI_{tf} is calculated along each frequency bin and $ACI_{tf\text{evenness}}$ is its inter-frequency distribution (Farina et al. 2016, 2017). ACI metrics can translate acoustic patterns that emerge from a Fourier transform applied to a sound file into numerical expressions in which we associate formal codes. In this way, codes are mathematical models that simulate the cognitive categorization that every individual may obtain through inborn or learned mechanisms.

The mathematical dimension of such codes outlines their properties. The translation of an assumptive species-specific meaning expressed by a sound into a numerical code is not automatic, but it is the only way to formalize the alleged sign. Like genetic codes are formalized by a sequence of bases, ecoacoustic codes are formalized by ACI metrics that convert a spectrographic representation of sounds (frequency *versus* time) in physically-formalized codes.

Specifically, ACI_{tf} is used in a singular way to code the first ecoacoustic level (Fig. 1), then the combination of ACI_{tf} , $ACI_{tf\text{evenness}}$, and $ACI_{tf\text{evenness}}$ is used to detect and identify ecoacoustic codes in acoustic communities and the soundscape level by adopting a three-digit ecoacoustic code (Fig. 2). The soundscape level is formalized after plotting every ecoacoustic code along a reasonable temporal interval (hour, half day, full day, distance from the sunrise/sunset, month) (Fig. 4) where typology, frequency, and sequence along a temporal interval concur with a coding syntax.

In acoustic communities, ecoacoustic codes only of biophonic origin are used to interpret ecoacoustic events, while at the soundscape level, coding uses a complete set of ecoacoustic events and their temporal sequence.

Conclusions

Ecoacoustic codes are obligate and unique mechanisms that transmit voluntary or involuntary information from individuals, species assemblages, and the environment to an active listener. Their ontogenesis, evolution, and adaptation change according to species, typology, local history of soniferous assemblages, geomorphology, vegetation conditions, and level of human intrusion (Francis et al. 2009, Wong and Candolin 2014). Ecoacoustic codes act in different ways according to the selected level at which a species interacts with the ecological complexity.

The soniferous species level is dominated by ecoacoustic codes that are the result of adaptation to environmental conditions to optimize intraspecific communication. The second level that results from interspecific communication within members of an ecoacoustic community has ecoacoustic codes that operate on ecoacoustic events that operate at an extremely short temporal scale given the ephemeral conditions of the behavioral processes and the great phenotypically plasticity of acoustic display. The third level is characterized by the frequency, distribution, and

sequence of the ecoacoustic events and has ecoacoustic codes common to mosaic-like species assemblages.

Despite the plasticity of the acoustic behavior, every acoustic phenomenon that masks or degrades the ecoacoustic network on the three levels, like environmental novelties of climate change and direct human intrusion (habitat degradation and noise), may have dramatic consequences on the composition and stability of ecosystems. In this context, it is important to improve our knowledge about the biology of disturbance to properly manage acoustic habitats and related physical habitats (Pavan, 2017).

The acoustic environment must be considered a fundamental component of the ecosystem and thus must be studied, preserved, and restored when altered by human actions to benefit ecoacoustic communities as well as human beings.

