

Acoustic indices for biodiversity assessments: Analyses of bias based on simulated bird assemblages and recommendations for field surveys



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ABSTRACT

Rapid acoustic surveys aim to estimate biodiversity based on the diversity of sounds produced by animal communities, and interest in this approach among conservation planners is increasing. Several indices of acoustic diversity have been proposed as proxies for species richness. However, in the field, the animal activity may be responsible for acoustic diversity to varying degrees. To evaluate how measures of acoustic diversity may depart from actual species richness, we selected seven acoustic indices and applied them to simulated recordings of bird assemblages under different field conditions. For a given sound, defined here as the song composition emitted by a species assemblage, we determined if the indices were i) only driven by animal sounds, ii) insensitive to species identity, and iii) independent of species evenness. Under the field conditions evaluated, none of the indices fulfilled the three criteria necessary for a perfect proxy of species richness. However, some indices may be appropriate as a measure of biodiversity under a more broad definition including phylogenetic and/or functional aspects of diversity. We provide recommendations for the application of these indices for biodiversity measurement under field conditions, such as the application of appropriate audio filters, the increase of the repetition rate of the recordings, and the identification of the main taxonomic groups occurring in the recorded communities.

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1. Introduction

Exhaustively describing all living organisms, from bacteria to large animals and plants, seems to be an impossible target despite the launch of all taxa biodiversity inventories (ATBIs) (Granjou et al., 2014; Lawton et al., 1998; Rossmann, 1998). Although an exact measure of biodiversity is currently out of reach, it is still possible to generate estimates from a subset of organisms. Traditionally, species inventories are created through sampling and then extrapolating the data over larger areas and time scales (Sutherland, 2006), but an accurate extrapolation requires a sampling protocol with a large spatial and/or temporal component, which requires lengthy and difficult fieldwork. In addition, the sampling and identification of different taxa depend on a high degree of expert taxonomic knowledge; even a drastic increase in the number of taxonomists might not meet this demand for expertise (Costello et al., 2013). For example, a recent study reported an average time of 21 years between the collection of a specimen in the field and a formal species description and name (Fontaine et al., 2012). This time lag is

especially prevalent for under-sampled areas, where taxonomic descriptions are still in progress (Pellens and Grandcolas, 2010).

To circumvent these difficulties, alternative methods of quantifying biodiversity that do not require a high level of taxonomic expertise have been developed. Most of these methods, known as rapid biodiversity assessments (RBAs), speed the inventory process by focusing on a particular taxonomic group (Kerr et al., 2000; Mazaris et al., 2008; Rosser and Eggleton, 2012) or by using para-taxonomic methods (Krell, 2004; Oliver and Beattie, 1996; Ward and Stanley, 2004). Another solution is to forego species identification by considering different ecological scales and moving from the levels of individuals and species toward communities by conducting rapid acoustic surveys of vocal animal communities (Sueur et al., 2008a).

The use of acoustic tools in biodiversity conservation is not new (Batista and Gaunt, 1997), but it has recently increased, especially as part of the management of large wild areas (Dumyahn and Pijanowski, 2011; Farina, 2014; Laiolo, 2010). There is a growing demand from park managers and local decision-makers to better understand acoustic sampling design and the automated analysis of sound. This high degree of interest is partly explained by the availability of autonomous and weather-resistant recorders, which are increasingly economically and technically accessible to local and regional authorities. However, these devices produce such a large quantity of recordings that they are difficult to analyze manually. Therefore, the interest in using

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acoustic indices in conservation planning is mainly due to the rapidity with which a large amount of data can be analyzed through standardized, automatic processes with minimal acoustical expertise. It is often difficult to monitor non-visible or local disturbances (e.g., invasive species, pollution) in large protected areas using traditional approaches (Turner, 2010). In such a situation, an acoustic alert system, identifying an unexpected change in acoustic patterns, could be helpful. Acoustic surveys could also be used to monitor the restoration process after a disturbance event and enable the long-term evaluation of a restoration plan. An acoustic approach may be even more valuable if noise is considered a potential disturbance to a protected area (Barber et al., 2011).

The main principle underlying a rapid acoustic survey is the quantification of the global acoustic variability in the sound emerging from an animal assemblage (or “soundtope” as defined in Farina, 2014). Hereafter, “sound” refers to the acoustic production of an assemblage of different species, and “song” refers to the acoustic sequence produced by a particular species. The rapid acoustic survey approach is rapid, non-invasive, sensitive to multiple taxa, and rather simple to apply over large areas and long time periods. An acoustic community is an assemblage of species that sing at a specific place during a limited time period, the diversity of which is named community acoustic diversity (CAD; Gasc et al., 2013a). Several acoustic indices have been developed to measure CAD (Depraetere et al., 2012; Gasc et al., 2013a, b; Pieretti et al., 2011; Sueur et al., 2008a; Towsey et al., 2014; Villanueva-Rivera et al., 2011), and we will refer to them as “acoustic diversity indices”. These indices have been shown to be promising tools for biodiversity assessment, as they have been positively linked to the number of song types (Pieretti et al., 2011; Sueur et al., 2008a), species richness (Depraetere et al., 2012; Towsey et al., 2014), and phylogenetic and functional diversity (Gasc et al., 2013a).

