Acta Acustica united with Acustica
Vol. 100 (2014) 772 – 781

DOI 10.3813/AAA.918757

Acoustic Indices for Biodiversity Assessment and Landscape Investigation

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Summary

Bioacoustics is historically a discipline that essentially focuses on individual behaviour in relation to population and species evolutionary levels but rarely in connection with higher levels of ecological complexity like community, landscape or ecosystem. However, some recent bioacoustic researches have operated a change of scale by developing acoustic indices which aim is to characterize animal acoustic communities and soundscapes. We here review these indices for the first time. The indices can be divided into two classes: the α or within-group indices and the β or between-group indices. Up to 21 α acoustic indices were proposed in less than six years. These indices estimate the amplitude, evenness, richness, heterogeneity of an acoustic community or soundscape. Seven β diversity indices were suggested to compare amplitude envelopes or, more often, frequency spectral profiles. Both α and β indices reported congruent and expected results but they may still suffer some bias due, for instance, to anthropic background noise or variations in the distances between vocalising animals and the sensors. Research is still needed to improve the reliability of these new mathematical tools for biodiversity assessment and monitoring. We recommend the contemporary use of some of these indices to obtain complementary information. Eventually, we foresee that this new field of research which tries to build bridges between animal behaviour and ecology should meet an important success in the next years for the assessment and monitoring of marine, freshwater and terrestrial biodiversity from individual-based level to landscape dimension.

PACS no. 43.80.+p

1. Introduction

Bioacoustics is usually defined as the scientific discipline that studies the emission, propagation and reception of sound produced by animal species. Bioacoustic studies dealing with humans are rather rare as research on human voice, audition or music is mostly related to medical sciences and musicology respectively. This definition has its origins in the paradigm of Shannon and Weaver [1] who describes communication as an emitter-receiver duo sharing information encoded in a signal. In terms of acoustics, an individual (the emitter) produces a mechanical vibration that embeds information (the signal) which propagates through a medium (air, water, vegetation, soil) and is received by another individual (the receiver). The reception of the signal may change the behaviour or the physiology of the receiver. The information is encoded by the emitter and decoded by the receiver through a code.

Received 9 January 2014,
accepted 9 May 2014.

This concept is extremely constructive as it builds a simple linear chain of events that are clearly identified and delimited (emission, propagation, reception). This explains why numerous bioacoustic studies refer, directly or indirectly, to the emitter-receiver paradigm. However, this scheme could also be viewed as a rather narrow concept as it suggests that communication simply works as a closed system between two individuals that share an encoding-decoding process. Studies on sound choruses clearly revealed that communication is structured in a network rather than in a one-to-one communication relation (for a review see [2, 3]). The emitter and the receiver rarely form an isolated pair but rather they combine into a piece of a communication web spun by several emitters and receivers like it happens in frog choruses (e.g. [4]). The study of networks and choruses increased significantly during the last years and the recent development of microphone arrays opens the possibility to track individual acoustic activity and, therefore, to better estimate the inter-individual interactions within a network of singing animals [5]. Even if cases of eavesdropping between species have

been reported [6] and inter-specific interactions have been explored (e.g. [7]), the encoding- decoding information system used by a dyad or a network of individuals is considered most often to be specific to each species [8]. This restriction to individuals from the same species is probably most often correct but inherently implies that animal communication is a locked system that prevents inter-specific interactions. Therefore, bioacoustics often focus on a single or a few species suggesting that bioacoustics is mainly a species-centered discipline.

Historically, ecology is the science that examines the interactions of organisms with their environment, including both biotic and abiotic factors. Although ecology covers by essence all organization scales, from genes to ecosystems, bioacoustics investigate mostly infra-specific and specific levels. Bioacoustic research led to fine art tools to monitor the acoustic activity of species, population and even of individuals in both marine and terrestrial habitats [9, 10]. However, bioacoustics showed little interest in higher levels like community, ecosystem and landscape. This scale mismatch between bioacoustics and ecology may explain why these two disciplines rarely met: bioacoustics is considered as part of animal behaviour discipline not of ecology.

