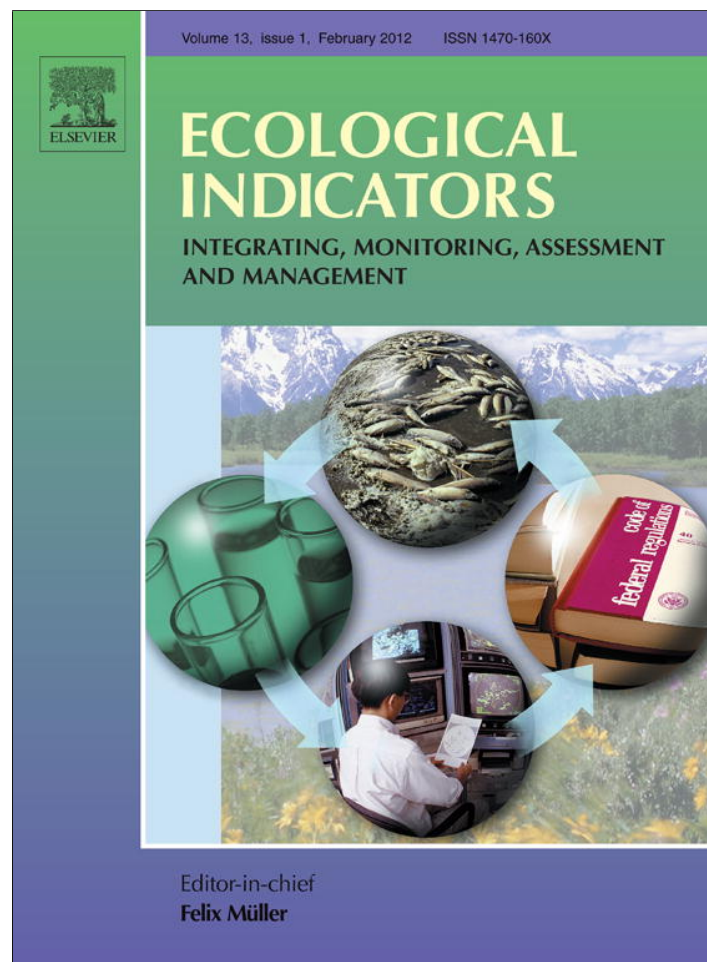


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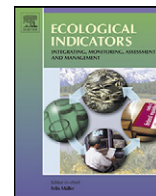
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Monitoring animal diversity using acoustic indices: Implementation in a temperate woodland

Marion Depraetere^a, Sandrine Pavoine^{b,c}, Frédéric Jiguet^b, Amandine Gasc^a,
Stéphanie Duvail^d, Jérôme Sueur^{a,*}

^a Muséum national d'Histoire naturelle, Département Systématique et Évolution, UMR 7205 CNRS OSEB, 45 rue Buffon, CP 50, F-75005 Paris, France

^b Muséum national d'Histoire naturelle, Département Écologie et Gestion de la Biodiversité, UMR 7204 CNRS-UPMC CERSP, 55-61 rue Buffon, CP51, F-75005 Paris, France

^c Mathematical Ecology Research Group, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

^d IRD (Institut de Recherche pour le Développement), UMR 208, IFRA, P.O. Box 58480, Nairobi, Kenya

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ABSTRACT

Biodiversity assessment is one of the major challenges for ecology and conservation. With current increase of biodiversity loss during the last decades, there is an urgent need to quickly estimate biodiversity levels. This study aims at testing the validity of new biodiversity indices based on an acoustic analysis of choruses produced by animal communities. The new Acoustic Richness index (AR) and the former dissimilarity index (D) aim at assessing α and β diversity respectively. Both indices were tested in three woodland habitats: a mature forest, a young forest and a forest-cropland ecotone within the Parc Naturel Régional of Haute-Vallée de Chevreuse (France). Three recorders running for 74 days generated 5328 files of 150 s for a total of 222 h of recording. All files were treated with frequency and amplitude filters to try to remove anthropogenic and environmental background noise. The AR index was in agreement with traditional aural identification of bird species. The AR index revealed an expected gradient of diversity with higher diversity values in the young forest that potentially provides a higher number of microhabitats. The D index also indicated expected differences in the acoustic environment across sites with distinct habitat structure. Both indices reveal significant peak during dawn chorus. These results suggest that diversity could be estimated through acoustics at both α and β scales. Our analyses reveal that, even if background noise needs to be considered with great care, the use of acoustic indices has the potential to facilitate animal diversity assessments over seasons or years and landscape scales.

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1. Introduction

In the last three decades, several indices have been developed to assess biodiversity. Most indices concerned species diversity and abundance including general density, average geometrical index or relative abundance, specific richness, Simpson or Shannon index (e.g. Margalef, 1958; MacArthur, 1965; Whittaker, 1972; May, 1975; Magurran, 2004; Buckland et al., 2005). Others indices have included characteristics of the species such as genetics, phylogenetics and functional traits (e.g. Faith, 1992; Pavoine et al., 2004; Petchey and Gaston, 2006). Interest has also been given to a simplification of these indices into α diversity, which measures the diversity within areas, and β diversity that evaluates differences among areas providing information on the turnover of specific diversity (Whittaker, 1972; Diserud & Odegaard, 2007). To evaluate changes in diversity pattern through time, both α and β diversity have to be assessed at different day or season times. Most methods

require large-scale data sampling at several locations and dates. However, traditional sampling methods are mainly based on slow inventories that may not be adapted to rapid assessment at large scales in particular when dealing with highly diverse groups as arthropods (Basset et al., 2000; Lawton et al., 1998). In addition, these sampling methods are in most cases invasive as relying on direct collection or trapping (Sutherland, 1996; Hill et al., 2005). We therefore propose to adapt non-invasive acoustic analyses to quickly reveal spatial and temporal patterns of variation in animal diversity.

