

Assessing biodiversity with sound: Do acoustic diversity indices reflect phylogenetic and functional diversities of bird communities?

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ARTICLE INFO

Article history:

Received 15 March 2012

Received in revised form 14 August 2012

Accepted 10 October 2012

Keywords:

Acoustic diversity

Biodiversity assessment

Bird community

Biodiversity indices

ABSTRACT

Measuring biodiversity is a challenging task for research in taxonomy, ecology and conservation. Biodiversity is commonly measured using metrics related to species richness, phylogenetic-, or functional-trait diversity of species assemblages. Because these metrics are not always correlated with each other, they have to be considered separately. A descriptor of animal diversity based on the diversity of sounds produced by animal communities, named here the Community Acoustic Diversity (CAD), was recently proposed. In many cases, the CAD could be easier to measure than other metrics. Although previous analyses have revealed that acoustic diversity might increase as species richness increases, the ability of CAD to reflect other components of biodiversity has not been formally investigated. The aim of this study is to test theoretically whether functional and phylogenetic diversities could be reflected by acoustic diversity indices in bird communities. Data on species assemblages were collated by the French Breeding Bird Survey describing spatial and temporal variation in community structure and composition across France since 2001. Phylogenetic and functional data were compiled from literature. Acoustic data were obtained from sound libraries. For each of the 19,420 sites sampled, indices of phylogenetic, functional and acoustic diversity of bird communities were calculated based on species' pair-wise distance matrices and species' abundances. The different aspects of biodiversity were compared through correlation analyses. The results showed that acoustic diversity was correlated with phylogenetic diversity, when the branch lengths of the tree were considered, and to functional diversity, especially body mass and reproduction. Correlations between phylogenetic, functional and acoustic distances among species did not entirely explain the correlations between phylogenetic, functional and acoustic diversity within communities. This result was interpreted as an effect of local ecological processes underpinning how bird communities assemble. Comparing the diversity patterns with a null model, phylogenetic and functional diversities were significantly clustered whereas acoustic diversity was not different from what was expected by chance. A comparison between acoustic indices showed that spectral component of acoustic diversity seems more appropriate to reveal bird phylogenetic diversity whereas temporal component seems more adapted to reveal functional diversity of a bird community. Overall, even if the processes at the origin of the different facets of biodiversity are different, CAD reveals part of phylogenetic diversity and some extent of functional diversity.

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1. Introduction

Diversity indices have been growing in number, but have been developed separately by different research fields related to evolution or ecology (Pavoine and Bonsall, 2011). At the community

level, indices mostly used to describe biodiversity include species richness, species relative abundance, and rarity. However, several recent studies have shown that these traditional metrics are insufficient to capture all facets of diversity and have proposed to focus instead on species functional and phylogenetic distinctiveness. Functional diversity is measured from functional traits that describe a variety of roles that different organisms play in their ecosystem (Petchey and Gaston, 2002). Depending on the ecosystem process analyzed, these traits might depend, for instance, on physiological, life-history, morphological, ecological or behavioral characteristics. In the last two decades, there has been an increasing

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number of functional diversity studies focusing on the local biotic and abiotic interactions that could explain the processes of species assemblages (Pavoine and Bonsall, 2011; Pillar et al., 2009). Phylogenetic diversity measures the dispersion of species belonging to a community over a phylogenetic tree (Faith, 1992; Pavoine et al., 2005a; Vane-Wright et al., 1991). In theory, phylogenetic diversity can reflect functional diversity if functional traits have a strong phylogenetic signal and thus if the phylogenetic distance between any two species reflects their difference in terms of a combination of functional traits (Webb et al., 2002). In practice, few studies have compared results collected from different aspects of biodiversity and some have shown that these were only partially correlated (Devictor et al., 2010; Pavoine et al., 2005a; Petchey and Gaston, 2002).

Working on phylogenetic and functional diversities can shed light on ecological processes. Indeed, functional traits could be affected by local ecological processes including competition and environmental filters. Competition leads to functional diversification contrary to environmental filters. Therefore, low functional diversity might be obtained with high species richness and abundance if environmental constraints filter species with similar traits (Holdaway and Sparrow, 2006; Petchey et al., 2007). Moreover, an evolutionary convergence of the functional traits of distantly related lineages can lead communities to include many lineages (high phylogenetic diversity) but which are functionally similar (low functional diversity) (e.g. Cavender-Bares et al., 2004; Grandcolas, 1993, 1998). In addition, in regions where species recently emerged by rapid radiation, high species richness might be attained with low phylogenetic diversity as species have diverged only recently (Slingsby and Verboom, 2006). Overall, although phylogeny and functional trait variations are becoming frequently used to assess biodiversity, they do not necessarily correlate due to evolutionary and ecological processes and have to be considered separately.