The use of acoustic indices in conservation planning is promising, but more studies are needed to interpret them properly. These indices measure acoustic heterogeneity over a few seconds or minutes of a sound sample using temporal and/or spectral analysis, and a few studies have found positive correlations between acoustic diversity indices and species richness (Depraetere et al., 2012; Towsey et al., 2014). Although the diversity of singing species would increase the acoustic heterogeneity of a recording, other sources of acoustic heterogeneity in field recordings might prevent these indices from being adequate proxies for the richness of singing species. The effects of these sources must therefore be investigated.

Here, we investigate five sources of heterogeneity:

- i) The ratio of sound duration to recording duration. Acoustic samples usually differ in their duration, and the proportion of a sound in a recording varies with the duration of a recording.
- ii) The amplitude level of the background noise. This unwanted component of the sound is a common issue in bioacoustics and may result in greater or lesser heterogeneity in a recording depending on both the quality of the original recording and the mathematical properties of the acoustic index. We used the definition of “background noise” as proposed by Towsey et al. (2014): “an acoustic energy which remains constant through the duration of a 1-minute audio segment regardless of its source.”
- iii) Sound composition. Two singing animal communities might have the same number of species with the same abundance but may be composed of different species. The songs of certain species might be similar or different from one another; thus, the degree of acoustic difference between songs might vary from community to community.
- iv) The relative amplitude of the songs composing the acoustic assemblage. Considering two animal communities with a similar number and composition of singing species, factors such as the distance of the individuals from the microphone, vegetation structure and density, and meteorological conditions might

affect the relative amplitude of the songs and the heterogeneity of the sound.

- v) The overlap interval between songs. The degree of overlap between songs within the acoustic assemblage can result in time and frequency masking.

2. Materials and methods

Using simulated bird assemblages, we tested the variation in seven acoustic diversity indices due to five sources of heterogeneity. The use of simulations allowed us to accurately and independently control the parameters associated with each source of heterogeneity. We artificially created these bird assemblages to mimic real assemblages of birds by generating simulations based on 100 real bird communities described in a previous study (Depraetere et al., 2012). We performed all of the acoustic and statistical analyses with “R” software (R Core Team, 2013) using the “seewave” (Sueur et al., 2008b) package. We set the type I error threshold at 5% for all statistical tests.

2.1. Acoustic diversity indices

We considered seven acoustic diversity indices (Table A1): (1) spectral entropy, H_f (Sueur et al., 2008a); (2) temporal entropy, H_t (Sueur et al., 2008a); (3) acoustic entropy, H , which is composed of H_f and H_t (Sueur et al., 2008a); (4) the acoustic complexity index, ACI (Pieretti et al., 2011); (5) the signal magnitude, M (Depraetere et al., 2012); (6) the acoustic richness index, AR , which is composed of the H_f and M indices (Depraetere et al., 2012); and (7) the number of frequency peaks, NP (Gasc et al., 2013b).

Both of the spectral indices (H_f and NP) were computed on a mean spectrum, which was the average of a short-term Fourier transform (STFT) with a non-overlapping Hanning window of 512 samples. For each index, mean spectra were scaled by their maxima to obtain values between 0 and 1. The temporal indices (M and H_t) were computed on the Hilbert amplitude envelope, which was scaled by its maximum to obtain values between 0 and 1. The ACI was computed on a non-scaled STFT with a non-overlapping Hanning window of 512 samples, and the values obtained for each acoustic index were scaled by their maxima to enable comparisons across indices. The parameters used for the calculation of each acoustic index are reported in Table A1, and the results are valid for the fixed set of parameters used to calculate the indices (see Table A1).