However, a change of scale in bioacoustics was recently achieved by trying to zoom out on sounds produced by entire communities or on considering the total acoustic elements of a landscape, known better as the soundscape [11, 12, 13]. In ecology, a community can be defined as an assemblage or collection of interacting species found in a particular prescribed area or habitat [14, 15]. An acoustic community is then an assemblage of vocal animals acoustically active at a given site and a particular time. These species may compete or cooperate for a limited acoustic space [7, 16, 17, 18, 19].

A landscape may be defined as a geographical area characterized by spatial characters (patterns) that influence composition and distribution of individual species, populations and communities [20], a cultural entity [21] or a species-specific cognitive dimension [22]. Despite the different epistemic perspective used to define a landscape, all sounds present in a landscape produce a soundscape defined by Pijanowski *et al.* [12, 13] as "the collection of biological, geophysical and anthropogenic sounds that emanate from a landscape and which vary over space and time". The soundscape is therefore divided into three main components: the biophony (biologically produced sounds), the geophony (geophysically produced sounds) and the anthrophony (human produced sounds) [12, 13].

The change of scale in bioacoustics is supported by the recent development of digital autonomous audio recorders that can collect in an unattended way the acoustic activity emanating from terrestrial, marine and aquatic environments [23, 24] (Figures 1 and 2). These devices can be deployed in large numbers to cover important areas and long periods of time. This technology for the first time allows sampling automatically the acoustical activity of animal communities and the sounds from landscapes.

Figure 1. Field recording of acoustic communities or soundscapes. An autonomous digital recorder (SM2, Wildlife acoustics) is settled in the Nouragues tropical forest in French Guiana with one microphone at a human breast heights and one microphone ready to placed in the canopy at a height of 20 meters. See [40] for details.

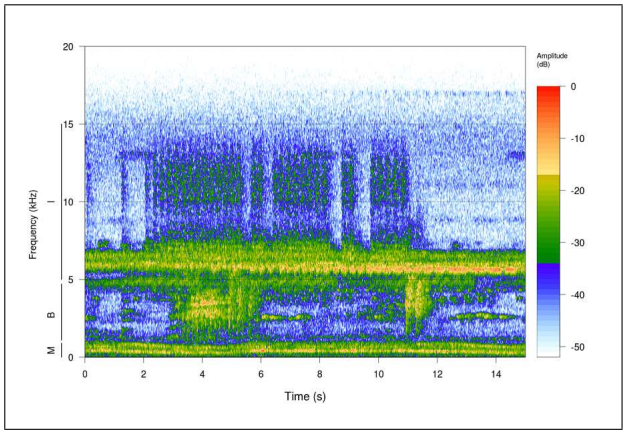

Figure 2. Sample of a community or soundscape recording. Spectrogram of a recording achieved at the Nouragues reserves in French Guiana on the 12nd of December 2010 at 6:30 am (point 04°05′18.99″ N, 52°40′27.68″ W). The recording include one mammal species (howler money, M) and several bird (B) and insect (I) species with lines indicating approximate respective frequency bands. Spectrogram specifications: 512 samples non-overlapping Hamming window with a 52 dB dynamic range. See [40] for details.

This, in turn, permits to address ecological and conservation questions at an ecological level. The massive audio dataset collected need to be managed and analysed with

efficient acoustic tools. In particular, research in ecology has a tradition of several indices that describe with a single value the ecological complexity from community to landscape scale (e.g. [25]). The requirement for acoustic tools leads to the concomitant development of acoustic-based ecological indices that could be used for biodiversity assessment, investigations on community dynamics and landscape patterns. We aim with this paper to review and comment some of these recent indices to better understand the relationship between environmental proxies and the acoustic complexity of vocal animals. All indices have been developed in terrestrial communities and landscapes so far. We will therefore focus our review on terrestrial environments even if several indices can be used without major conceptual and technical issues to marine and freshwater environments [26].