Beyond these components of biodiversity, acoustic diversity recently emerged as a possible relevant indicator of biodiversity for several reasons (Obrist et al., 2010; Sueur et al., 2008b). First, there are practical advantages to using passive acoustic methods in conservation surveys. Acoustics allows exploring habitats that are difficult to access such as canopy (Riede, 1997), marine and freshwater habitats (Luczkovich et al., 2008), soil and interior structures of plant (Mankin et al., 2000), and dark environments (Meyer et al., 2011; Obrist et al., 2004). Moreover, compared to classic methods of biodiversity assessment based on field inventories, passive acoustic censuses are less costly especially when automatic recordings are used which can ensure large temporal and spatial scale surveys. The description of sound provides information on acoustic diversity at individual (Pollard et al., 2010), population (Dawson and Efford, 2009; Forrest, 1988), species (Brandes et al., 2006; Skowronski and Harris, 2006), community (Cardoso and Price, 2010; Diwakar and Balakrishnan, 2007; Riede, 1997, 1993) and landscape levels (Pijanowski et al., 2011). At the landscape scale, a soundscape ecological approach distinguishes three components in the soundscape, namely the biophony, the geophony and the anthrophony. Biophony is mainly defined as “a collection of sounds produced by all living organisms in a given habitat over a specified time” (Pijanowski et al., 2011). The present paper considers the diversity of the acoustic community here named for the first time Community Acoustic Diversity (CAD). Biophony is very closely related to acoustic community. However, the concept of community includes not only the species assemblage but also the interactions between species that are supposed to compete for the acoustic resource. The CAD considers the competitive interaction for the sound space, structured by the sound resource. Contrary to biophony, community acoustic diversity intends to reflect all ecological processes that determine how many diverse biotic sounds

co-occur in a community. Acoustic output of an animal community is generally analyzed using three approaches: species identification by an expert, species identification using automatic recognition and global acoustic measure without species identification. As species identification of singing individuals is necessary and requires a high level of expertise, identification has to be achieved by trained experts (Dickinson et al., 2010) or by automatic classification processes (e.g. Acevedo et al., 2009; Han et al., 2011). Both approaches are difficult to apply due to song overlap observed in rich acoustic communities. Consequently, new indices have been recently developed to obtain a global measure of acoustic diversity without any species identification. For instance, an entropy-like index based only on the frequencies recorded was proved to increase with the number of species. Likewise, a dissimilarity index based on the variations of frequencies collected was shown to be inversely correlated with the number of shared species between two focal communities (Depraetere et al., 2012; Sueur et al., 2008b). An acoustic variability index was also shown to evolve with the dynamics of bird communities (Farina et al., 2011; Pieretti et al., 2011).

These approaches generally support a correlation between the CAD and species richness, and the CAD and abundance, but whether and how CAD can be related to other biodiversity components has never been investigated. Rather than working on pure simulated communities as Sueur et al. (2008a,b) did it first, we chose to test the dissimilarity index and to try to understand the information it can provide by working on bird communities that were described through data gathered by local field workers. A theoretical analysis was performed on data extracted from different sources: (i) bird community composition from the French breeding bird survey, (ii) phylogenetic and functional data corresponding to each species from literature and (iii) acoustic data corresponding to each species from different sound libraries to answer the following questions: (i) Do spectral and temporal parts of an acoustic signal have different impacts on acoustic diversity calculation? (ii) Does the acoustic diversity reflect phylogenetic and/or functional diversities of bird communities? (iii) Do the acoustic, phylogenetic and functional diversities result from the same ecological and evolutionary processes?

2. Materials and methods

Acoustic, phylogenetic and functional diversity indices were computed using the quadratic entropy index (Chave et al., 2007; Pavoine et al., 2004, 2005b; Pavoine and Bonsall, 2011; Rao, 1986). The quadratic entropy index was applied to abundance data describing bird communities and a pair-wise distance matrix among species for each diversity type (i.e. acoustic, phylogenetic, and functional diversity) (Fig. 1). Two types of data were necessary to calculate diversity indices: the detail of bird community assemblage in terms of species' abundances and acoustic, phylogenetic and functional data used to calculate the distances between species.

2.1. Data

2.1.1. Bird communities

Bird community compositions were extracted from data collected by the French breeding bird survey (FBBS; Jiguet et al., 2012). This survey is based on a standardized protocol conducted by a volunteer network coordinated by the Muséum national d'Histoire naturelle (Paris, France, Jiguet et al., 2012; Julliard et al., 2006). A sampling quadrat of 2 km × 2 km is randomly localized in a 10 km circle around a location chosen by a volunteer. Ten points are then located homogeneously and proportionately to the habitats occurring in the quadrat. Points have to be separated by at least 300 m.

