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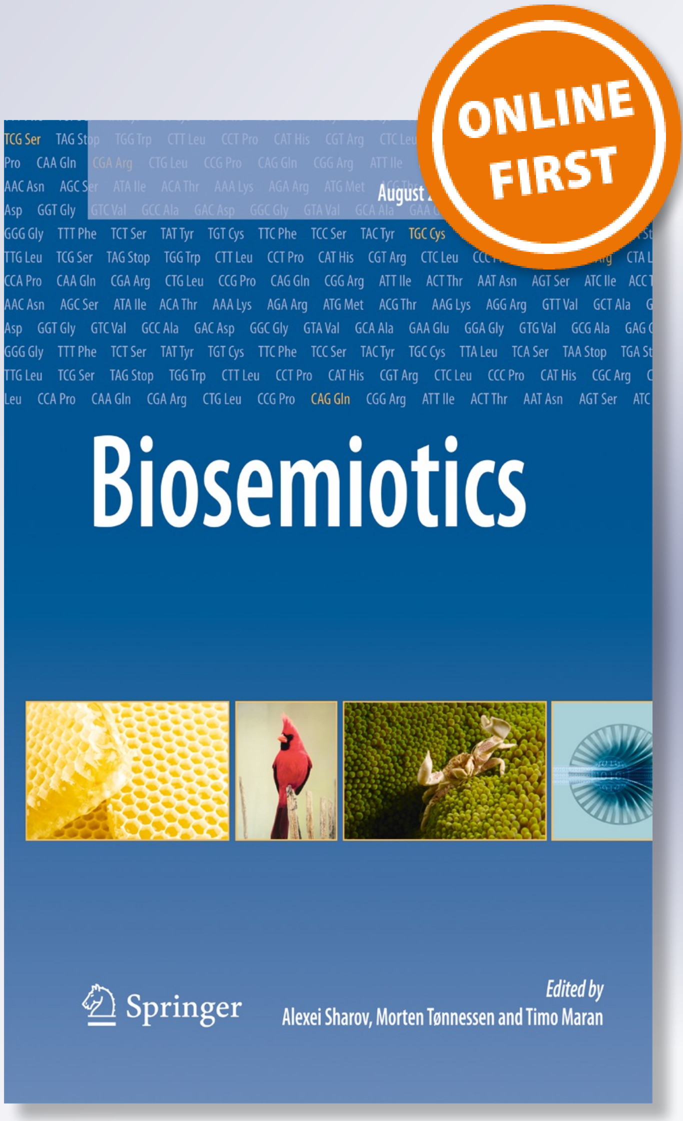

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SHORT COMMUNICATION

Ecoacoustics: the Ecological Investigation and Interpretation of Environmental Sound

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Abstract The sounds produced by animals have been a topic of research into animal behaviour for a very long time. If acoustic signals are undoubtedly a vehicle for exchanging information between individuals, environmental sounds embed as well a significant level of data related to the ecology of populations, communities and landscapes. The consideration of environmental sounds for ecological investigations opens up a field of research that we define with the term *ecoacoustics*. In this paper, we draw the contours of ecoacoustics by detailing: the main theories, concepts and methods used in ecoacoustic research, and the numerous outcomes that can be expected from the ecological approach to sound. Ecoacoustics has several theoretical and practical challenges, but we firmly believe that this new approach to investigating ecological processes will generate abundant and exciting research programs.

Keywords Ecoacoustics · Sound · Large-scale research · Discipline framework

Introduction

In the last years, the growing interest in the use of environmental sounds as a non invasive reliable proxy for investigating ecological complexity has opened up new perspectives in ecology (Farina 2014; Towsey et al. 2014a). This new field of research was mainly related to the contribution of passive acoustics and to the development of new acoustic metrics. Passive acoustic approach is based on listening techniques elaborated to detect and to monitor individuals without interfering with their behaviour