2.2. Simulations

2.2.1. Basic artificial bird assemblages

We simulated artificial bird assemblages that mimic the species compositions of real bird assemblages recorded in a temperate woodland by Depraetere et al. (2012). These simulations were based on i) the description of the compositions of real bird species assemblages and ii) recordings of the isolated songs of individual species from sound libraries (Fig. 1 and Fig. A1). Three SM1 digital audio recorders (Wildlife Acoustics, 2009) equipped with two omni-directional microphones (flat frequency response between 20 Hz and 20 kHz) were placed in the Parc Naturel de la Haute Vallée de Chevreuse in France from 24 March to 5 June 2009 (sampling at 44.1 kHz with digitization to 16 bits). Birds were the main source of acoustic activity in this region and during this season. Bird species were aurally identified in these recordings, leading to descriptions of the compositions of real bird assemblages (Depraetere et al., 2012). From this dataset, we selected a sub-sample of 100 assemblages with no anthropophonic or geophonic sounds. These assemblages were composed of a total of 24 species with an average of 4 species, a minimum of 1, and a maximum of 8 species per assemblage (see Table A2 in the supplementary information); thus, an assemblage could be composed of a single species. As

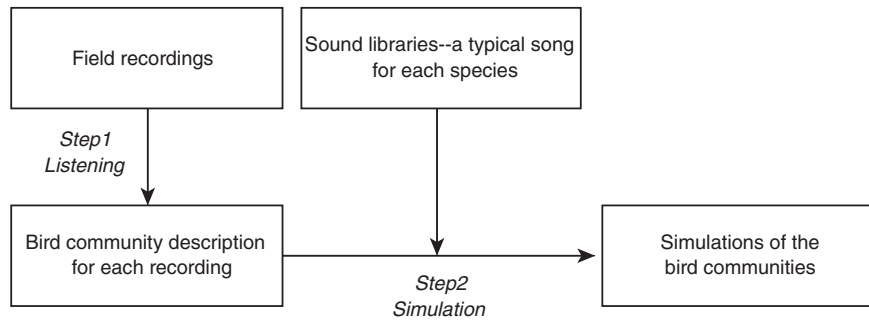


Fig. 1. From field recordings to the simulation of the 100 bird communities. Step 1 corresponds to the aural identification of the bird species in each recording. Step 2 corresponds to the simulation of the bird communities from the description of the communities and a pool of species-specific recordings available from sound libraries.

recommended by Toledo et al. (2015), the collected recordings will be deposited in the sound library of the National Museum of Natural History in Paris, and the identification codes associated with the recordings used in this paper are reported in Table A3.

To simulate the sound of each real bird assemblage, we combined the songs of the individual species acquired from different sound libraries (as specified in Table A2). We selected these songs based on two conditions: (i) the song had to be emitted by an isolated individual, and (ii) the signal to noise ratio (SNR) of the recording had to exceed 10 (20 dB). This ratio was estimated as follows: $SNR = 100 \times (rms(S)/rms(N))$, where S and N are the probability mass functions of the amplitude envelope of both 0.5 s of signal and 0.5 s of noise randomly chosen from the recording and rms is the root-mean-square. The duration of each species recording was set to 30 s, and the amplitude was scaled between -1 and $+1$.

2.2.2. Modification of the ratio of sound duration to recording duration (S/R)

A real recording of a species assemblage can contain a substantial amount of background noise, which becomes more apparent when there is a lack of singing birds. We tested whether the index values calculated for a 30 s recording, which only captured the sound, would be similar to a longer recording that captured both the sound and some of the background noise. To correctly reflect the acoustic activity of the animals, indices should be insensitive to the duration of the sound produced by a species assemblage in comparison to the duration of a recording.

We tested the impact of variation in the S/R ratio on the values of each index. As explained in Section 2.2.1, we simulated the sound of each of the 100 assemblages, and each sound was successively extended by 0 s, 30 s, 60 s, and 90 s of a background noise selected from the data set of Depraetere et al. (2012). This manipulation led to different recording durations (30 s, 60 s, 90 s, and 120 s, respectively), which made comparisons between the recordings irrelevant. We added silence (i.e., 0 values that do not affect the acoustic heterogeneity of the recording and thus the values of the indices) to the 30 s, 60 s, and 90 s recordings to reach a similar duration of 120 s.

We calculated the indices of the 400 sounds (100 sounds * 4 durations). For each index, we applied a Friedman test to estimate the effect of the S/R ratio on the index value.

2.2.3. Modification of the amplitude level of the background noise

To correctly reflect the acoustic activity of the animals, indices should be insensitive to the addition of an abiotic noise, such as the background noise. To test the effect of the amplitude levels of the background noise on the index values, we added a background noise selected from the recordings made by Depraetere et al. (2012) to the 100 simulated acoustic assemblages (see Section 2.2.1). We repeated the simulation three times using three amplitudes of the background noise: the amplitude level recorded in the field and levels fifty and one hundred times higher than that recorded in the field (oscillograms

of one sound at the three noise levels are available in the supplementary information, Fig. A2). We calculated the indices for all of the sounds, and for each index, we applied the Friedman test to the values obtained for the three levels of background noise.