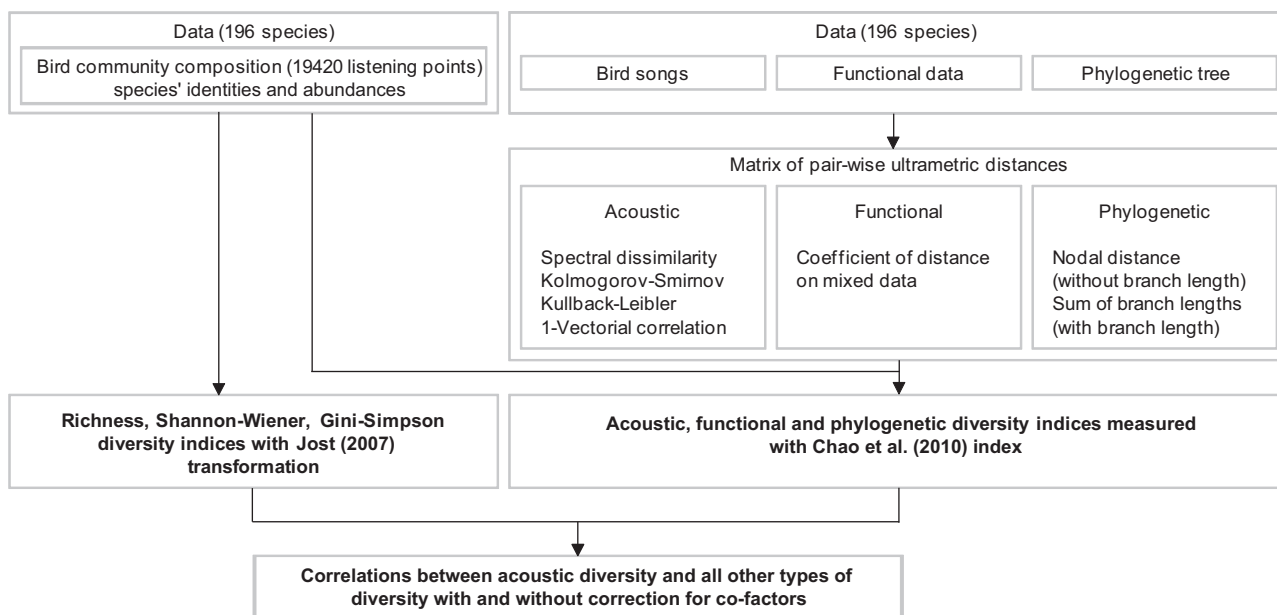


Fig. 1. From data to indices: process used for the computation of diversity indices. The five functional categories were diet, reproduction, behavior, body shape and body mass.

Every spring, each volunteer spends 5 min on each point at two dates before and after May 8th. For each species, the volunteer counts the number of detected individuals, which is considered as an index of species abundance. For each point visited at least one year between 2001 and 2010, average species abundances over all available years were calculated, for a total of 19,420 points. Among the species detected in at least two points, 196 species were selected based on song recording availability (see Section 2.1.2 and list of species in supplementary information in Table S1).

2.1.2. Bird songs

A species-specific territorial song of each bird species was selected (Bossu and Charron, 2004, 1998; Deroussen, 2001, 2011; Deroussen and Jiguet, 2006; Roché, 1990; Xeno-canto, <http://www.xeno-canto.org>) according to 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. This ratio was estimated following: $SNR = 100 \times (rms(S)/rms(N))$, where S and N are the probability mass functions of the amplitude envelope of 0.5 s of signal and of 0.5 s of noise both randomly chosen along the recording considered, respectively, and rms is the root mean square. This recording selection constituted our acoustic data.

2.1.3. Phylogenetic data

The phylogenetic tree came from a mega-phylogeny approach performed by Thuiller et al. (2011) who combined supertree and supermatrix approaches with sequences obtained from GenBank. This tree has branch lengths that can be defined in terms of time since speciation. Within the 340 bird species composing the tree, a tree of 192 species was sub-sampled. This tree was completed with four missing species (*Lanius meridionalis*, *Anas strepera*, *Ardea alba*, *Larus fuscus*) using literature data (Davis, 2008). The final tree was composed of the 196 bird species selected for acoustics.

2.1.4. Functional data

Forty-eight functional traits were extracted from Devictor et al. (2010, $n = 17$), Cramp et al. (2004, $n = 17$), Davies et al. (2004, $n = 13$) and BirdLife International (2004, $n = 1$) (see supplementary information Table S2). The traits were organized in five functional categories: behavior (social, migration, nocturnal), diet (type,

foraging, substrate), morphology (body size, tarsus size, tail size, span), reproduction (habitat type, nest construction, parental behavior), and body mass. Morphological variables were highly correlated to body mass. In order to have an idea of body shape, independently to body mass, the morphological variables were transformed as follow:

$$Vmc = \frac{Vm}{Vp^3}$$

with Vmc is the morphological variable corrected, Vm is the morphological variable and Vp is the body mass variable.

In the following text, the transformed morphological variable will be referred to “body shape”. A logarithmic transformation was applied on “body shape” and “body mass” variables.

2.2. Distance matrices

From the data described in the previous subsection distinct matrices of distances among species were calculated and used to obtain measures of acoustic, phylogenetic, and functional diversities.