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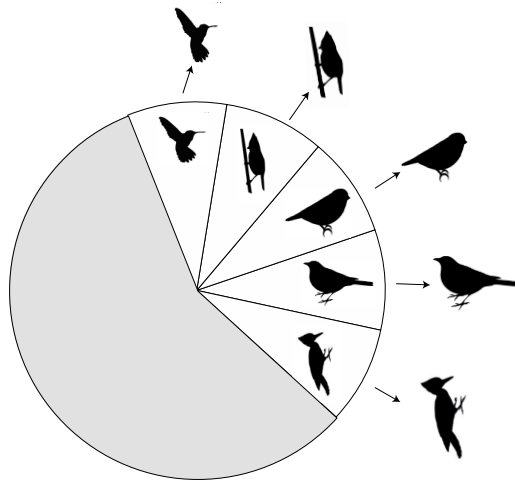
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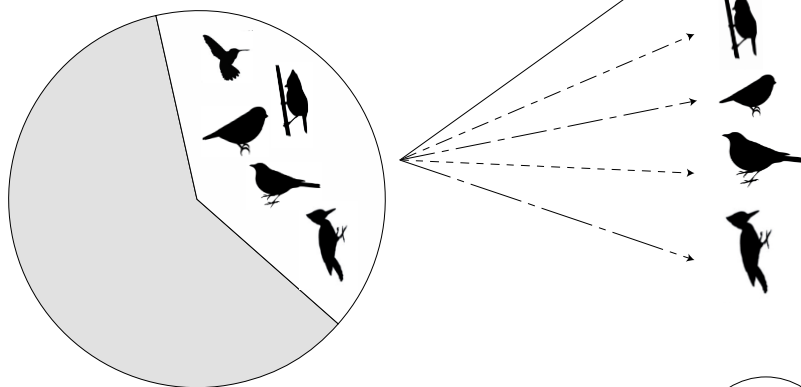
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A) Individual soniferous species



B) Ecoacoustic community



C) Soundscape

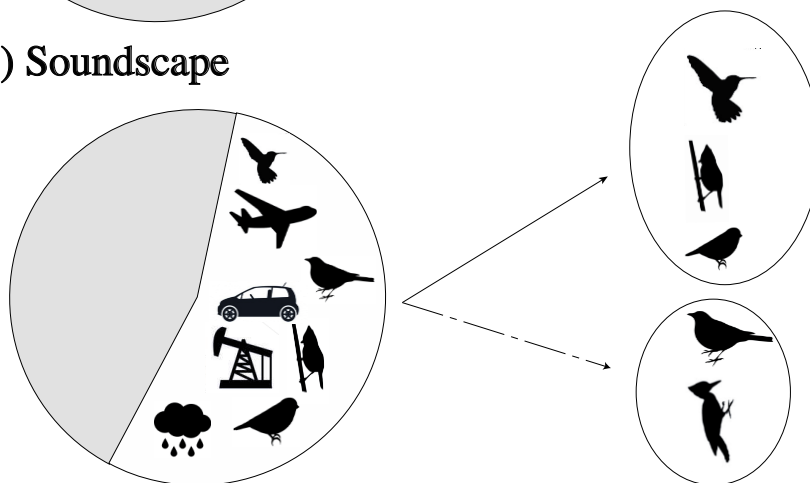


Fig. 1 - Simplified representation of the three ecoacoustic levels at which every species interacts. At the soniferous species level (a), every species interacts with individuals of the same species; at the community level (b), every species interacts with signals that emerge from the acoustic community to which it temporarily belongs. At the soundscape level (c), groups of species have a common reaction to ecoacoustic events that occur.