2.2.4. Modification of the composition of the sound

To act as a reliable proxy for species diversity, an acoustic diversity index should vary in the same way when a new song is added to an assemblage regardless of the type of song. We added one song to each of the 100 simulated acoustic assemblages defined above and examined the variation in the indices. We selected three songs based on their distinct frequency inter-quartile ranges (IQR) to represent a high degree of spectral diversity: the song of *Sitta europaea* (Eurasian nuthatch), with a low frequency IQR (516 Hz); that of *Phylloscopus collybita* (common chiffchaff), with a medium frequency IQR (1378 Hz), and the song of *Turdus philomelos* (song thrush), with a high frequency IQR (2584 Hz). We compared values of the indices before and after the addition of a new song as follows.

Given an assemblage of bird species A , A_0 was obtained by removing, if present, the songs of *S. europaea*, *P. collybita* and *T. philomelos* from A . Then, new assemblages (A_1 , A_2 , and A_3) were created through the addition of one of the selected songs to A_0 .

For A_0 , A_1 , A_2 , and A_3 , we computed the seven indices, denoted as $\alpha(A_0)$, $\alpha(A_1)$, $\alpha(A_2)$, and $\alpha(A_3)$. We then calculated the variation in an index that resulted from the addition of each tested song by comparing $\alpha(A_1) - \alpha(A_0)$, $\alpha(A_2) - \alpha(A_0)$, and $\alpha(A_3) - \alpha(A_0)$ using a Friedman test. A_0 was considered a control, and A_1 , A_2 and A_3 were the acoustic treatments applied to assemblage A .

2.2.5. Change in the relative amplitude of the songs comprising the acoustic assemblage

Acoustic indices should be insensitive to the relative amplitude of the songs comprising the assemblage (i.e., the relative distances of the emitter-receivers) so that they can correctly reflect the number of different songs (i.e., the number of singing species). To test the impact of the relative amplitude of songs on index values, we simulated acoustic assemblages with different amplitude levels attributed to each song. We multiplied each song by an amplitude coefficient randomly chosen from a vector of values ranging between 0.1 and 1 with a step of 0.1. This process was applied to the 90 assemblages composed of at least two species.

For each of the 90 assemblages, we i) repeated the simulations 100 times and randomly varied the amplitude coefficients at each iteration, ii) calculated the indices for each simulation, and iii) calculated the standard deviation of the 100 index values to generate one standard deviation per assemblage. The standard deviation reflects the variation in the index due to the variation in the relative intensities.

2.2.6. Change in song overlap

Ideally, an acoustic index that acts as a reliable proxy for species richness (here, song richness, as a species is associated with a single

characteristic song in our simulations) should not be affected by the temporal overlap of a fixed number of songs. To estimate the potential effect of song overlap, which could lead to time and frequency masking, we simulated 100 artificial assemblages each composed of six songs randomly sampled from the pool of 25 songs. Each sound was simulated by combining six songs with three different time shifts separating the songs: 0 s (no time shift leading to complete overlap, i.e., synchrony), 15 s (half-time shift leading to each song overlapping its predecessor by half of its duration, i.e., middle) and 30 s (maximal shift leading to an absence of overlaps, i.e., alternation). We obtained a total of 300 sounds (100 assemblages * 3 overlap variations), and we added silence (i.e., zero values) to the simulated recordings to create the same duration for all sounds. For each index, we applied the Friedman test to the values obtained for the three different time shifts.

3. Results

The significance levels of the results given below are provided in Table 1.

The *Hf*, *M*, and *ACI* indices increased as the *S/R* ratio decreased (Fig. 2). The *Ht* and *H* indices decreased with the *S/R* ratio, whereas the *AR* and *NP* indices varied little.

The effect of the amplitude level of the background noise differed significantly among indices (Fig. 3). The values of the *H*, *Hf*, *Ht*, and *M* indices increased with an increase in background noise level, whereas those of *AR* and *ACI* decreased. The *NP* index was not significantly affected by the amplitude of the background noise.

The values of all indices varied significantly with the type of song added (Fig. 4). Although the values of the *Hf*, *Ht*, *H*, and *M* indices increased, on average, with the addition of a new song, the *NP* and *ACI* indices increased or decreased depending on the species added. Among the indices that increased with the addition of a new song (i.e., *Hf*, *Ht*, *H* and *M*), *Ht* was the least affected by song type (lowest difference in the diversity values after the addition of the species, in contrast to *M*, which displayed the highest difference; Fig. 4). On average, the *AR* index varied with the addition of a species, but this variation did not depend on the type of song added and it could be positive or negative depending on the community in which the song was added.

The impact of the relative intensities of the songs differed significantly among indices (Fig. 5). The *AR* index showed the highest standard deviation in response to a change in the relative intensities of songs, followed by the *M* and *NP* indices, with intermediate standard deviations, and the *Ht*, *Hf*, and *ACI* indices, with low standard deviations.

The values of the *M*, *ACI* and, to a lesser extent, *Hf* indices increased as the overlap between songs decreased (Fig. 6), whereas those of *Ht* and *H* decreased. The *AR* and *NP* indices did not vary significantly with temporal overlap.