2.2.1. Acoustic distances

Evolution might not have been constant for all song features (Robillard and Desutter-Grandcolas, 2011). For this reason, the acoustic indices used in this paper are not based on classical acoustic parameters but on a single distance measure embedding temporal and/or spectral characteristics. Four types of pair-wise acoustic distances between species were computed:

- (i) A spectral dissimilarity index (D_f), as described in Sueur et al. (2008b), was based on the difference between a pair of mean spectra. Each spectrum was computed as the average of a Short Time Fourier Transform with a non-overlapping sliding window (length = 512 points, time precision = 0.012 s, frequency precision = 86 Hz). Each spectrum was transformed into a probability mass function $S_i(f)$ and vectorial difference was calculated between the two spectra to be compared.
- (ii) Kolmogorov–Smirnov distance (KS), which was defined as “the maximum value of the absolute difference between two

cumulative distribution functions" (Rachev, 1991), was computed between cumulated spectra.

- (iii) Symmetric Kullback–Leibler (KL) distance was estimated by computing the relative entropy between two probability frequency spectra (Kullback and Leibler, 1951).
- (iv) The similarity RV correlation coefficient was used as developed by Escoufier (1973) and Robert and Escoufier (1976). RV correlation measures the correlation between two matrices. Short Time Fourier transform with a non-overlapping sliding window was computed for each recording leading to a data matrix. The columns of each matrix were the successive spectra computed along the time scale with a time precision of 0.012 s and a frequency precision of 86 Hz. RV was computed according to Kazi-aoual et al. (1995) and Josse et al. (2008). The complement $1 - RV$ was computed to obtain a dissimilarity measure.

2.2.2. Phylogenetic distances

Phylogenetic distances were calculated as the number of branches on the shortest path that connects two species in the phylogenetic tree without branch length. A phylogenetic distance including branch lengths was also calculated as the sum of branch lengths on the shortest path that connects two species.

2.2.3. Functional distances

Functional distance matrices were computed using Pavoine et al.'s coefficient of distance calculated from species-specific traits (Pavoine et al., 2009). This index, based on Gower distance (Gower, 1971), allows measuring functional distances from any type of variables (e.g. quantitative, nominal, ordinal, proportional, binary, circular). The types of the traits here considered are given in Table S2. Details on these types of traits can be found in Pavoine et al. (2009). Quantitative traits and (rank-transformed) ordinal traits were treated by formula 3 in Pavoine et al. (2009, Euclidean metric). The distance between two species based on a nominal trait was 1 if the two species had similar attributes and 0 elsewhere. Proportional (fuzzy) variables were treated by formula 11 in Pavoine et al. (2009). Multichoice variables were treated by Jaccard (1901) index. Five distance matrices were separately calculated using the five functional groups defined a priori (diet, behavior, body shape, weight, reproduction, Table S2). These functional groups contained several traits each (see Table S2). An average distance over all traits per group was obtained as defined in Pavoine et al. (2009). Traits were weighted to take account of their pair-wise correlations as defined by Petchey et al. (2009). All functional distance matrices were transformed into ultrametric distances using the UPGMA (Unweighted Pair Group Method with Arithmetic Mean) method (Legendre and Legendre, 1998).

2.3. Diversity indices

Species richness (number of species – 1), Shannon and Gini-Simpson indices were calculated for each community (Magurran, 2004). In order to respect the replication principle, Shannon and Gini-Simpson indices were corrected using the exponential of Shannon and the inverse of Gini-Simpson index as $1/(1 - \text{Gini-Simpson values})$ (Jost, 2007). These indices equal zero for a community with a single species. Acoustic, phylogenetic and functional diversity indices were computed using the quadratic entropy from the distances previously calculated and species' abundances within bird communities (Fig. 1). In Chao et al. (2010), the authors proposed a new correction for the quadratic entropy to comply the replication principle. This correction was applied and the resulting index will be called Chao et al.' index in the following text. The resulting diversity estimates had symmetric distributions. A part of the correlation observed between the acoustic, phylogenetic and functional diversity indices could possibly be driven by the intrinsic

mathematic property of these indices associated with the inverse Gini-Simpson index. All diversities calculated following Chao et al. (2010) index shared this co-variable due to the mathematical formula. To correct for this co-variable, the three diversities values (acoustic, phylogenetic and functional) were divided by $1/(1 - \text{Gini-Simpson values})$.

2.4. Statistical analyses

Acoustic, phylogenetic and functional diversities were computed with the same mathematical methodology that depends on pair-wise distances between species and species' abundances. This led to a dependency between the three diversities. Indeed, if two pair-wise distance matrices were strongly correlated (i.e. pair-wise acoustic and phylogenetic distances between species were strongly correlated), and the corresponding values of the diversity index were correlated as well (i.e. the acoustic and phylogenetic diversities of the bird communities were also strongly correlated), the similarity between two aspects of diversity (i.e. phylogenetic and acoustic diversity) could be explained only by the similarity of the distances between species and not by the assemblage processes that underpin bird communities. By contrast, a difference in the correlations calculated between distances at species level and those calculated between diversities at community level would indicate that diversity at the community level could not be considered just as the random addition of pair-wise species distances but that the community structure, in terms of how species assemble, had an influence on the diversity of the community. Finally, if two matrices of pair-wise distances between species were not (or moderately) correlated, then the corresponding values of the diversity index within communities might still be correlated if similar stochastic, or deterministic ecologically based processes, influence the community composition. To counteract this issue, statistical analyses were achieved at species level based on the distance matrices and at community level based on the calculation of the diversity indices (see below).