Acoustics can be used for animal movement tracking (Hammer and Barrett, 2001; Mennill et al., 2006), automatic species identification (Brandes et al., 2006; Brown et al., 2006; Chen and Maher, 2006; Villanueva-Rivera, 2007; Brandes, 2008; Bardeli et al., 2010), animal conservation (Laiolo, 2010), singing activity estimation (Pieretti et al., 2011) and Rapid Biodiversity Assessment (RBA) (Brandes, 2005). RBAs based on animal vocalisations can provide simple biodiversity estimations through aural identification or recording of acoustic communities (Herzog et al., 2002; Rempel et al., 2005; Villanueva-Rivera, 2007) and can also determine community structure (Diwakar and Balakrishnan, 2007a,b;

* Corresponding author. Tel.: +33 1 40 79 33 98; fax: +33 1 40 79 36 99.
E-mail address: sueur@mnhn.fr (J. Sueur).

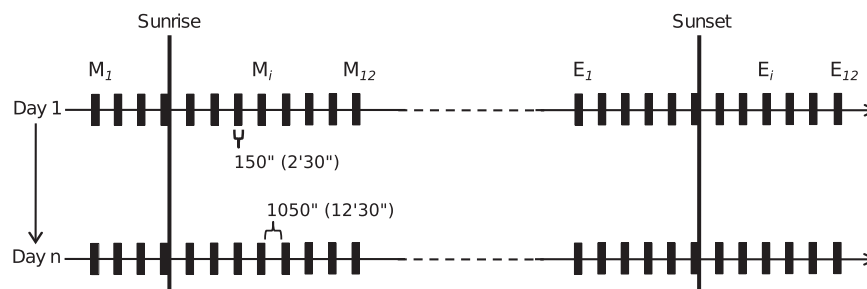


Fig. 1. Diagram showing the daily frequency of recording according to two periods of sampling. The first period starts one hour before sunrise and ends two hours afterwards. The second period starts one hour and half before the sunset and ends one hour and half afterwards. For each period, each recording lasts 150 s every 15 min.

Riede, 1993, 1997). Among these RBA programs, the Automated Digital Recording System (ADRS), which allows automatic data collection, generates a large amount of high-quality data (Acevedo and Villanueva-Rivera, 2006), considerably reduces human related costs (Parker, 1991; Penman et al., 2005) and avoids any invasion of the prospected habitat (Diwakar et al., 2007).

Accordingly, a new RBA method through acoustics has been recently developed (Sueur et al., 2008b; Obrist et al., 2010). The main principle of this method is to obtain a holistic view of the local animal community that produces sound. The method avoids species or morpho-species identification, a pre-requisite of other inventory methods, All Taxa Biodiversity Inventory (ATBI) and RBAs included.

Recently an acoustic method has been proposed also to infer the singing activity of avian communities (Pieretti et al., 2011). The number of bird vocalisations produced within a community is estimated through an algorithm that computes the variability of the sound intensities. This method looks promising but cannot be used to assess species diversity and has not been employed yet to compare the acoustic composition of different communities. Based on a simple analysis of the signal, acoustic indices inferring α and β animal diversity were previously developed to summarize the variety of choruses produced by animal communities (Sueur et al., 2008b). The acoustic indices, named H and D , respectively, were first tested on artificial choruses whose specific diversity was known, and later successfully applied *in situ* in a coastal tropical forest of Tanzania where animal diversity is not known in detail (Sueur et al., 2008b). Here, we test and develop the indices in a temperate habitat where the diversity is lower than in Tanzania and the background noise due to human activity (anthrophony *sensu* Qi et al., 2008 and Pijanowski et al., 2011) may be prominent. In particular, we tested during springtime the acoustic indices in three distinct habitats: (i) a mature open forest with few vegetation strata and low tree density, (ii) a young closed forest with several vegetation strata and high tree density, and (iii) a forest-cropland ecotone with a crop field inhabited by a few species. We mainly focused our test on singing birds that are the major source of sound diversity during spring. Amphibian vocalisations were scarce and insect stridulations were notably absent. Following previous studies on bird richness in different woodland habitats (Blondel et al., 1973; Fuller and Crick, 1992; Tellería et al., 1992), a higher bird diversity can be expected in the younger forest than in the mature forest and at the forest-cropland ecotone.

Computing the acoustic H and D indices in such habitats, we estimated that local background noise can significantly impair the results provided by the H index. This led us to develop a new α index, named Acoustic Richness (AR), based on the temporal entropy and amplitude of the signal. We then addressed the following questions regarding both AR and D acoustic indices temperate habitats: (i) do the indices match with results provided by a classical bird inventory? (ii) could the indices follow the variation of daily animal activity? and (iii) could the indices

highlight expected biodiversity differences between different habitats?

2. Materials and methods

2.1. Study area and recording

Fieldwork was carried out in the Parc Naturel Régional of Vallée de Chevreuse (24,300 ha), a protected area located 40 km southwest of Paris, France. The area is deeply transformed by human activities with a land cover of 20% dwellings, 40% crop fields, and 40% temperate mixed deciduous forest.

The recording equipment consisted of three digital audio field recorders Song Meter SM1 (Wildlife Acoustics, 2009). These off-line and weatherproof recorders are equipped with an omni-directional microphone (flat frequency response between 20 Hz and 20 kHz). The recording level of all recorders were set to the same value. The signals were sampled at 44.1 kHz with a 16 bits digitization. The files were saved in the lossless compressed format *.wac* and then transformed into the format *.wav* with the software WAC to WAV Converter Utility version 1.1 (Wildlife Acoustics, 2009).