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(e. g., Cato et al. 2006; Zimmer 2011; Marques et al. 2012). Several acoustic metrics, mostly deriving from ecological indices, were coined to qualify and quantify environmental sounds (e.g., Wimmer et al. 2013; Sueur et al. 2014; Farina et al. 2014). Empirical evidence has suggested that: biological and non-biological sounds could have a relevant role in animal population aggregation, community composition, and more in general in environmental dynamics. Sounds could also be regarded as appropriate material for examining and interpreting ecological processes as the change of ecosystem resilience under climatic changes (e.g. Botero et al. 2009; Møller 2010) or the disturbance regime dominated by human intrusion in fragile systems (e.g., deforestation: Tucker et al. 2014). Following these developments, we recently organised a meeting in Paris (Ecoacoustics : ecology and acoustics, emergent properties from community to landscape. Paris, France, 16–18 June 2014, Muséum national d'Histoire naturelle and University of Urbino) where, for the first time, the role of environmental sounds was discussed according to theoretical, methodological and application perspectives. The attendees reached a broad consensus on the opportunity to create an independent field of research named ecoacoustics.

This paper, which reflects the outcomes of the meeting, as well as our own views, offers a synthesis of formal theories, concepts, principles, standard techniques and applications to be followed in the new field of ecoacoustics.

Definition and Scope

Ecoacoustics is defined as a theoretical and applied discipline that studies sound along a broad range of spatial and temporal scales in order to tackle biodiversity and other ecological questions. The use of sound as a material from which to infer ecological information enables ecoacoustics to investigate the ecology of populations, communities and landscapes (Fig. 1).

Ecoacoustics is closely related to bioacoustics, but differs markedly in that ecoacoustics considers sound to be a component and an indicator of ecological processes, whereas bioacoustics is an animal behaviour discipline that studies mainly sound as a signal that transfers information between individuals (Fletcher 2007). Covering all ecological organisation levels, ecoacoustics includes *ipso facto* soundscape ecology, which is a field of research specifically dedicated to the study of the sounds emerging from the landscape (Schafer 1977; Porteous and Mastin 1985; Truax 1999; Pijanowski et al. 2011). Ecoacoustics can be viewed as an umbrella discipline under which soundscape ecology can harbour.

One of the most salient features of ecoacoustics is the fact that sampling operates on a large observation scale, targeting large-scale ecological organisations as populations, communities, or landscapes. The main advantage of using sound is that sound can be recorded remotely and autonomously with rather cheap sensors, costing a few hundreds of Euros or US dollars depending on the digitization quality and whether the equipment is dedicated to air- or water-borne sound. These sensor units can be synchronised, deployed in large numbers to large areas up to several square km and precisely scheduled to ensure an appropriate sampling. Ecoacoustics also includes studies that record a single population for extended periods, or use dense spatial sampling over a relatively short period, can also be included in ecoacoustics (van Opzeeland et al. 2013; Farina and Pieretti 2014; Risch et al. 2014; Rodriguez et al. 2014; Furnas and Callas