2.4.1. Species level

A preliminary Mantel test with Spearman correlation and 999 permutations (Hardy and Pavoine, 2012; Mantel, 1967) was used to compare the four acoustic dissimilarity indices. The Mantel test was also applied to compare acoustic distances with phylogenetic and functional distances. The equality between phylogenetic distances and acoustic distances between species would imply evolutionary-based mechanisms such as the Brownian model of evolution if the phylogeny has branch lengths or punctuated evolution of species' acoustic properties if the phylogeny has no branch lengths (Brooks and McLennan, 1991; Legendre et al., 2008; Robillard and Desutter-Grandcolas, 2011). Similarly, the equality between functional distances and acoustic distances between species would imply that species' acoustics could depend directly, or indirectly via a correlation with a co-factor, on the trait(s) analyzed.

2.4.2. Community level

Spearman correlation coefficients were calculated between the different aspects of biodiversity at the community level (see the description of the diversity indices above). No test was performed because the high number of communities (19,420) is known to lead to significant tests (low p -values) even with a correlation coefficient close to zero. In that case, analyzing the correlation coefficient was more informative than tests.

To reveal if ecological processes can explain the observed composition of bird assemblages, Webb et al. (2002) suggested to compare the observed diversity within each community with the one expected according to a null model. The following null model

Table 1

Mantel correlations, based on Spearman method with randomization, between the different matrices of pair-wise acoustic distances between species: frequency distance (D_f), Kolmogorov–Smirnov distance (KS), symmetric Kullback–Leibler (KL) and dissimilarity RV correlation ($1 - RV$).

Acoustic distances	D_f	KL	KS
KL	0.902, $p=0.001$		
KS	0.864, $p=0.001$	0.912, $p=0.001$	
$1 - RV$	0.785, $p=0.001$	0.838, $p=0.001$	0.841, $p=0.001$

was used: for each community, the distribution of species abundances, and the number of species were fixed but species identities were randomly extracted from the 196 species pool (model 1p in Hardy, 2008). For each aspect of biodiversity (functional, phylogenetic and acoustic diversity), Chao et al. (2010) index was calculated for the corresponding artificial communities. This process was repeated 999 times. At the end for each aspect of diversity and each community, 1000 theoretical diversity values were calculated (one obtained from the real communities and 999 obtained based on the null model). Then a new diversity value within the community considered was defined by: $D^* = (D_{obs} - \bar{D}_{sim}) / SD_{Dsim}$ where \bar{D}_{sim} is the mean of the 1000 theoretical diversity values, D_{obs} is the observed diversity value and SD_{Dsim} the standard deviation of the theoretical diversity values. The index D^* was calculated for each of the 19,420 communities. The null model chosen assumed that the distribution of species within communities was not dependent on species phylogenies, traits or acoustics. Negative values of the corrected index were expected if the species with close characteristics tended to co-occur in local communities. In contrast, large positive values were expected if species co-occurring within local assemblages tended to have distinct characteristics. A value close to zero indicated that the composition of the community supported the null model. These trends were visualized with histograms.

All calculations were achieved with the R software (R Development Core Team, 2010) including the packages ‘seewave’ (Sueur et al., 2008a), ‘ade4’ (Dray and Dufour, 2007), ‘vegan’ (Oksanen et al., 2011), and ‘FactoMineR’ (Husson et al., 2011).

3. Results

3.1. Species level

Correlations between the acoustic distances were all significant (Table 1). All distances associated with the spectral component only (i.e. D_f , KL and KS) were highly correlated. Even if high, the lowest correlations were between $1 - RV$ and the other indices. Due to high redundancy between D_f , KS and KL and because these three indices measure the same sound component, only D_f and $1 - RV$ indices were considered in the following analyses.

Correlations between the acoustic distances and the functional distances were all significant except between reproduction category and $1 - RV$. The significant values were low to moderate ranging from 0.061 to 0.307 (Table 2). The highest values were observed between acoustic distances and distances among species defined by differences in their body mass and in their body shape. The correlations between acoustic distances and phylogenetic distances were significant but moderate (ranging from 0.124 to 0.296). The highest correlation was observed with phylogenetic diversity including branch lengths.

3.2. Community level

Most pair-wise correlations between Chao et al. (2010) index applied to acoustics, phylogeny and functional traits had high values. A high correlation coefficient was observed for Chao et al. (2010) index of diversity between acoustic and phylogenetic diversity especially when time-scaled branch lengths were

Table 2

Results of the Mantel test, with randomization using Spearman correlation coefficient, between the different distance matrices. Notations are: frequency distance (D_f) and dissimilarity RV correlation ($1 - RV$).