Three sampling sites were chosen according to a gradient of tree density (Supporting information, Fig. S1). The sampling sites were spaced at least 300 m from each other. This distance ensured to avoid overlapping between recording points. Sampling site A (48°37.628N, 01°55.294E, 174 m) was a mature forest composed of a regular grove of pedunculate oak (*Quercus robur*), sessile oak (*Quercus petraea*) and downy birch (*Betula pubescens*). Sampling site B (48°38.519N, 01°56.155E, 166 m) was a young forest mainly made up of hornbeam (*Carpinus betulus*). Sampling site C (48°38.319N, 001°57.527E, 160 m) was at the frontier between an open habitat (cornfield) and a forest composed by hornbeam (*Carpinus betulus*) and European ash (*Fraxinus excelsior*). Recorders were all positioned on a tree at a height of 2 m and microphones pointing horizontally. The distance from the closest road was 300 m, 900 m and 210 m for the sites A, B and C, respectively. Files were uploaded every week from the SD cards of the digital recorders by one of us (M.D.).

2.2. Sampling and signal pre-processing

Recordings were taken between the March 24th and the June 5th 2009. During this period, birds are the main source of acoustic activity (Bas et al., 2008; Moussus et al., 2009) with some amphibians (mainly common toad *Bufo bufo*) and mammals (primarily roe deer *Capreolus capreolus* and wild boar *Sus scrofa*). Using the software Song Meter Configuration Utility version 1.6 (Wildlife Acoustics, 2009), a programme was written to record 150-s periods every fifteen minutes around sunrise (3 h) and sunset (3 h) generating 24 recording periods each day, identified as M1 to M12 for the morning and as E1 to E12 for the evening (Fig. 1). Recording periods 4 and 18 corresponded to sunrise and sunset time, respectively. The schedule produced a total number of 5328 recordings (24 recording

periods × 74 days × 3 recorders) of 150 s each (=222 h). The duration of each recording was limited to 150 s because of computing time limits. This schedule was chosen because a peak of acoustical activity was expected around sunrise. This intense singing period is known as the “dawn chorus” during which species compete for signal broadcast (Staicer et al., 1996; Brown and Handford, 2003). A reduction of acoustical activity was expected at sunset when the activity of diurnal birds decreases.

A procedure was achieved to directly estimate the number of bird species at the sampling sites. A sample of the recordings was listened by one of us (F.J.) who is trained in bird aural identification. The files were regularly collected every seven days (11 dates) and every four time steps (6 times per day) for each recording period at each sampling site (3 sampling sites), for a total of 11 dates × 6 times × 3 sites = 198 files. Each file was listened once. Each vocalising species was identified and its presence noted for each file.

2.3. Data pre-processing

The Parc Naturel Régional de Vallée de Chevreuse is occupied by human settlements and therefore constitutes a noisy environment. Background noise was due to car and plane traffic, and to agricultural machinery. A band-pass filter between 1 kHz and 13 kHz was applied with Goldwave[®]. Due to the permanent background noise caused by wind, vegetation rustle and/or rain (geophony *sensu* Qi et al., 2008 and Pijanowski et al., 2011), it was necessary to apply a second filter. The amplitude median of the quietest signal including noise was assessed at a level of 90 points, with a maximum value of 2^{15} . This energy level was used as a reference to apply an amplitude filter to all files. The filter removed all signal sections that were below a threshold of 90 points. The filter was applied using the package *seewave* (Sueur et al., 2008a) within the statistical environment R (R Development Core Team, 2010).

Weather conditions were monitored for each recording day. Minimum and maximum temperatures, precipitation and solar radiation were taken from a national weather station located in Trappes (48°46.638'N, 02°0.150'E) (Météo France, 2009). Average wind speed was measured at a local weather station in Saint-Rémy-Chevreuse (48°42.384'N, 02°4.349'E).

Computing the acoustic dissimilarity D was highly time consuming in terms of computer calculations. Given the large quantity of recordings (2556 pairs of recordings), the files were combined by time of the day and by site. This generated a matrix including 72 comparisons: $A_{M1}B_{M1}$, $A_{M1}C_{M1}$, $B_{M1}C_{M1}$, $A_{M2}B_{M2}$, $A_{M2}C_{M2}$, $B_{M2}C_{M2}$... $A_{E12}B_{E12}$, $A_{E12}C_{E12}$, $B_{E12}C_{E12}$, with major letters indicating the recording site and the subscript indicating the step of time in the morning (M_i) and in the evening (E_i). For instance, $A_{M1}B_{M1}$ means that the first recording of the day (morning) in site A is compared to the first recording of the day in site B. This matrix provided information on temporal changes in the dissimilarities among the sites.

2.4. Acoustic indices

Sueur et al. (2008b) first developed an acoustic entropy index (H) of α diversity composed of two sub-indices: the temporal entropy index H_t and the spectral entropy index H_f according to $H = H_t \times H_f$ with $0 \leq H \leq 1$. H_t and H_f are computed following:

$$H_t = - \sum_{t=1}^n A(t) \times \log_2(A(t)) \times \log_2(n)^{-1} \quad \text{and}$$

$$H_f = - \sum_{f=1}^N S(f) \times \log_2(S(f)) \times \log_2(n)^{-1}$$

where n = length of the signal in number of digitized points, $A(t)$ = probability mass function of the amplitude envelope, $S(f)$ = probability mass function of the mean spectrum calculated using a Short Term Fourier Transform (STFT) along the signal with a non-overlapping Hanning window of $N = 512$ points.

The overall amplitude of the signal, that was not previously taken into account in the H index, was here considered for the first time leading to a new acoustic index named M that is the median of the amplitude envelope following:

$$M = \text{median}(A(t)) \times 2^{(1-\text{depth})} \quad \text{with } 0 \leq M \leq 1,$$

where $A(t)$ = amplitude envelope and depth = signal digitization depth (here, 16 bits).

Values of M were very low (mean = 0.002 ± 0.002 , min = 0.923×10^{-3} , max = 0.048). To obtain values of M varying between 0 and 1, a second standardization was calculated by dividing M with its maximum value.