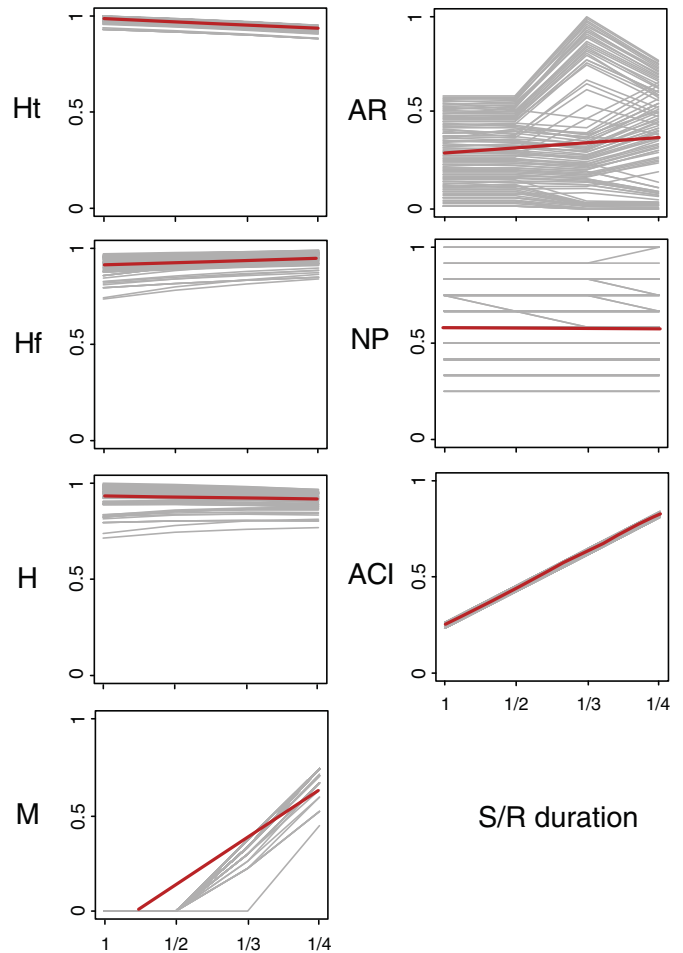


Fig. 2. Variation in the values of the acoustic diversity indices with different sound to recording duration (*S/R*) ratios. Each gray line links four values calculated for one 30 s assemblage with 30 s, 60 s, 90 s, and 120 s of recording corresponding to a ratio of 1, 1/2, 1/3 and 1/4, respectively. For each index, the red line (bold line) is the linear model explaining the index values by recording duration. The values on the x-axis increase with the recording duration and thus decrease as the *S/R* ratio increases; the flatter the resulting red line, the lesser the impact of variations in the *S/R* ratio on the index. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

We demonstrated that acoustic diversity indices can be impacted by the five acoustic conditions examined above. Here, we will (i) discuss the use of acoustic diversity indices as proxies for the diversity of singing species and (ii) propose recommendations to reduce the effects of each source of acoustic heterogeneity on the indices during field surveys.

Table 1

Variation in acoustic diversity indices due to five sources of acoustic heterogeneity. The variation due to the relative amplitude of the songs is given as the median of the standard deviation of the value of each index. The variation due to the other four sources corresponds to the Friedman chi-square value. A symbol representing the significance level of the test is associated with each chi-square value: ^{ns} is for a non-significant p-value; * is for a p-value between 0.05 and 0.01; ** is for a p-value between 0.01 and 0.001, and *** is for a p-value less than 0.001.

Index	Sound to recording (<i>S/R</i>) duration. chi-square value	Background noise. chi-square value	Composition. chi-square value	Relative amplitude. Median value	Song overlap. chi-square value
<i>Ht</i>	300***	200***	167***	0.005	200***
<i>Hf</i>	300***	200***	196***	0.020	91***
<i>H</i>	130***	200***	163***	0.000	165***
<i>M</i>	299***	196***	163***	0.084	200***
<i>AR</i>	12**	13**	7*	0.300	0.32 ^{ns}
<i>NP</i>	8*	6 ^{ns}	108***	0.099	4 ^{ns}
<i>ACI</i>	300***	192***	143***	0.019	200***