	Acoustic distances, D_f	Acoustic distances, $1 - RV$
Phylogenetic distances		
Tree with branch length	$r=0.266, p=0.001$	$r=0.296, p=0.001$
Tree without branch length	$r=0.124, p=0.001$	$r=0.124, p=0.001$
Functional distances		
Body mass	$r=0.307, p=0.001$	$r=0.289, p=0.001$
Body shape	$r=0.295, p=0.001$	$r=0.254, p=0.001$
Reproduction	$r=0.061, p=0.008$	$r=0.009, p=0.323$
Diet	$r=0.064, p=0.011$	$r=0.075, p=0.007$
Behavior	$r=0.136, p=0.001$	$r=0.079, p=0.004$

Table 3

Spearman correlation coefficients between acoustic diversity indices. The acoustic diversity indices were considered without and with correction by the inverse Gini-Simpson index. Phylogenetic, functional and acoustic diversities were calculated by entropy quadratic index corrected by Chao et al. (2010) method.

	Acoustic diversities			
	No correction		Inverse Gini-Simpson correction	
	D_f	$1 - RV$	D_f	$1 - RV$
Phylogenetic diversities				
Tree with branch length	0.621	0.610	0.506	0.446
Tree without branch length	0.501	0.493	0.351	0.266
Functional diversities				
Body mass	0.428	0.422	0.301	0.223
Body shape	0.419	0.481	-0.002	-0.080
Reproduction	0.515	0.585	0.284	0.415
Diet	0.352	0.481	0.064	0.243
Behavior	0.362	0.469	0.094	0.206
Others diversities				
Inverse Gini-Simpson	0.615	0.707		
Exponential Shannon	0.564	0.654	0.302	0.497
Richness	0.370	0.441	0.185	0.324

available (Table 3). All types of functional diversity were from moderately to highly correlated with acoustic diversity with correlation coefficients ranging from 0.352 to 0.516 for D_f and 0.422 to 0.649 for $1 - RV$. The $1 - RV$ index showed slightly higher values than D_f index.

All correlations decreased when Chao et al. (2010) index of diversity was corrected by $1/(1 - \text{Gini-Simpson index})$ (Table 3). The highest correlation was still obtained with phylogeny with branch lengths. The correlations between D_f and the functional diversities were low except for reproduction and body mass categories. However, a high correlation was observed between $1 - RV$ and the diversity in reproduction strategies and moderate correlations were obtained with diversities in diet habits, behaviors, and body masses. D_f and $1 - RV$ were not correlated with body shape diversity. Regarding exponential Shannon and richness indices, the correlations were higher with $1 - RV$ than with D_f . Besides, comparing exponential Shannon and richness indices, correlations between acoustic indices and exponential Shannon were higher than between acoustic indices and richness.

Chao et al. (2010) index standardized by the null model revealed mostly negative when applied to functional diversity and especially