The index H was successfully tested in a tropical forest (Sueur et al., 2008b). This habitat is known to include a high number of singing species generating a high level of acoustic activity. The signal-to-noise ratio is then high. However, in the context of a temperate habitat, the acoustic activity is much lower and the background noise due to wind and rain is higher in amplitude. This can bias H_f , generating false high values when wind and rain dominate over animal calls (see Section 3). A new index, called Acoustic Richness (AR), was then elaborated based on H_t and M and computed with *seewave* (Sueur et al., 2008a) following:

$$AR = \frac{(\text{rank}(H_t) \times \text{rank}(M))}{n^2}, \quad \text{with } 0 \leq AR \leq 1.$$

The acoustic dissimilarity index D estimates β diversity between two acoustic communities (Sueur et al., 2008b). D is made of two sub-indices: the temporal dissimilarity index D_t and the spectral dissimilarity index D_f according to $D = D_t \times D_f$ with $0 \leq D \leq 1$. D_t and D_f are computed according to:

$$D_t = 0.5 \times \sum_{t=1}^n |A_1(t) - A_2(t)| \quad \text{and} \quad D_f = 0.5 \times \sum_{f=1}^N |S_1(f) - S_2(f)|$$

where $A_1(t)$, $A_2(t)$ = probability mass functions of the amplitude envelope for the two recordings under comparison, and $S_1(f)$, $S_2(f)$ = probability mass functions of the mean spectrum (see above) for the two recordings.

2.5. Statistical analyses

Redundancy analysis (RDA) (Rao, 1964) was used to evaluate the impact of climatic parameters on the diversity estimations. Data obtained with AR and D indices and those obtained by the trained observer were compared by summarizing data on cloud of points (Cleveland, 1981). Given evident temporal autocorrelation among consecutive recordings, the values of the indices AR and D were compared among sites and pairs of sites with randomization process by assuring that the randomizations conserve the pattern of temporal autocorrelation so that nothing changes during a randomization except the effect of interest (null models, Gotelli and Graves, 1996). Data were first averaged per day or half day (morning vs. evening), as specified. The statistic used corresponded to Wilcoxon signed rank test. This statistic was computed on the real data set and after each randomization leading to theoretical values of the statistics. The randomization consisted in permuting per day (by considering only the morning or the evening as specified) the values of AR (or D) obtained for two distinct sites (or two distinct pairs of sites for D). The observed value was compared to the distribution of theoretical values to obtain the p -value (denoted p

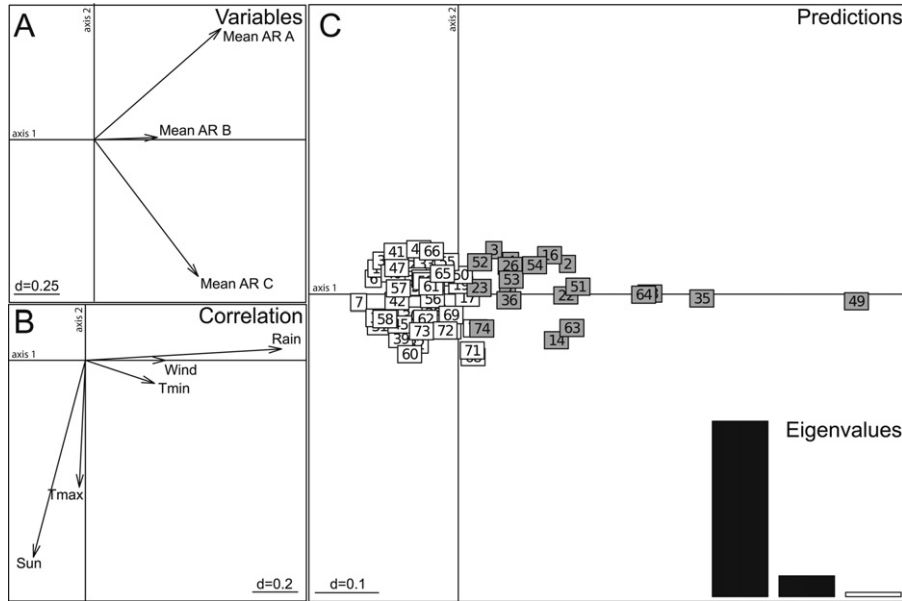


Fig. 2. Redundancy analysis (RDA) carried out on acoustic α diversity AR averaged per site (A, B and C) and day explained by meteorological variables. (A) Directions in which the average values of the Acoustic Richness index (AR) increase for site A (*mean AR A*), B (*mean AR B*) and C (*mean AR C*). (B) Directions in which each meteorological variable increases. (C) Positions of each recording day. Grey background identifies bad weather days subsequently removed out of the analysis. The insert reports the relative values of the Eigenvalues of the axes. The positions of the recordings in (C) are explained by the direction of the response variables in (A) and the explanatory variables in (B). T_{min} and T_{max} are the minimal and maximal temperature of the day, respectively.

below). The RDA analysis led to remove several recordings where bad weather conditions affected the acoustic signals (see below). This implied that there were a few mismatches in the dates for which the recordings were available for the three sites. Accordingly, the number of recordings considered is indicated below for each statistical test where the three sites were compared. We made sure that for each test the subsets of data compared between two sites matched exactly in terms of recording days and hours. All statistical analyses were achieved with R 2.10.1 (R Development Core Team, 2010) with the ade4 package (Dray and Dufour, 2007).