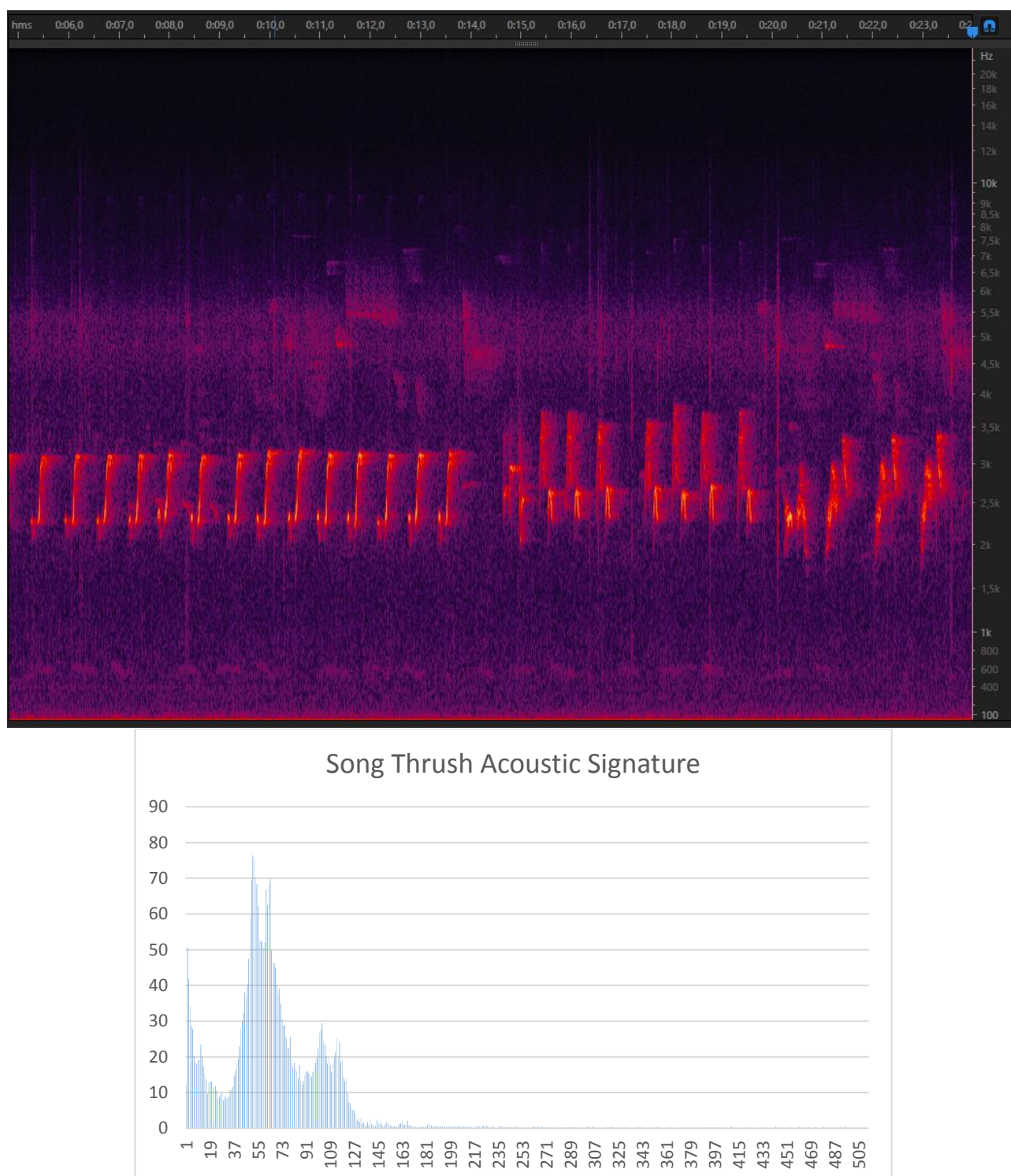


Fig. 2 - Spectrogram and acoustic signature of a Song Thrush (*Turdus philomelos*) song. The x axis indicates time and the y axis the frequency in a logarithmic scale. The intensity of the color is related to the sound magnitude.

The ecoacoustic code (Acoustic signature) for this first ecoacoustic level is the sequence of values created by the application of the $ACIt_f$ metric to a matrix of acoustic intensity.