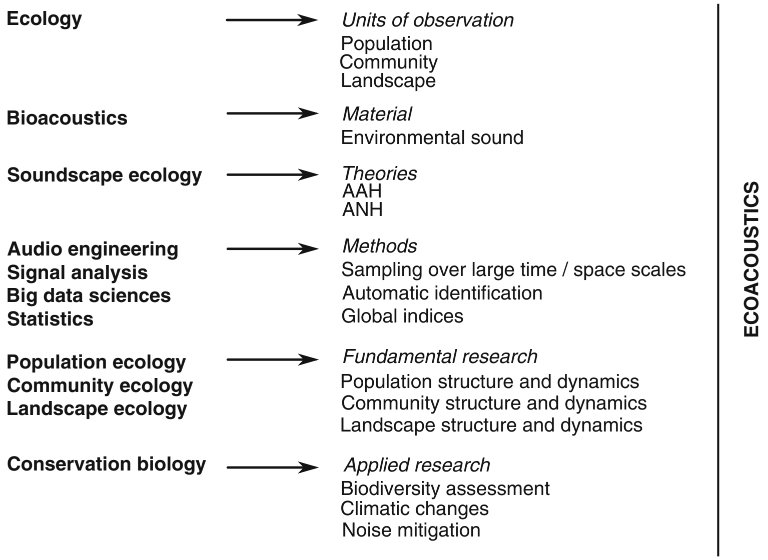

Fig. 1 Contributing disciplines, concepts and scopes of ecoacoustics. The figure shows on the left the different academic disciplines that are beyond the several concepts and scopes grouped by ecoacoustics. For instance, the discipline ecology suggest to observe sound at the population, community, and landscape scale rather than at the individual or species scales. *ANH* Acoustic niche hypothesis, *AAH* Acoustic adaptation hypothesis

2015). Ecoacoustics is able to investigate several types of media including air, marine and fresh water, soil and vegetation, and can operate in pristine environments and in human-modified systems. Conducting large-scale research entails the development of automatic systems that process massive amounts of data. As such, ecoacoustics is closely linked to ecoinformatics (Michener and Jones 2012), and has to meet the main 'big data' scientific challenges (Hampton et al. 2013).

Background Theories

The acoustic niche hypothesis (ANH) and the acoustic adaptation hypothesis (AAH) comprise the main theoretical background of ecoacoustics. The ANH is derived from empirical observations that the sounds produced by species vocalising at the same time in a location little overlap leading to an acoustic partitioning of the acoustic space (Krause 1993). The ANH directly refers to the ecological niche concept (Hutchinson 1957) and can be linked to the semiotic niche concept adding a sensory dimension to the space surrounding an organism (Hoffmeyer 2008). Even if studies dealing with both terrestrial and marine acoustic communities have challenged this theory (Amézquita et al. 2011; Chek et al. 2003; Tobias et al. 2014), numerous observations suggest the occurrence of acoustic partitioning in both time and frequency domains (Sueur 2002; Luther 2009; Schmidt et al. 2012; Sinsch et al. 2012; Schmidt and Balakrishnan 2014; Ruppé et al. 2015).

The AAH, meanwhile, stipulates that the acoustic properties of habitats, which are created by ground morphology and plant structures, have shaped animal sounds, resulting in the maximisation of their propagation (Morton 1975; Marten and Marler 1977;

Boncoraglio and Saino 2007; Ey and Fischer 2009). According to the AAH, every habitat and, on a larger scale, every landscape generates an emergent unique acoustic signature (Krause 1987; Briefer et al. 2010; Bormpoudakis et al. 2013). This phenomenon has been indirectly proved by the orientation of animals towards habitats through hearing (Slabbekoorn and Bouton 2008) like the case of coral reef fish (Simpson et al. 2005). We believe that the acoustic signature, which has long been tested on an individual level, should be utilised at the higher level of organisations for long-term ecological monitoring as already explored in tropical forests (Sueur et al. 2008), coral reefs (Piercy et al. 2014) and temperate landscapes (Farina et al. 2011).

The AAH and ANH deal with two main evolutionary constraints that act on signals: acoustic interference due to the sound produced by co-occurring species and sound degradation caused by obstacles obstructing the transmission of signal between emitters and receivers. These two constraints drive species-specific features in opposite directions, leading respectively to an acoustic divergence or convergence, that is to an increase or decrease of acoustic niche differences. These opposite effects have often led to consider the AAH and ANH separately when in fact they are probably related through the natural selection. We therefore advocate that these two theories should be considered together for a better understanding of the patterns and processes of population, community or landscape acoustics.