3. Results

3.1. Meteorological factors

The RDA applied to AR (matrix with sites as columns, the days as rows, and AR averaged values as entries) and meteorological parameters as factors revealed the importance of precipitation (Fig. 2). Precipitation was strongly correlated ($r=0.95$) with the

first axis that explained 87.5% of variation. AR mean was also positively correlated with the first axis, i.e. positively increased with precipitations and, to a lesser extent, wind. The first canonical plan showed an opposition between bad weather environmental factors and environmental factors related to sun radiation and maximal temperature. Precipitation and wind ($r=0.39$) were correlated with the first axis whereas sun radiation and maximum temperature were strongly correlated with the second axis, which explained only 10.4% of variation (sun radiation: $r=-0.95$, T_{max} : $r=-0.61$). Overall, sun radiation and maximum temperature added residual explanatory strength to the values of AR. This residual effect was a correlation between sunny days and higher acoustic diversity (AR) in sampling site C than in sampling sites A and B. The RDA revealed a set of 20 days that were most affected by a heavy rain and/or intense wind (Fig. 2). We selectively removed those days to avoid any over-estimation of the indices due to wind or rain interference.

Regarding the D index, the RDA confirmed the importance of temperature. The maximum temperature was strongly negatively correlated with the first axis ($r=-0.87$) that explained 90.2% of the

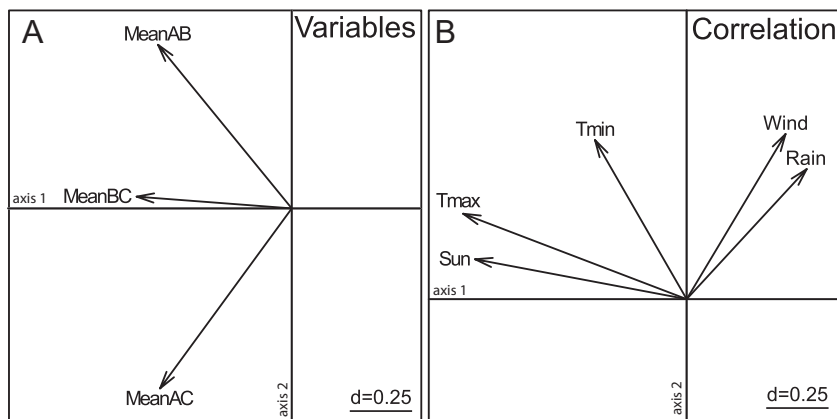


Fig. 3. Redundancy analysis (RDA) carried out on acoustic dissimilarity index D averaged per combinations of sites (AB, AC and BC) and per day explained by the meteorological variables. (A) Directions in which the average values of D (β diversity) between sites A and B (*mean AB*), sites B and C (*mean BC*) and sites A and C (*mean AC*) increase. (B) Directions in which each meteorological variable increases. T_{min} and T_{max} are the minimal and maximal temperature of the day, respectively.

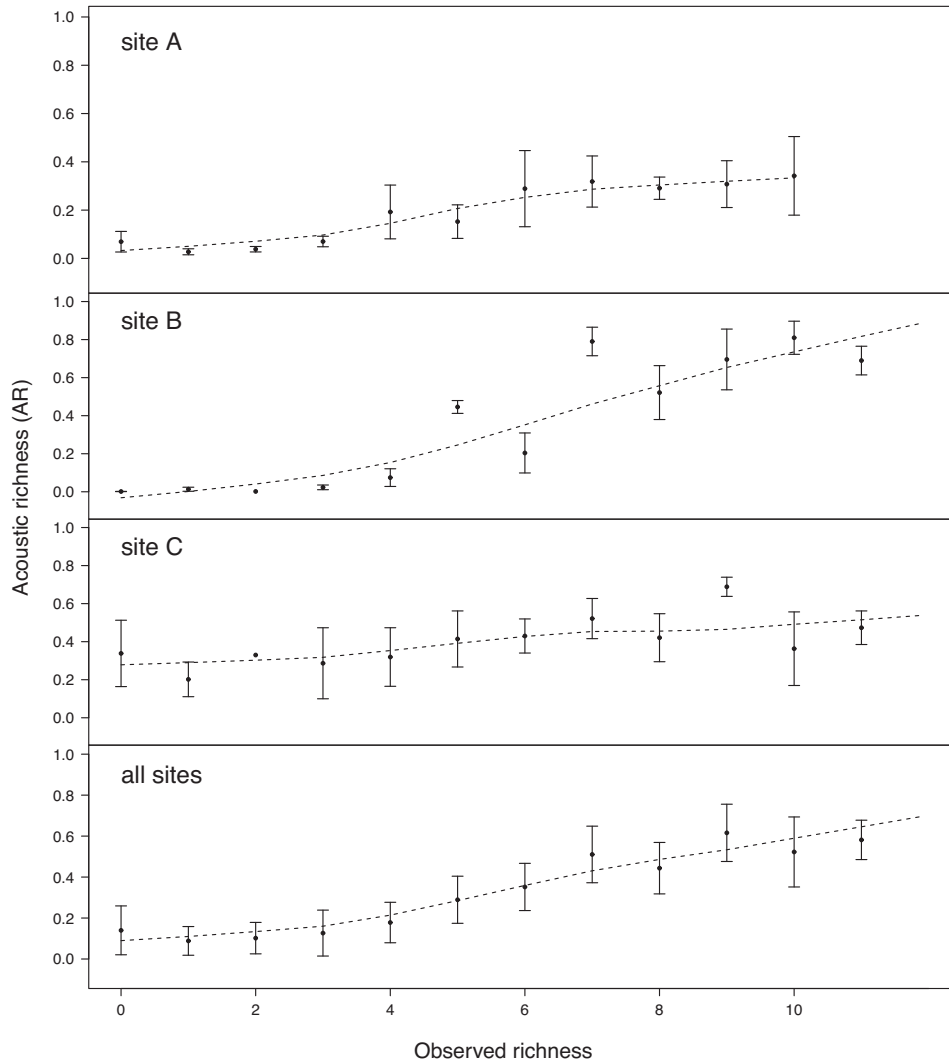


Fig. 4. Species richness estimated with a classical aural inventory (observed richness) and with the Acoustic Richness index (AR). Species richness and AR were compared for each sampling site and for all sites. The points represent the mean, the error-bars represent the standard deviation, and the dashed line is the result of lowess smoothing.

variation (Fig. 3). Sun radiation was also strongly negatively correlated with the first axis 1 ($r = -0.82$). All D values were negatively correlated with the first axis. Accordingly, the dissimilarities among sites were higher during sunny, warm days.