2. Biodiversity indices

An index of biodiversity is a mathematical function designed to evaluate some aspects of biodiversity. In biodiversity assessment, numerous indices have been developed to describe several diversity facets of animal and plant communities. These indices aim to quantifying, among others, richness, evenness, regularity, divergence or rarity in species abundances, traits, or phylogeny [27, 28, 29]. A usual distinction in biodiversity assessment is made between the within- and between-group diversity, a group being a sample unit as a site, a habitat or a time event. The within-group diversity was named the α diversity and the between-group the β diversity [30]. Both α and β diversities are computed from the list of entities belonging to a sample unit. Main α diversity indices are related to the number of entities (richness) and the relative abundance of each entity (evenness) in a specific collection. Main β diversity indices try to estimate similarity or dissimilarity between the lists of entities recorded at each site. In most cases, these entities are species, but other entities can be used including genes, evolutionary units, and functional traits (e.g. related to behaviour, morphology or ecology) to assess genetic, phylogenetic or functional diversity [28].

Indices developed for biodiversity assessment were very recently adapted for the estimation of sound diversity emanating from natural environments. The entity to be assessed is therefore an acoustic community or a soundscape. Before, several indices were used to describe the perception and categorization of urban [31] and rural soundscapes [32, 33] according to a human perspective. These urban soundscape indices mainly rely on human perception scales [34] and their results are therefore difficult to compare due to potential differences in perception. However, recent efforts have been done to produce objective acoustic parameters that are not observer biased [35]. In this context, the idea of applying biodiversity indices to the analyses of acoustic recordings rose by trying in most cases to collect objective data.

Animal sound emission can be sampled within a group – a community, a landscape – or in different groups at the same time. It becomes then necessary to assess both within- and between-group acoustic diversity. Several α acoustic indices have been developed to try to assess the richness or complexity of an acoustic community or soundscape and some β acoustic indices have been proposed to evaluate a level of acoustic disparity between acoustic communities. We will review these two families of indices successively.

3. Within-group indices: α acoustic diversity

Acoustic indices estimating within-group diversity can be divided into three categories: (1) indices using the amplitude, or intensity *i.e.* sound energy, (2) indices that estimate a level of complexity in terms of time, frequency and/or amplitude, and (3) indices that take into account the three components (biophony, geophony, and anthrophony) of a soundscape (Table I).

3.1. Intensity indices

A simple measure of an acoustic community or a soundscape consists in measuring sound intensity. Almost all measurements are sound level parameters L expressed in deciBel with different frequency weighting and time averaging leading to a plethora of indices (e.g. $L_{\mathrm{C,peak}}$, $L_{\mathrm{A,eq}}$, L_{day}, L_{evening}) [35]. These measurements are traditionally used for noise level assessment in urban soundscape (e.g. [36]) and occasionally in an ecological or conservation context [37, 38, 39]. However, accurate sound level measures require the use of numerous and expensive sound level meters and miss important information regarding the frequency and temporal patterns of sounds. These measures should be then accompanied with other indices working on the time and frequency dimensions. Two recent papers used amplitude measurements to estimate natural soundscape intensity [40, 41]. In French Guiana, the ambient acoustic amplitude of the audio files generated by 24 recorders was estimated by computing the root-mean-square (RMS) of the absolute value of the raw signals [40]. This information was successfully used to draw amplitude-based maps of the forest area sampled but was completed with metrics based on the frequency content of the soundscape. Soundscape power was also measured in a recent study in a deciduous and coniferous North American forest [41]. However this was not a standing alone metric as sound power was also measured for 11 frequency intervals taking therefore into account the frequency dimension of sound (see section Soundscape indices). Eventually, a set of six metrics related to amplitude was tested to estimate avian richness of an Australian site [42] .

3.2. Complexity indices

The concept of "complexity indices" is based on the assumption that the acoustic output of a community or a landscape will increase in complexity with the number of singing individuals and species. An index that captures the heterogeneity of sound should then give a proxy of animal acoustic activity. The first index developed in a context community and landscape was an index that assesses

Table I. Summary of α and β acoustic diversity indices.