Techniques and Methods

An important part of ecoacoustics is devoted to the audio methods with which to reinforce each step of the workflow: recording, database managing, signal analysis, quantification, and statistics. In ecoacoustics, active processes, such as those used by sonar-like systems, are not required. The data are acquired in a passive way mainly through the use of automatic sensors or with the help of a large group of citizens running manually the recorders. These recording procedures can considerably reduce the time of operation. Nonetheless, settling and scheduling the equipment is not a trivial matter. The number of recording sites, the space volume covered by each sensor, and the duration and repetition of the recording sessions must be fully thought out in relation to the next steps in the workflow, particularly with regard to the audio data weight, the signal analysis time consumption, and the statistical power. As ecoacoustics examine large ecological units, it is necessary to simultaneously conduct recordings using several omni-directional sensors to capture all significant events. Ecoacoustics will therefore benefit from the design of low-cost recording devices that could be deployed over large matrices of sampling points (Farina et al. 2014). Such sampling protocols generate massive datasets that need to be saved and managed by audio-dedicated archives (Kasten et al. 2012; Toledo et al. 2015). Once acquired and archived, sound samples can be treated with signal analysis techniques like the Fourier and wavelet decompositions that are commonly used in acoustic-related disciplines, but need to be applied to massive datasets with fast procedures. The sound samples can be joined to non-audio data, such as weather, elevation, or vegetation data. In the best option, the sampling of all data types should be synchronized and achieved in a passive way to keep the cost of sampling as low as possible. However, data based on active techniques that are uncoupled with the audio recordings, such as those obtained by satellite remote sensing (Smith et al. 2013) or LIDAR technique (Pekin et al. 2012), can be processed and introduced in an ecoacoustics analysis as well.

Signal transformation is a necessary step for retrieving the features that are specific to each recording. The signals embedded in the audio samples can be labelled automatically on an individual, population or species level through machine-learning techniques (Potamitis 2014). This procedure can be extremely informative, as it can return presence/absence data in relation to time and space, which is a fundamental requirement for addressing ecological researches. To achieve universality, automatic sound labelling should be an unsupervised process, that is, it should not require any manual data labelling (Stowell and Plumbley 2014). However, this research route can be tortuous, due to the intrinsic properties of environmental sounds that are made up of a complex mix of intricate sounds with a high level of intra-specific variation. Ecoacoustics has opened up another way to quantify sound samples by developing mathematical indices that aim to quantify the properties of a single recording (α indices) or to measure a dissimilarity between two recordings (β indices) (Sueur et al. 2014). This global parametrisation is attractive, as it does not require major computations and can be applied to the majority of acoustic environments. The method has returned promising, but also mixed results, suggesting that it still needs to be improved and better calibrated. Finally, the information extracted from the audio samples has to be plotted using graphics that summarise several variables at the same time along many dimensions, thus representing a challenge for big data visualisation (Gage and Axel 2014; Towsey et al. 2014c).

Main Tasks and Future Directions

Ecoacoustics should lead to new research that tests the ANH and AAH through playback experiments run at the community rather than the individual level. Following the niche concept, the ANH is mainly based on the idea that species compete through acoustic interference. However, we believe that species belonging to the same assemblage not only interact through direct competition or amensalism, but also through mutualism and commensalism (Malavasi and Farina 2013). Even if main information transfer relies on species-specific encoding-decoding systems, there is no reason to believe that species communicate in a totally hermetic system (McGregor 2005). We believe that research focusing on species interactions should test whether species interact acoustically in a positive way, either by exchanging information with mutual benefits or by eavesdropping on the signals of other species. This would suggest that sounds are working as both direct, active cues used by animals, and as indirect sources of information inside a cognitive public space. In addition, we think that the ANH should be confronted with the neutral theory, which suggests that biodiversity patterns, including community structures, could arise from random processes based on an equivalence of competitors within the community (Hubbell 2011). Acoustic community patterns may actually result from the combination of deterministic (Hutchinson's niche model) and stochastic processes (Hubbell's neutral model) as suggested for other types of communities (Chase and Myers 2011).