3.2. Aural identification

Listening to a selection of files led to the identification of a total of 43 bird species. Sampling site A included 31 species across all recordings listened for a total of 270 contacts, sampling site B included 23 species for 386 contacts, and sampling site C included 33 species for 349 contacts (Supporting information, Table S1). There was a higher average species richness per recording during the morning (8.04 ± 2.16 , $n = 144$) than during the evening (2.63 ± 2.53 , $n = 144$). In the morning, average species richness per recording decreased from sampling site B (9.00 ± 1.70 , $n = 144$), through sampling site C (8.21 ± 2.30 , $n = 144$), to sampling site A (6.92 ± 1.86 , $n = 144$). Accordingly despite the fact that sampling site B had the lowest absolute species richness with only 23 species over all recordings, it had the highest average species richness per recording, which means that more species sing simultaneously on a short period of time. In the evening, average species richness per recording decreased from sampling site B (3.38 ± 2.75 , $n = 144$),

through sampling site C (2.58 ± 2.48 , $n = 144$), to sampling site A (1.92 ± 2.21 , $n = 144$).

Regarding the differences among sites, sampling sites B and C were in the morning the most different (with only 1 species shared), followed by sites A and B (with 3 species shared) and sampling sites A and C (with 4 species shared). In the evening all sites shared a few species only (1 shared between sampling sites A and C and 2 between the other pairs of sites) (Supporting information, Fig. S2).

3.3. Acoustic richness index (AR)

AR values ranged between 1.85×10^{-6} and 0.99 with a mean of 0.33 ± 0.29 . AR was on average higher during the morning (0.48 ± 0.28 , $n = 1907$) than during the evening (0.17 ± 0.21 , $n = 1836$) ($W = 1275$, $n = 50$, $p < 0.001$) confirming that acoustic diversity recorded was higher during the morning than the evening. In the morning, AR decreased from sampling site B (0.62 ± 0.25 , $n = 635$), through sampling site C (0.52 ± 0.24 , $n = 636$), to sampling site A (0.31 ± 0.24 , $n = 636$); (test for $H_0: AR_B = AR_C$, $H_1: AR_B \neq AR_C$: $W = 139446$, $p < 0.001$, $n = 635$; test for $H_0: AR_C = AR_A$, $H_1: AR_C \neq AR_A$: $W = 173255$, $p < 0.001$, $n = 636$). In the evening ($n = 612$), AR decreased from sampling site C (0.24 ± 0.23), through sampling site B (0.19 ± 0.23), to sampling site A (0.08 ± 0.15); (test