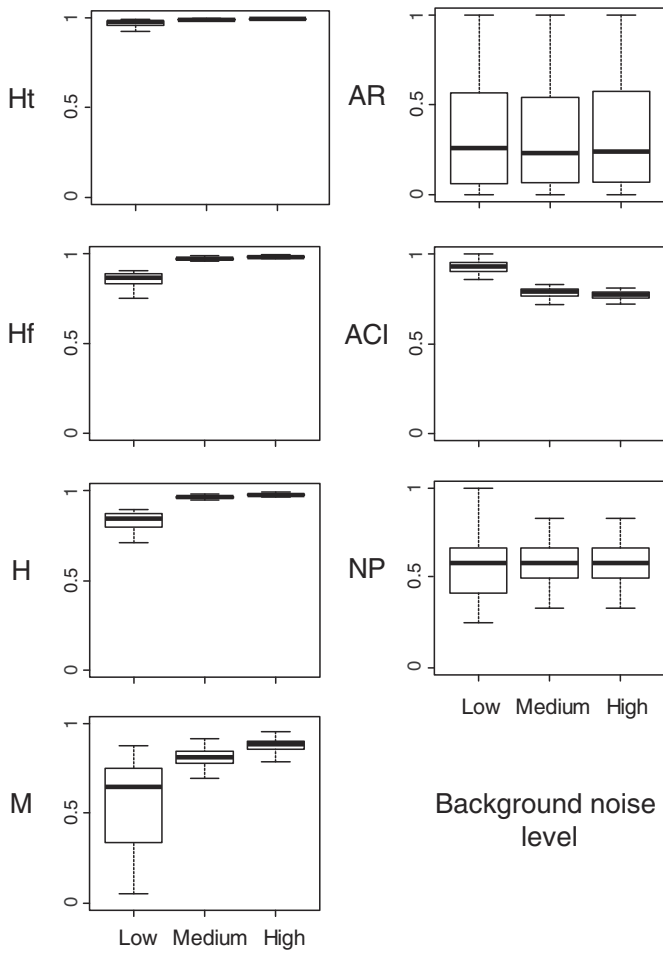


Fig. 3. Boxplot of the values of the indices of acoustic diversity for 100-song assemblages with low, medium, or high background noise levels.

If, in theory, acoustic diversity index values increase with the number of singing species, in practice, field conditions can have an impact and must be investigated in depth (Fig. A3 shows that all indices increase with the species richness of the simulated assemblages but do not always increase when applied to the corresponding field recordings). Different indices have different mathematical properties, which explains why they behaved differently in our simulations. Overall, an acoustic diversity index should

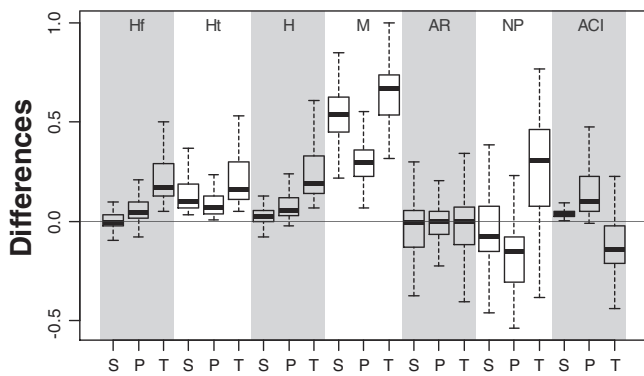


Fig. 4. Boxplot of the differences in the acoustic diversity values per index due to the addition of each of the three types of song: S is for *Sitta europaea*, P is for *Phylloscopus collybita*, and T is for *Turdus philomelos*. A value close to 0 indicates that the indices were not altered by the addition of a new species.

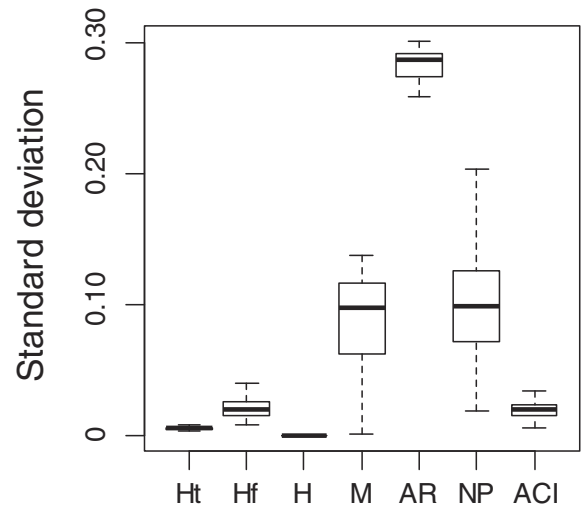


Fig. 5. Boxplots of the standard deviation values of the species assemblages for each acoustic index. Each standard deviation value is associated with one assemblage, and the boxplots represent the standard deviation of the acoustic index values when the relative amplitude of the songs composing the assemblage is varied randomly. Lower standard deviation values associated with an index indicate that the index is less impacted by the relative intensity of the variation in the songs.

- (i) only be driven by the sound of animals to serve as a measure of biodiversity.