Full name	Abbreviation	Principle	Reference
α indices			
Relative avian abundance	–	Area under spectrum in relation with an amplitude threshold	[43] [43]
Temporal Entropy	H_t	Envelope complexity	[44]
Spectral Entropy	H_f	Spectrum complexity	[44]
Acoustic Entropy Index	H	Envelope and spectrum complexity	[44]
Ratio of biophony to anthrophony	ρ	Ratio of biophony to anthrophony	[54]
Acoustic Complexity Index	ACI	Spectrogram complexity	[50]
Biophony	–	Biophony level	[45]
Biophony peak	bioPeak	Biophony level	[56]
Acoustic Entropy Index	AEI ($= H$)	Envelope and spectrum complexity	[45]
Shannon's Index	H'	Spectrum complexity	[46]
Acoustic Richness	AR	Envelope complexity and intensity	[48]
Median of amplitude envelope	M	Median of amplitude envelope	[48]
Normalised Difference Soundscape Index	NDSI	Ratio of anthrophony to biophony	[55]
Acoustic Diversity Index	ADI ($= H'$)	Spectrum complexity	[47]
Sound pressure level parameters	L	Ratio of sound pressure relative to a reference value	[35] [35]
Number of peaks	NP	Spectrum complexity	[19]
Mid-band activity	–	Fration of spectrum above an amplitude threshold	[42] [42]
Entropy of spectral maxima	H_m	Spectrum composition	[42]
Entropy of spectral variance	H_v	Spectrum complexity	[42]
Spectral diversity	–	Number of clusters	[42]
Spectral persistence	–	Duration of repeated clusters	[42]
β indices			
Spectral Dissimilarity	D_f	Spectrum dissimilarity	[44]
Temporal Dissimilarity	D_t	Envelope dissimilarity	[44]
Acoustic Dissimilarity Index	D	Envelope and spectrum dissimilarity	[44]
Kolmogorov-Smirnov distance	KS	Spectrum dissimilarity	[60]
Kullback-Leibler distance	KL	Spectrum dissimilarity	[60]
Vectorial correlation coefficient	RV	Spectrum similarity	[60]
Cumulative Dissimilarity	D_{cf}	Spectrum similarity	[61]

the relative abundance and composition of bird communities [43]. This index computes the area under the frequency spectrum above a specific dB threshold and within a specific frequency range. This metric, which is a function of both sound level and the number of frequency bands used by the bird community, facilitated the monitoring of species across Hawaiian bird submontane ecosystems [43].

One year later, one of the most used indices in biodiversity assessment, the Shannon Shannon evenness index, was applied on sound emitted by animal communities by computing two acoustic sub-indices H_f, and H_t [44] . The Shannon index derives from the computation of entropy. For a set of S species, this index is calculated with the equation

$$H = \left(- \sum p_i \ln p_i \right) / \ln S, \quad (1)$$

where p_i is the proportion of individuals found in the ith species.

The spectral entropy, H_f, was therefore obtained by applying Shannon evenness to the average frequency spectrum scaled by its integral with species being replaced by frequency bins. Similarly, the temporal entropy, H_t, was computed on the amplitude envelope obtained with the Hilbert transform of the signal, scaled by its integral as well. These two indices were multiplied to obtain an acoustic entropy named H ranging between 0 and 1, with low values indicating pure tones and high values sound with numerous and even frequency bands. This index returned expected results on recordings made in a Tanzanian forest where animal acoustic activity was high and background noise due to wind, rain and human activity very low leading to a high signal-to-noise ratio [44]. A slight modification of the spectral entropy index H_f was later introduced by reducing the frequency resolution of the average spectra to 1 kHz or by applying Shannon diversity (=Shannon evenness/ln *number of frequency bins*) (index H' and *AEI* [45]; index H' [46]; index *ADI* [47]). It later appears that entropy, in particular its spectral component H_f, could give counter-intuitive results when applied to recordings where background noise dominates over animal sound production as it often occurs in temperate habi-