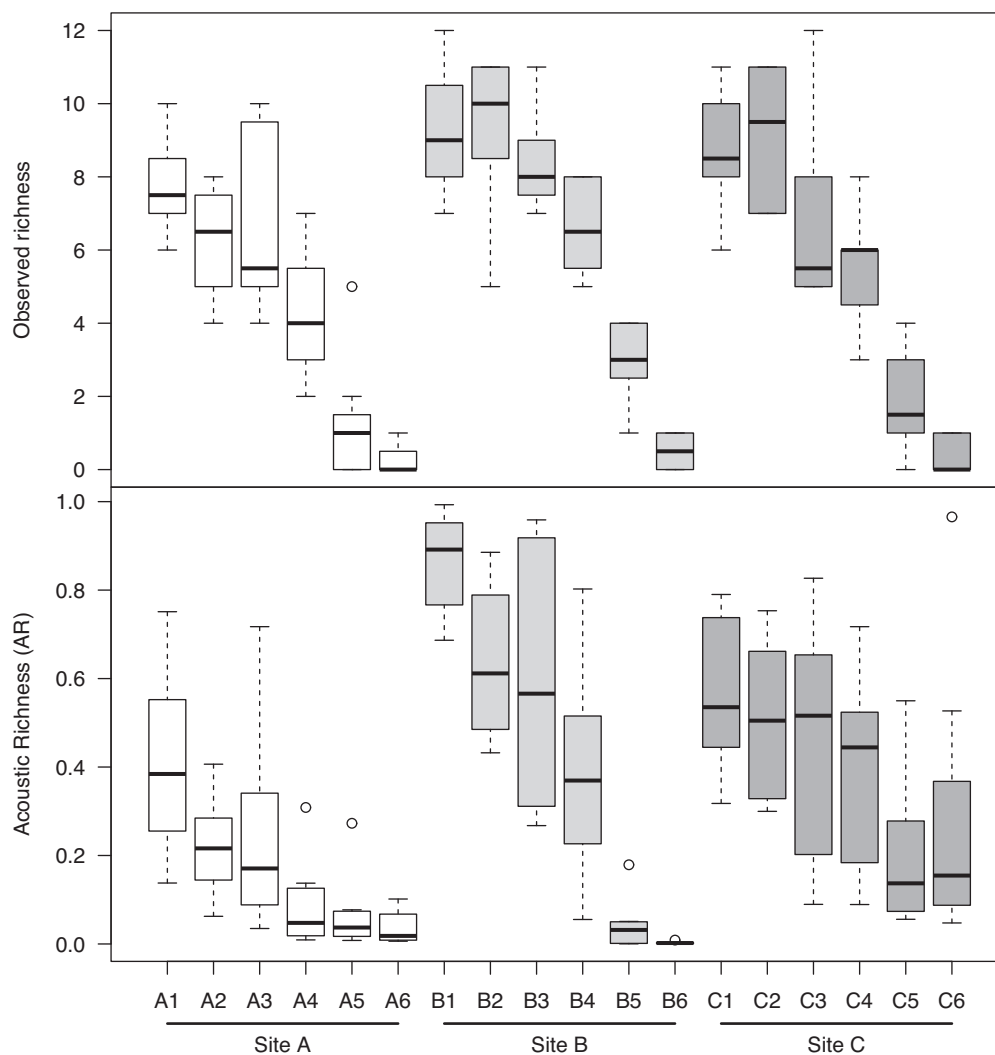


Fig. 5. Species richness estimated with a classical aural inventory (observed richness) and with the Acoustic Richness index (AR). There were six time periods from sunrise to sunset for each site (A, B and C): 15 min before sunrise (A1, B1, C1), 60 min after sunrise (A2, B2, C2), 120 min after sunrise (A3, B3, C3), 45 min before sunset (A4, B4, C4), 30 min after sunset (A5, B5, C5), and 90 min after sunrise (A6, B6, C6). Horizontal bar marks the median, boxes mark second and third quartiles and whiskers mark the range.

for $H_0: AR_C = AR_B$, $H_1: AR_C \neq AR_B$: $W = 119420$, $p < 0.001$; test for $H_0: AR_B = AR_A$, $H_1: AR_B \neq AR_A$: $W = 136179$, $p < 0.001$.

AR increased with the observed species richness for sampling sites A and B (Fig. 4). Regarding sampling site C, relation between observed richness and AR was less obvious with larger variability. When considering variations around sunrise and sunset, changes in species richness estimated by aural identification and AR showed similar profiles (Fig. 5).

The evolution of H_f along the day showed an unexpected decrease around sunrise and a slow increase around to sunset motivating the development of the new index AR (Supporting information, Fig. S3). There was a consistent profile of H_t , M (Supporting information, Fig. S4) and consequently AR variations during the daytime for the three sites (Fig. 6). By considering only averaged values per time unit, indices increased quickly until reaching a maximum just before sunrise and then decreased gradually. Except for site C, AR decreased after falling night.

3.4. Dissimilarity index (D)

D values ranged between 0.012 and 0.349 with an average of 0.035 ± 0.027 . D was on average higher during the morning (0.045 ± 0.026 , $n = 1908$) than the evening (0.024 ± 0.023 , $n = 1836$)

suggesting that there was more difference among community acoustic structures in the morning than the evening. This was supported by significant differences in D between the morning and the evening (data averaged per day, $W = 1272$, $n = 50$, $p < 0.001$). The index D (Fig. 6) and its sub-indices D_f and D_t (Supporting information, Fig. S5) showed a standard variation profile around sunrise and sunset similar to the profile of AR. They increased just before sunrise, then decreased regularly just after sunset. The difference among community acoustic structures was thus more important at sunrise and decreased as the day progressed. We compared the distances D among pairs of sites, separating the morning from the evening data. On the morning, the distances were ordered as follows ($n = 636$): $BC (0.049 \pm 0.030) > AB (0.045 \pm 0.024) > AC (0.042 \pm 0.026)$; (test for $H_0: BC = AB$, $H_1: BC \neq AB$: $W = 119236$, $p < 0.001$; test for $H_0: AB = AC$, $H_1: AB \neq AC$: $W = 112226$, $p = 0.018$). On the evening ($n = 612$), the distances were even $BC (0.025 \pm 0.023) \approx AB (0.025 \pm 0.023) \approx AC (0.023 \pm 0.023)$; (test for $H_0: BC = AB$, $H_1: BC \neq AB$: $W = 91967$, $p = 0.693$; test for $H_0: AB = AC$, $H_1: AB \neq AC$: $W = 93331$, $p = 0.940$; test for $H_0: BC = AC$, $H_1: BC \neq AC$: $W = 92759$, $p = 0.789$). These tendencies confirmed the results obtained above with aural identification: B and C were most different in the morning, followed by A and B, and A and C; all sites shared a few species only in the evening.