Ecoacoustics encompasses a rarely met spectrum of investigations in ecology, due to the numerous ecological scales on which the investigations are conducted. Ecoacoustics can achieve indeed several tasks in connection with biodiversity assessment, habitat assessment, population ecology, community ecology, landscape ecology and conservation biology (Table 1). These tasks, which ranges from the detection of a

Table 1 The main tasks of ecoacoustics grouped by related disciplines. A single reference is given as key example and should not be considered as the only reference treating the topic

Discipline and tasks	Reference
Biodiversity assessment	
Detection of the occurrence of species of interest	Bardeli et al. (2010)
Estimation of the number of species	Towsey et al. (2014b)
Estimation of animal acoustic diversity changes over time and space	Rodriguez et al. (2014)
Habitat assessment	
Habitat monitoring through an habitat acoustic signature	Bormpoudakis et al. (2013)
Assessment of habitat quality changes	Piercy et al. (2014)
Assessment of habitat selection by animal species	Figueira et al. (2015)
Analysis of soundscape orientation by migrating animals	Slabbekoorn and Bouton (2008)
Population ecology	
Estimation of population distribution, including migration patterns	Risch et al. (2014)
Estimation of population density	Lucas et al. (2015)
Estimation of population viability	Laiolo et al. (2008)
Estimation of population structure	Laiolo and Tella (2006)
Estimation of the effects of global changes	Llusia et al. (2013)
Analysis of the dynamics of species invasion	Both and Grant (2012)
Community ecology	
Description of acoustic community composition and dynamics	Sueur et al. (2008)
Assessment of the community acoustic diversity	Gasc et al. (2013)
Testing the partitioning hypothesis within the community	Ruppé et al. (2015)
Deciphering the acoustic interactions within the community	Tobias et al. (2014)
Landscape ecology	
Ecoacoustic theory and methods in landscape analysis	Mazaris et al. (2009)
Interaction between landscape and acoustics	Farina et al. (2010)
Analysis of landscape properties through acoustics	Tucker et al. (2014)
Develop landscape planning through acoustics	Brown and Muhar (2004)
Estimation of changes of soundscape along landscape gradients	Joo et al. (2011)
Conservation biology	
Estimation of the relative importance of noise in the environment	Barber et al. (2011)
Estimation of the effects of noise on acoustic communities	Pieretti and Farina (2013)
Suggestion of conservation planning through acoustic assessment	Laiolo (2010)
Estimation of the effects of noise on populations	Azzellino et al. (2011)
Acoustic community and soundscape archiving	Kasten et al. (2012)

single species of interest to the analysis of soundscape properties, all aim at a better understanding of ecological patterns and processes.

More specifically, at the population level, ecoacoustics can be used to estimate population density, population internal structure, population viability, population distribution in space and time and the effects of global changes. Ecoacoustics can also be called to monitor the dynamics of invasive species populations. When focusing on communities, the ecoacoustic approach aims to describe the acoustic composition of the community, the potential partitioning of the acoustic space by its members, the variation in space and time of one or several communities, and the acoustic interactions between species within a community. The emerging acoustic environment or soundscape can be used to investigate the structure of landscapes, the effect of spatial patterns like the structure of the patch mosaic (size and shape of the edges), the contagion property of the land mosaic, the insularisation effects, and the effect of land uses (e. g., deforestation, logging and prescribed burns).

Ecoacoustics plays a central role in biodiversity assessment by potentially detecting the occurrence of species of interest, and by estimating species acoustic diversity changes over time and space. The acoustic signature can be extracted to assess the habitat selection of species and the changes in habitat quality. Ecoacoustics also aims to assess the importance of anthropogenic noise in shaping species sound diversity (Rabin et al. 2003; Barber et al. 2009; Francis et al. 2009; Kight and Swaddle 2011).

Although ecoacoustics relies on automatic recorders, it is not yet a true remote-sensing field. The next generation of sensors must be able to send data, whether raw or interpreted, through a wireless connection. The automatic identification of acoustic items must achieve a higher level of accuracy, while the global acoustic indices need to be more resistant to unwanted external factors. These improvements are essential if the ecoacoustics field plans to offer applications for smartphones or other handheld devices for use in citizen science programs (Snaddon et al. 2013).

This short essay proves that the new ecoacoustics discipline is, in essence, multi-disciplinary within the wider field of life sciences, but we are also convinced that progress will only be possible if strong bridges are built between ecoacoustics and other non-biological disciplines like electronics, data mining, big data, omics, and social sciences.

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