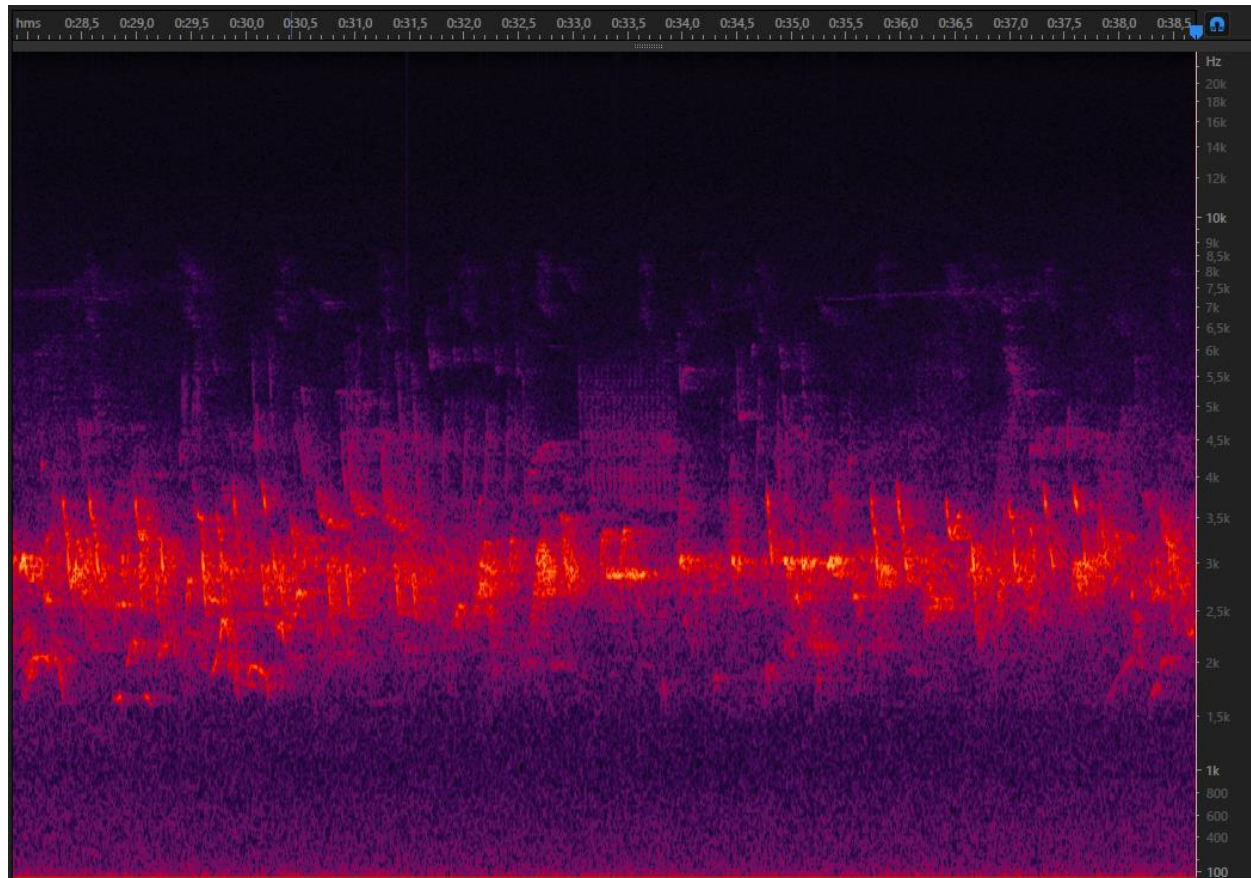


Fig. 3 - Spectrographic representation of an acoustic community (dawn chorus at 0431 am of May 20 2016 at MColli2 location, $44^{\circ} 12' 29.84''$ N, $10^{\circ} 03' 33.08''$ E, 246 m a.s.l., slope exposition: North East). The ecoacoustic code of this community is 993. This code is obtained by applying the EEDET sub-routine of the EEDI procedure (Farina et al. 2016, 2017). The x axis indicates time and the y axis the frequency in a logarithmic scale. The intensity of the color is related to the sound magnitude.