Abiotic sounds, produced by geological events such as rain, wind,

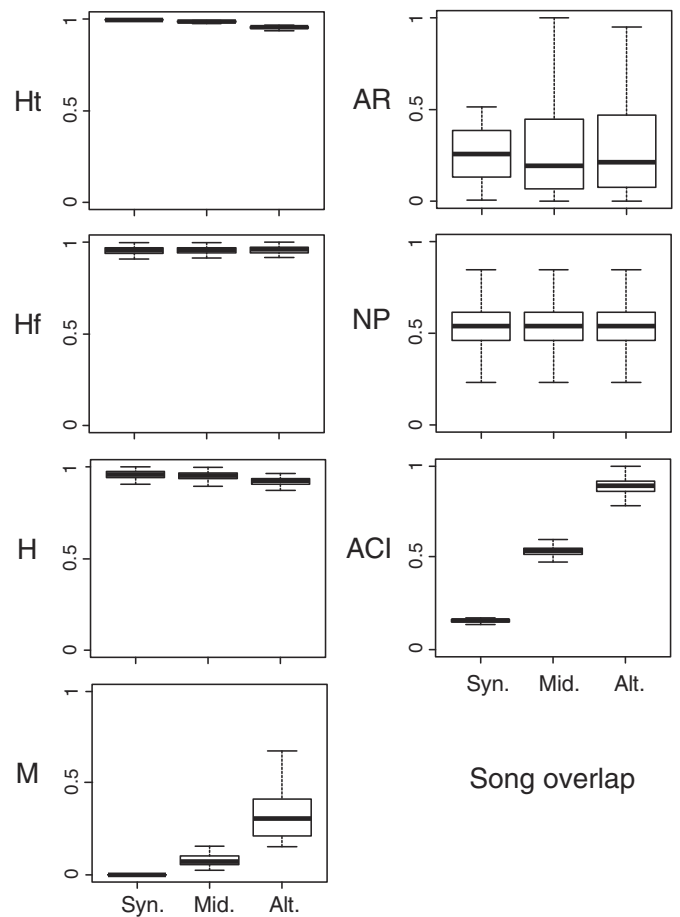


Fig. 6. Boxplot of the values of the indices of acoustic diversity for 100-song assemblages with three levels of overlap between songs: synchrony (Syn.), middle (Mid.), and alternating (Alt.).

rivers, thunder (geophonic sounds) and/or by human activities such as road or aircraft noise (anthropophonic sounds), can greatly affect acoustic diversity. These unwanted sounds can be reduced through careful selection of the location of a recorder in the landscape, the application of filters or by coupling recordings with meteorological data to identify and potentially exclude noise (Depraetere et al., 2012). However, even after avoiding and removing unwanted sounds, background noise can remain. The choice of index can also help minimize the effect of background noise. For example, of the diversity indices examined in this study, *NP* and *AR* displayed the lowest sensitivity to the amplitude of the background noise and the S/R ratio. Therefore, apart from *NP* and *AR*, all of the indices might only reflect biodiversity if background noise has been preliminarily removed. The effect of background noise can also be mitigated with amplitude threshold cut-off filters (i.e., *ACI*, Farina and Pieretti, 2014), and downstream methods can also reduce the impact of background noise, such as through the use of combined frequency and amplitude filters (i.e., *AR*; Depraetere et al., 2012), spectrum subtraction (i.e., *NP*; Gasc et al., 2013b) or spectrogram subtraction (Gustafsson et al., 2002; Towsey, 2013). Such noise reduction processes can increase the ability of acoustic indices to reveal species richness, as has been demonstrated in marine habitats (using *H*; Parks et al., 2014).

- (ii) be insensitive to the identity of species to serve as a proxy for species diversity.

The basic characteristic of a species diversity index is that it should not be impacted by substituting one species with another in a set while maintaining the abundance distribution (evenness). None of the acoustic diversity indices tested in this study satisfied this condition; all were sensitive to species identity and are thus deficient as perfect proxies of species diversity. The impact of a single species on the global acoustic diversity will vary with the features of its song. For some indices, such as *NP*, *AR*, and *ACI*, the acoustic properties of a species can decrease the global acoustic diversity value by adding a song with a flat amplitude envelope and/or frequency spectrum. The effect of the addition of a song might also depend on the species richness and composition of the community into which the new song is added. Among acoustic diversity indices, the value of *Ht* increased with the addition of a new species and was one of the least affected by species identity. Therefore, *Ht* could better reflect species diversity than other indices. However, intra-specific variability (i.e., repertoires and geographic variation in the songs of species; see Krebs and Kroodma, 1980) was not explored here as a source of heterogeneity, but the link between acoustic diversity indices and species richness is not straightforward also because of intra-specific variability. Future studies should thus consider the link between acoustic diversity indices and the number of song vocalizations (Pieretti et al., 2011) or song types (Gasc et al., 2013b; Towsey et al., 2014).