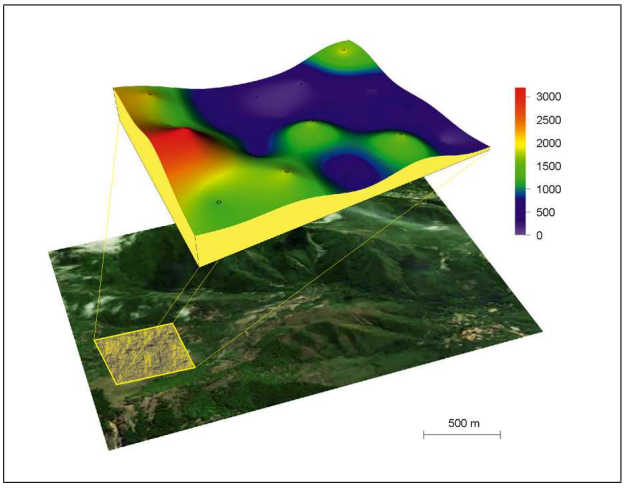

Figure 3. α acoustic diversity of a Mediterranean landscape. Interpolation map representing the acoustic dynamics arising from the processing of one recording session via the computation of Acoustic Complexity Index (*ACI*) [50]. Twenty H4 recorders (Zoom Corporation, Japan; sample rate 44.1 kHz, 16 bit, stereo) were placed in an ecotonal area of a beech wood in the Tuscan-Emilian Apennine National Park, Fivizzano, Italy (central point 44°16′00.07″ N, 10°12′49.40″ E, 1060 meters a.s.l.) for two hours at dawn in Spring 2011.

tats where diversity is lower than in tropical forests. This motivated the design of another index, named Acoustic Richness (AR) that combined temporal entropy and amplitude but not spectral entropy [48]. This index AR reported values in agreement with bird species richness estimated aurally in a French temperate woodland [48]. The H index also proved to work coherently when applied to marine according as soon as the raw data were filter out to remove noise due to seismic airgun activity [26].

At the same time, the Gini index [49] was applied to a binned frequency spectrum above a specified amplitude threshold leading to the Acoustic Evenness Index (*AEI*) [46]. The same year (2011), an acoustic complexity index, *ACI*, was developed to produce a direct quantification of soundscape complexity by computing the variability of the intensities registered in audio recordings, despite the presence of constant human-generated-noise [50, 51]. The *ACI* works on the matrix returned by a short-term Fourier transform (STFT) applied to the complete recording or to a series of successive windows. The computation mainly consists in summing up the absolute difference between two adjacent values of intensity, $I_k - I_{k+1}$, where k is the kth position in the intensity values recorded along a single frequency bin of the STFT. The *ACI* was successfully applied in different Mediterranean soundscapes mainly composed with bird and cicada sound [50, 51, 52] (Figure 3).

Recently, eight metrics were used to search for an acoustic signature of different habitats in Northern Greece [53]. These metrics were all based on the frequency spectrum, including the spectral centroid, standard deviation, kurtosis, skewness, zero-crossing rate, entropy, spectral flatness, and Spearman correlation to pink ($1/f$) noise. None of these parameters were considered as an index but they were used as a set of descriptors. A random forest algorithm with all these metrics yielded to a classification of six habitat types with a very low error rate ($< 1\%$). The most significant descriptors in the classification were the centroid, the spectral flatness and the entropy suggesting that they can participate to habitat specific ambient sound patterns and could be used to characterise and discriminate habitats.

Another index of sound complexity, named *NP*, was built by simply counting the number of major frequency peaks obtained on a mean spectrum [19]. This index results from the assumption that spectral complexity of a sound can be assessed by the number of frequency bands occupied. It is indeed expected that a sound produced by $n + k$ species should contain more frequency peaks than a sound due to n species only. The *NP* index is also supposed to be insensitive to noise that does not perfectly match with the sound of interest as residual frequency peaks due to background sound can be easily discarded. However, some bias may also appear as a single species producing a noise-like sound, like some cicadas do, may return a higher *NP* index than several species producing pure tone sound. This bias may also affect other indices.