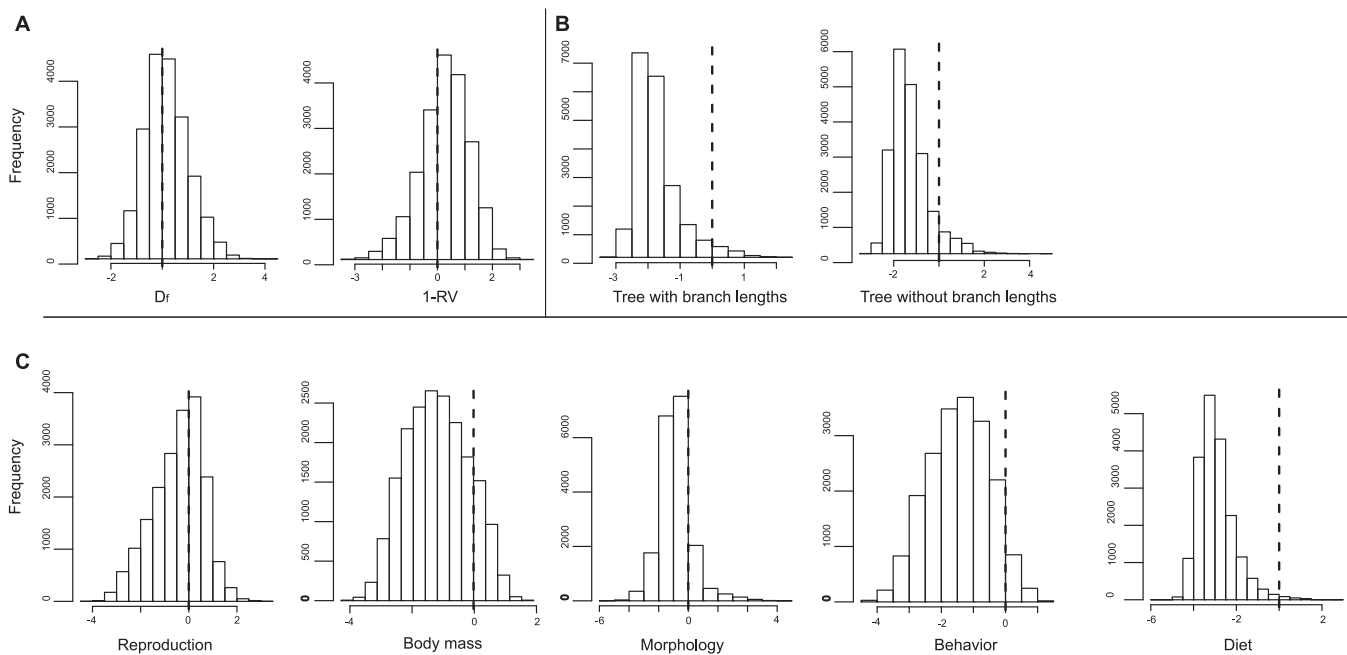


Fig. 2. Histogram of diversities corrected with the null model: (A) acoustic diversities; (B) phylogenetic diversities; (C) functional diversities. The vertical dashed line represented the value zero where the occurrence of a species within a community is independent of its functional, phylogenetic and acoustic characteristics. On the negative side, the community is considered as clustered, and on the positive side it is considered over-dispersed.

phylogenetic diversity (Fig. 2b and c). In contrast, the distribution of the standardized Chao et al. (2010) index applied to acoustic diversity had a bell shape centered near 0 (Fig. 2a).

4. Discussion

Interest in using acoustic methods as a new tool for the identification of singing species, the monitoring of species or populations, or the evaluation of global acoustic diversity is rapidly increasing (Acevedo et al., 2009; Blumstein et al., 2011; Obrist et al., 2010). In particular, the evaluation of global acoustic diversity (e.g. Sueur et al., 2008b) appears as an innovative method in conservation biology as it can be deployed over large spatial and temporal scales and can facilitate the assessment of numerous communities simultaneously. The previously observed correlations between acoustic diversity and number of species (Depraetere et al., 2012; Sueur et al., 2008b) reinforce the interest of acoustic diversity studies to evaluate the biodiversity. Before applying passive acoustic diversity analyses at large scales, there is a critical need to know whether acoustic aspects reflect phylogenetic (Faith, 1992; Isaac et al., 2007; Pavoine et al., 2005a; Vane-Wright et al., 1991) and/or functional diversity (Dalerum et al., 2009) levels. An important database on bird community was therefore used to theoretically assess the relative parts of phylogenetic and functional diversities embedded in the measures of acoustic diversity.

To complete the first acoustic distance produced by Sueur et al. (2008b) (D_f), three other dissimilarity measurements based on spectral (KS, KL) or time and spectral ($1 - RV$) profiles were first used. It appears that the mathematical method used to calculate spectral dissimilarity between two sounds does not significantly impact the result as shown by the high correlation between D_f , KL and KS. We found differences between $1 - RV$ and the others diversities. However, $1 - RV$ is quite more costly in terms of computational time and might be difficult to obtain when handling large datasets. In practice, the choice of the index will result in a trade-off

between the processing time and the accuracy of the expected results.

At the species level, the moderate correlations between acoustic distances and body shape and body mass distances among species indicate that the more different species are in their body mass and body shape the more different their songs are likely to be. This implies that species acoustics could depend directly or indirectly via a correlation with a co-factor on these traits. This could be explained by morphological constraints known to occur on the frequency range produced by birds. Body weight is negatively correlated to the mean song frequency in passerine birds (Wallschläger, 1980). This relationship can be extended to several bird taxa (Martin et al., 2011), and even to vertebrates for which the optimal communication frequency is inversely proportional to body mass (Fletcher, 2004).

High correlations between acoustic and phylogenetic distances based on the tree with branch length available suggest the occurrence of evolutionary-based mechanisms that have led to a phylogenetic signal embedded in the songs of extant species. Overall, branch lengths seem to have a decisive impact on the correlation between phylogenetic and acoustic distances. Given the assumption that the phylogenetic tree with branch length is clockwise, acoustic behavior evolution may be associated to clockwise evolution; although this hypothesis should be tested on larger data sets. Another explanation might be that the data set included a large number of Passerine birds ($n = 105$). Consequently, the consideration of branch lengths in the calculation of phylogenetic diversity increased the importance given to the phylogenetic distinctiveness of the non-passerine species, which also contained several of the most acoustically distinct species. This greater differentiation among bird orders might be responsible for the increased detection of phylogenetic signal in acoustic distances among species.

At the community level, the expected correlation between acoustic diversity and richness (Depraetere et al., 2012; Sueur et al., 2008b) was confirmed when considering the diversities calculated by Chao et al. index without any corrections. The strong correlation between acoustic diversity and the inverse Gini-Simpson index

was expected as Chao et al. index is mainly based on inverse Gini-Simpson index. The high correlation between acoustic, functional and phylogenetic diversity indices suggest that acoustic diversity index, as calculated here, could be used as an acceptable surrogate of phylogenetic and functional diversities indices.