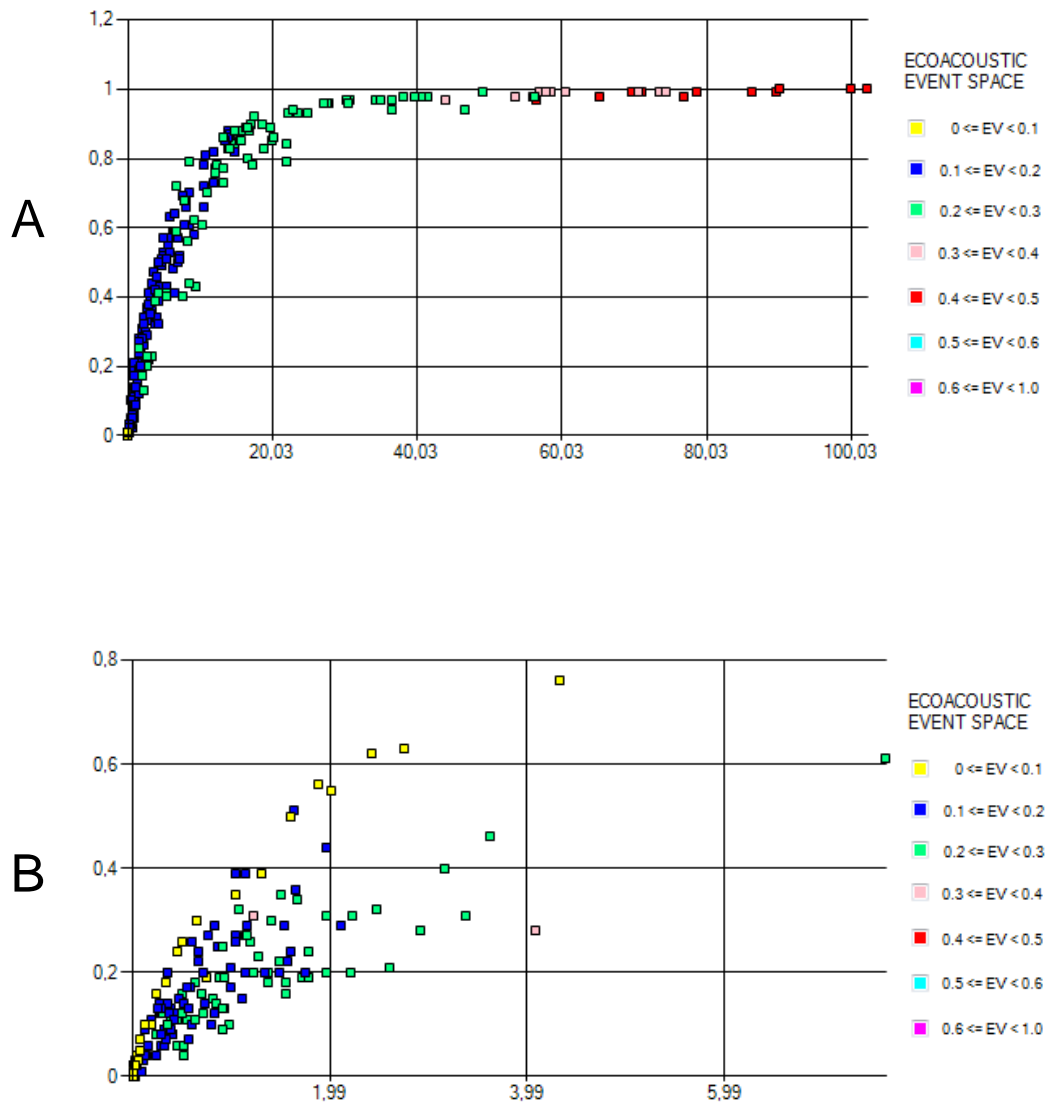


Fig. 4 - Two soundscape patterns encoded according to the sub-routine EEDET (Farina et al. 2016, 2017). The distribution of ecoacoustic events throughout a day depicts the third ecoacoustic level. The soundscape of each day has been sampled one minute of every 5, totaling 240 wave files, then processed and converted into a three-digit ecoacoustic codes. In abscissa (x) $ACIf_t$, in ordinate (y) $ACIf_{evenness}$. In color the values of $ACIf_{evenness}$. A) Biophonic activity associated to a high geophonic sources (rain) on 01 June 2016. In B) Modest biophonic activity on 04 April 2016. Data from MColli2 location, 44° 12' 29.84" N, 10° 03' 33.08" E, 246 m a.s.l., slope exposition: North East.