Five new indices were very recently designed: (i) mid-band activity or the fraction of spectrogram cells in the mid-band (482–3500 Hz) where the spectral amplitude exceeds a specific threshold, (ii) entropy of spectral maxima H_m which is an entropy-like index focusing on the 4282-8820 Hz frequency band, (iii) entropy of spectral variance H_v that is based on the same principle of the spectral index H_f but computes the variance instead of the average of each frequency bin, (iv) spectral diversity that estimates the number of distinct spectral clusters, and (v) spectral persistence which is related to spectral diversity by estimating the average duration of clusters that persist along time [42].

3.3. Soundscape indices

Another family of indices, derived directly from the concept of soundscape ecology, which divides a soundscape into biophony, geophony and anthrophony. The main idea is to estimate the relative contribution of biophony compared to geophony and anthrophony. To separate the sources of these three components is not an easy task. Therefore a simplified approach was used that splits the spectral profile of the soundscape into two main regions: (1) the frequency band between 0.2 and 2 kHz would mainly consist of mechanical signals (anthrophony), and (2) the frequency band between 2 and 8 kHz would be primarily occupied by animal sound production (biophony). The sound due to wind or rain would cover the entire spectrum with more energy in the lower frequencies [54]. These limits, that were first defined empirically, were controlled later with recordings taken along an urban-rural gradient [45]. Nonetheless these limits might be slightly artificial as it is known that animals may produce sound below 2 kHz and above 8 kHz. In particular, these limits will likely be different in tropical habitats where animal

acoustic diversity is not typically limited within the 2–8 kHz frequency band. A level of energy per soundscape component, i.e. per frequency band, can be assessed on the frequency spectrum, which has been discretized to a 1 kHz resolution. It is then possible to quantify a relative level of energy of anthrophony (a) and biophony (b) and to compute their ratio (b/a) leading to the first soundscape index that essentially estimates the relative level of biophony. This ratio was first symbolised with the Greek letter ρ [54]. A variation of the ρ index, termed Normalised Difference Soundscape Index (NDSI), was introduced by computing the ratio $(b-a)/(b+a)$ [55]. NDSI index ranges between -1 and 1, with low and high values indicating the prevalence of the anthrophonic and biophonic sound, respectively. The index NDSI was used in a soundscape library to qualify online samples [55] and to examine and map changes in soundscape composition in a North American lacustrine forest habitat [41]. The anthrophony and biophony energy level can also be treated independently without computing a ratio as it was done when investigating the spatial and temporal patterns of soundscape characteristics in an urban-rural landscape gradient (value *biophony* [45]; value *bioPeak* [56]).

4. Between-group indices: β acoustic diversity

A β acoustic diversity should help in determining how much two or more acoustic communities or soundscapes are acoustically different, or in assessing the changes between two dates of a focused community or landscape. The measure of sound divergence is not straightforward as sound can vary independently along three dimensions, i.e. time, frequency and amplitude, and homology along each of these three dimensions might not be clear. In addition, in the particular case of outdoor recordings, the distance between the sources (the calling animals) and the sensor (the audio recorders) can induce amplitude variations among recordings that should not be interpreted as relevant differences.

The comparison of one-dimension contours (envelope, spectrum) is not trivial as revealed in other disciplines than acoustics [57, 58, 59]. There is therefore no universal metric that properly estimate sound similarity or difference. Current acoustic indices in use for ecology might therefore not be optimal but they returned expected results so far (Table I).

A first attempt to compare the acoustic output of animal communities was made comparing Hilbert amplitude envelopes and average frequency spectra [44]. The dissimilarity index, named D, is the multiplication of two-sub indices, D_t and D_f. D_t is obtained by computing the Hilbert amplitude envelope of each sound, scaling each envelope by its integral, and computing the difference for each time sample. Similarly, D_f, is obtained by computing the average of the STFT of each sound, scaling each average spectra by its integral, and computing the difference for each frequency bin. D is the multiplication of D_t and D_f,