As expected, the correlations among different aspects of biodiversity differed with and without correction by inverse Gini-Simpson index. This difference was due to the important co-variable role of species' abundance distribution within all diversity indices computed with Chao et al. (2010) index. However, the high correlation between tree with branch length and acoustic diversity was conserved, which indicates that the evolution time information is included in the acoustic diversity of the bird community. Our results also suggested that spectral information may be sufficient to reflect phylogenetic diversity even if temporal variation participates to the diversity and encoding processes of bird songs (Catchpole and Slater, 1995 for a review). Considering the functional diversities, the corrections also pointed out a difference between D_f and $1 - RV$. The temporal information supported by $1 - RV$ appears to have higher links with functional information, especially with diversity in reproduction strategies. This result supports the fact that sexual selection of several bird species is based on temporal features of male song (Catchpole and Slater, 1995 for a review). It was in particular demonstrated that male song rate is associated to reproductive success and territory quality (Alatalo et al., 1990; Greig-smith, 1982). The diversity of frequencies supported by D_f , was nevertheless also related to diversity in reproduction. A moderate correlation between D_f and $1 - RV$ and body mass was maintained after the correction for the co-factor. The spectral diversity seems thus to better reflect phylogenetic diversity whereas temporal diversity would better reflect functional diversity.

Acoustic diversity was correlated with species richness, exponential Shannon index and inverse Gini-Simpson index. When corrected for the inverse Gini-Simpson index, it was still correlated with the exponential Shannon index and to a lesser extent with species richness. Inverse Gini-Simpson, exponential Shannon and the richness indices differ in the importance they give to rare vs. abundant species (Patil and Taillie, 1982). A correlation between acoustic diversity, exponential Shannon index and species richness, even after a correction by the inverse Gini-Simpson suggest that less abundant species are important in explaining the level of acoustic diversity in a community. This might be due to the high abundance of passerine species in French bird communities and to the acoustic distinctiveness of less abundant non-passerine species whose occurrence in a community impacts the overall level of acoustic diversity despite their lower abundance.

The correlations found between different aspects of distances among species (functional, phylogenetic vs. acoustic distances) were different from the correlations found between different aspects of diversity within communities. Several researches focused on the environment filtering and the competitive interaction as two contrasting processes underlying community assembly, as reviewed in Emerson and Gillespie (2008). Our results highlight that the community structure, in terms of how species assemble within communities, is likely to have an influence on the diversity of the community. Bird communities are not just random assemblages of species but depend on ecological processes. According to the FBBS protocol, each local community was investigated within a homogeneous habitat. Environmental filters within each habitat are therefore likely to filter species based on their functional traits (Lebrija-Trejos et al., 2010).

In our case study, phylogenetic and functional clustering was indeed found in local communities, which means that co-occurring species tend to be closely related and to share similar traits. In

other words, communities tend to have closely related species with similar traits and similar phylogenetic history. Phylogenetic and functional clustering might simply be explained by limits in the geographic distribution range of related species with similar traits (such as Devictor et al., 2010) and also by local ecological processes, especially habitat filtering. Species found in the same habitat type are expected to share functional traits (Cornwell et al., 2006) and phylogenetic positions (Emerson and Gillespie, 2008). However, in contrast to the observed phylogenetic and functional clustering, bird communities continuously ranged from acoustically clustered, through random to over-dispersed patterns. Within a homogeneous habitat, acoustic overdispersion is expected because specificity ensures an efficient communication between congeners (Chek et al., 2003). However, acoustic clustering is expected if the pressure of habitat type leads to acoustic adaptation of the species. In that case acoustic features are dependent on particular habitats (Boncoraglio and Saino, 2007). For instance, closed habitats have greater reflections than tree trunks and leaves (Slabbekoorn, 2004; Wiley and Richards, 1978). These opposed processes could lead to different community acoustic assemblies, from clustered to over-dispersed. Even if the acoustic diversity seems to be positively correlated with phylogenetic and body mass diversities, the processes that structure the acoustic diversity are thus expected to be partly different than those that structure phylogenetic and functional diversity.

In conclusion, a means of estimating a finer definition of acoustic diversity at the community level was suggested. The Community Acoustic Diversity (CAD) contains all the variability that can be extracted out of a sound produced by an animal community. Traditionally, two components of the sound, frequency and time structure are used to describe this variability. The number of species (Depraetere et al., 2012; Sueur et al., 2008b) and the number of signals (Farina et al., 2011; Pieretti et al., 2011) can potentially be assessed by the CAD. The present work showed that, in bird communities, the CAD contains a phylogenetic signal with evolution time information. Still in regard to the data used here, the CAD contains also a functional signal essentially linked to body mass and reproduction and more slightly to diet and behavior. This preliminary work is theoretical and it raised new hypotheses that now have to be tested on real community songs. However, it supports the idea that biodiversity assessment through acoustics could then provide valuable information on different biodiversity facets. The CAD could be used on real animal choruses through data collected by automatic devices settled in the fields. To applied the CAD index on the field, this theoretical work needs to be complete by tests on real choruses.

Acknowledgements

This work was supported by a CNRS INEE PhD grant and the FRB BIOSOUND program. Authors would like to thank Pierre-Yves Henry, Marsha Schlee, Grégoire Lois, Philippe Clergeau, Camila Andrade for their help when we collecting bird functional traits. We greatly thank the hundreds of volunteers who have been taking part in the national breeding bird survey (FBBS program). We thank Ryan Calsbeek for improving the language of the manuscript and the two anonymous referees for their helpful comments on the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2012.10.009>.

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