- (iii) be independent of species evenness and overlaps between songs to serve as a proxy for species richness.

To be independent of species evenness, all species must be evenly weighted, as is done with incidence (or presence–absence) data. However, we know that songs vary greatly among species in their amplitude, time (i.e., duration and level of repetition) and frequency (i.e., dominant frequency and frequency modulation). Our results demonstrated that the relative amplitude associated with the songs in an assemblage can impact the values of an index; *Ht* was the index least affected by species evenness and was only slightly affected by song overlap. The temporal organization of songs within a community can be driven by external processes, such as the influence of temperature and luminosity on choruses (Hutchinson, 2002). To reduce the potential bias due to extrinsic features, we propose greater sampling

repetition for each animal community. Increasing the number of recordings at each location would allow for the capture of the songs of species from different spatial positions relative to a recorder. Alternatively, several recorders could be distributed throughout the same site to capture the same acoustic species assemblages from different locations and reduce the difference in species detection due to both distance from the microphone and intrinsic differences in song intensity. The number of recordings from the same recorder and/or the number of recorders required to obtain a fair estimation of the CAD remain to be investigated through field studies.

The criteria above are nested so that for an acoustic diversity index to act as a proxy for species diversity, it should satisfy both criteria (1) and (2), and to act as a proxy for species richness, it should satisfy all three criteria. Criterion (1) is a basic, necessary condition for acoustic diversity to reflect the properties of the community rather than the abiotic environment. Criteria (2) and (3) are necessary only if one is more interested in species diversity and richness than in the diversity of the acoustic characteristics of a community. From our results, *NP* and *AR* were found to be the best biodiversity indices (i.e., the least affected by background noise). However, none of the acoustic diversity indices tested satisfied all three criteria; thus, none can be considered to be good proxies of species richness under field conditions. Nevertheless, the above recommendations are likely to improve the application of acoustic diversity indices in the field.

The choice of an index could depend on the acoustic properties of the dominant taxa in the recordings. For example, crickets and birds produce very different sound patterns. Crickets usually repeat the same scheme without frequency modulations, and birds produce complex songs with important amplitude and frequency modulations. Because they are less impacted by the temporal overlap of songs, the *NP* and *AR* indices would be best for cricket stridulations, and the *ACI*, which is thought to capture amplitude and frequency modulations, would be more suited to bird songs. However, as emphasized above, *NP*, *AR*, and *ACI* are sensitive to species identity and could decrease with the addition of species. Thus, they are likely to depart from species diversity. *Ht* was among the least affected by species evenness and overlap in songs, and among those indices that increased with the addition of a species, it was the least sensitive to the identity of the species added. Among the indices tested, *Ht* is the most promising proxy for species richness once the background noise has been removed.

It is possible that the effects demonstrated in this paper would vary according to species richness, a factor that would change depending on the location of the survey. Indeed, acoustic diversity is expected to first increase with species richness and then reach a threshold where it remains steady due to redundancies in the acoustic characteristics of the species (as observed by Sueur et al., 2008a). The existence of such a threshold in the relationship between functional diversity and species richness has long been recognized (e.g., Petchey and Gaston, 2002); thus, acoustic diversity indices are likely to be proxies for species richness below that threshold. Our simulations were based on local communities from the same region with limited species richness (a maximum of eight species per assemblage), and these effects may also vary depending on the number of individuals singing. The chosen recording duration will influence the number of individuals and the number of species captured by the recording, and it will also change the proportion of the sound in the file. Considering a 5 s song in a 5 s recording, and then considering the same 5 s song in a 60 s recording, the weight of this song in the values of some of the indices will decrease with the longer recording duration. We have observed differences in acoustic sampling duration in the literature, including 1 min (Gasc et al., 2013b), 5 min (Depraetere et al., 2012), 15 min (Villanueva-Rivera et al., 2011), and 2 h (Pieretti et al., 2011). We thus recommend the use of a standardized recording duration to calculate indices; a short

time window would allow for rapid computation of the values and better detection of acoustic variation. However, to capture all of the acoustic variability due to animal activity, the duration could be chosen based on the length of a complete song phrase related to the species or the taxonomic group being studied. A recent paper investigated the use of 1 minute recordings to devise an acoustic diversity index (Pieretti et al., 2015).

5. Conclusion

Based on the analyses described in this paper, we advise careful interpretation of acoustic diversity indices as proxies for species richness because acoustic diversity can be influenced by other sources of acoustic heterogeneity. Thus, the development of acoustic indices dedicated to the evaluation of species richness should be investigated further, and we also encourage the consideration of acoustic diversity per se as a facet of biodiversity that is linked to other facets, particularly functional diversity and phylogenetic diversity. We hope that such work will help decision makers more accurately interpret acoustic diversity indices, which could reduce potential biases related to acoustic surveys in the field.

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