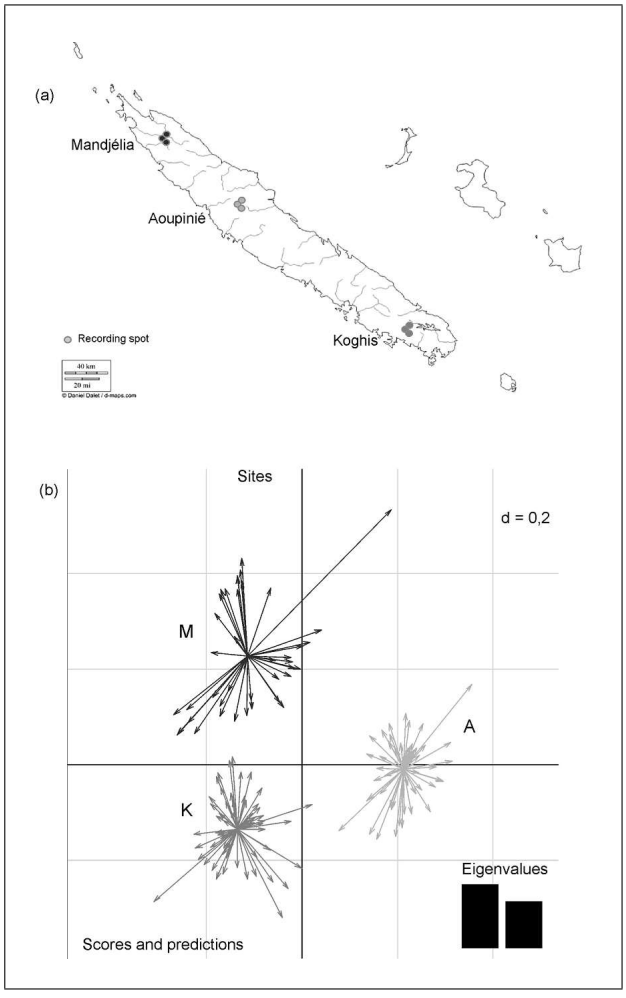

Figure 4. β acoustic diversity at a regional scale in New Caledonia. (a): The sound of three acoustic communities were sampled in three sites with three recording points at each site: Aoupinié (A), Koghis (K) and Mandjélia (M). (b): Results of Redundancy Analysis applied to the principal coordinates analysis of acoustic distances among all recordings, with a factor "Site" as an explanatory variable, revealing a clear acoustic difference between the three acoustic communities. The length of the arrows represents residuals: each arrow connects the position of a recording predicted by the site in which it was done (where the arrow starts) to its real position based on raw data (real acoustic composition where the arrow ends). Modified from [60].

tends towards 0 for similar sound and towards 1 for distinct sound. This index was applied when comparing two Tanzanian forest communities [44] and analysing temperate woodland bird communities [48]. However, it also appears that the index D_t requires a perfect temporal homology between the amplitude envelopes to be compared. This strict homology may not be met even with synchronised recordings. The sub-index D_t was therefore not used in other analyses and only the sub-index D_f was kept. The D_f index revealed clear temporal and geographical variation of distant New Caledonian sites [19] (Figure 4) and also highlighted time and spatial patterns within a patch of a tropical rainforest in French Guiana [40].

Four other distance metrics were used to compare the average spectrum of bird songs: (1) the Kolmogorov-Smirnov distance that is the maximum distance between two cumulated frequency spectra, (2) the symmetric Kullback-Leibler distance that computes the relative entropy between two probability frequency spectra, (3) the similarity RV vectorial correlation coefficient that measures the correlation between two matrices [60], (4) the cumulative frequency dissimiliarity D_{cf} [61]. The index D_{cf} works as D_f but takes cumulative frequency spectra as inputs. This index has the advantage to be sensitive not only to the spectral overlap between two spectra but also to the mean distance between the different frequency peaks of the two spectra. All indices, including D_f, were proved to be highly correlated generating similar results. D_f and D_{cf} could be preferred due to their simplicity in terms of computation.

5. Comments and prospectus

To find a single index that summarizes all biodiversity facets is undoubtedly utopian. There will not be any single value that will reliably estimate all levels of local or regional diversity. The motivation to find such a unique parameter derives probably from the request of managers, politicians and policy makers who need a single and easy to understand value to take conservation decisions [62, 63]. The same phenomenon seems to happen with acoustic indices: there is a current search for a single index that would give the most reliable and complete information on the acoustic and diversity states of a population, a community or a landscape. This explains why, after a few years only, several indices have been proposed in the same time but have been used very rarely together [45] (Table I).

The α acoustic indices achieved an important success probably because they aspire to give a single value, a kind of signature, to an acoustic community or a soundscape. These indices returned congruent results revealing, for instance, changes in bird species richness in accordance with aural identification [48] or complex patterns of the soundscape across different temporal scales [51]. However it is important to note that they may be affected by several factors like transitory or permanent background noise, variation in the distance of the animals to the sensor, the relative intensity and calling repetition of the calling animals, time and/or frequency overlap between sounds arising from different sources. These variations should be evaluated soon in different contexts, such as different habitats (vegetation structure and composition) and different sampling efforts. In addition, a clear correlation between the α indices and the level of community diversity or soundscape complexity has not been established yet. There is therefore still a need for a confrontation between classical direct field-based data like individual and/or species aural counting by volunteer observers and acoustic inferences. The research of α indices is currently in development: the improvement of former indices and the emergence of new indices are expected in the next years. As an example, acoustic diversity indices used so far were mainly based on the Shannon evenness index but other classical indices, like the exponential of the entropy or the Hill index [64, 65] could inspire quickly new α acoustic indices. However, it is highly probable that a single index will never cover all biodiversity facets and be reliable in all contexts. Combinations of indices could lead to more efficient results as already explored by [42]. We therefore recommend the use of several complementary α indices.

Compared to the important number of α indices, few β indices have been conceived so far (Table I). Bioacoustics shows a great interest in sound comparison to identify automatically species or individuals [66, 67, 68, 69, 70]. However, the comparative methods used in these contexts are adapted to closely related sounds, as vocalisations produced by a single individual, but are in most cases irrelevant to compare sounds emerging from communities and landscapes where strict time and frequency homologies are difficult to define. The β acoustic indices in current use are all based on simple distances between time envelopes or spectral profiles. These indices are very simple and might need a refinement. In particular, they may not be optimal as they are all based on a pointwise comparison. This is particularly the case of the D_f index that operates a subtraction of homologous frequency bins. These indices, like D_f, can return unexpected important differences for two frequency spectra with similar shapes but only slightly shifted in frequency. Other metrics that compare vectors of proportions (here frequency spectra) can be envisaged to replace the index D_f used so far. Such metrics could be for example the Orlóci chord distance [71] and the Morisita-Horn metric [72, 73]. Eventually, another method to compare community or landscape acoustics could be to use the symbolic aggregate approximation (SAX, [74]) [55]. SAX consists in converting a numerical series into a character string by transforming the data into a discrete string of letters. The size of the string can be chosen as well as the length of the alphabet. This results in a dimensionality reduction and lower bounding. SAX is currently in use for data mining, in particular for online search of similar soundscapes (see http://lib.real.msu.edu/) but it could be used to address ecological questions where spectral dissimilarities have to be computed.

All the developments in relation to acoustic indices for biodiversity assessment and landscape ecology can be considered as a new turn in bioacoustics with a change of scale from species to community and landscape. A major issue in ecology is to collect data over large areas and long time periods with a high and regular repetition rate [75]. By investigating acoustic communities and soundscapes, bioacoustics provides an efficient way to sample large ecological units. If the scaling up towards communities and landscapes sounds a promising avenue for bioacoustics and ecology, this process should not discredit the historical species-specific approach that provides accurate information on populations and species dynamics. Forthcoming efforts should consider all units of the ecological

scale shedding new light on the acoustic behaviour and acoustic ecology of animals.

Acknowledgement

We thank Stuart Gage and Eric Kasten for having checked the section dealing with landscape indices. Jerôme Sueur and Sandrine Pavoine were supported by a Fondation pour la Recherche sur la Biodiversité (FRB) grant and JS by the SABIOD MASTODONS Big Data CNRS MI project 2012-2017.

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