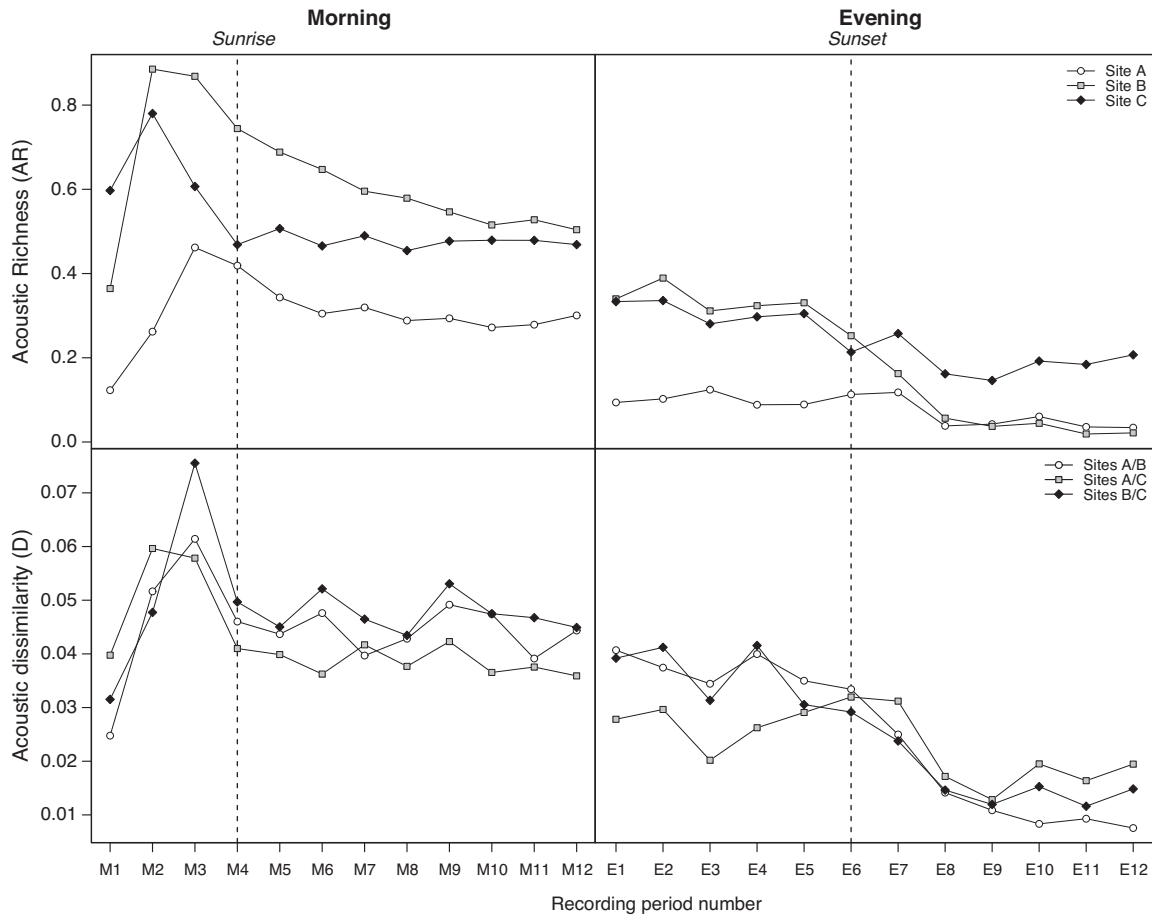


Fig. 6. Temporal changes in the acoustic richness, AR, the acoustic dissimilarity index, *D*. Acoustic indices averaged per site (A, B, C) for AR and pair of sites (AB, AC, BC) for *D*, and per time period. Time periods represent the time ranges corresponding to 150 s every 15 min around sunrise (*M_i*) and sunset (*E_i*).

4. Discussion and conclusions

Animal diversity is traditionally estimated with species inventories. However, such inventories rely on a series of difficult tasks. In most cases, specimens have first to be collected in the field. Once brought back in a Museum collection, specimens have to be sorted out, prepared for examination, and eventually each specimen needs to be identified by a taxonomic expert. Alternatively, vocalising species can be estimated in the fields through aural identification with trained human listeners (Petrauborg et al., 1953; Bridges and Dorcas, 2000; Rempel et al., 2005; Diwakar et al., 2007). Such remote sampling can produce a large dataset only if it relies on a massive network of observers (Devictor et al., 2008). A global assessment of animal diversity through remote and automatic methods of acoustics cues appears then as an attractive solution to fastidious species inventories. Based on a global analysis of the sound produced by an animal community, two indices were initially developed (Sueur et al., 2008b). The first Shannon-like acoustic index *H* aimed at assessing α diversity by measuring the entropy of the community sound. The second index is a simple dissimilarity acoustic index *D* to estimate β diversity. These indices were successfully tested in Tanzania, where the intensity of animal sound was high and the background noise was particularly low. Such highly favourable acoustic conditions are rarely met in a temperate habitat where animal species density is low and anthropogenic noise prevails. The first question addressed was then to know whether the indices were still reliable in a typical temperate habitat surrounded by human activity. It quickly appeared that frequency content of the spectral entropy index named *H_f* could

hardly give reliable results even after having treated raw signals with adapted frequency and amplitude filters. Background noise due to plane, car, farm machinery or train can severely impair the measure by generating a fairly flat spectrum and hence false *H_f* high values. Such a bias did not affect the index *H_t* that is based on the amplitude envelope of the signal. *H_t* was thus used as an indicator of the diversity of animal vocalizations. In that case, the amplitude filter was efficient by removing the noisiest parts of the recordings. Neither *H_f* nor *H_t* can estimate the density of the community, i.e. the number of animals vocalising. This can be achieved potentially by taking into account the sound level of the community. An index *M* was computed on the amplitude of recordings as an indicator of the number of animal vocalizations. Taking into account sound amplitude might be constraint by several factors including the microphone-emitter distance and the structure of the habitat. We tried to normalise as much as possible the recordings in the three sampling sites by using similar equipment, similar settings and by selecting similar positions in the habitat. Both *H_t* and *M* were eventually associated in a new index, the acoustic richness index AR.

In addition to anthropogenic noise, meteorological conditions impacted on recording quality. Bad weather had the strongest impact on AR variation, with wind and rain generating an over-estimation of AR. The RDA approach has the potential to reveal those unsuitable days, characterized by strong precipitation and/or intense wind. Bad weather days can be easily removed for further analysis. This procedure can significantly increase the reliability and speed of the method by using objective and automatic exclusions of potentially biased recordings. Solar radiation and

maximum temperature impacted variations in the *D* index, which might reveal a real biological correlation rather than a technical result. On the one hand, when the weather is cloudy, rainy, or cold compared to the season average, the animal community seems to react in a similar way in any habitat, with a decrease in singing activity, leading to lower differences between sites. On the other hand, during favourable days with sunshine and high temperature, song activity is higher (Bas et al., 2008). Species specific to each habitat are then better captured by the acoustic index *D* that reveals thus differences in community structures.

After considering the issue of noise, the results obtained from the index *AR* matched those obtained through aural identification traditionally used in bird ecology. On average, the values of *AR* increased with the richness observed in spite of an important variability. This suggests that such an automatic procedure can potentially support or even replace the observations made by a human expert. Ultimately, these results are encouraging as species richness, which is a simple measure of taxonomic diversity, was only considered. Further tests are needed to improve the connections between the acoustic approach and traditional ones. Future analyses could compare the *AR* index to more complex indices of biodiversity that take into account the acoustic repertoire (alarm calls, social calls, territorial songs), and the duration, amplitude, and frequency characteristics of bird vocalisations. It is also particularly important to identify which kind and which amount of biodiversity (taxonomic, functional or phylogenetic) the acoustic indices capture (Purvis and Hector, 2000; Magurran, 2004). In addition, classical analyses of species richness now integrate corrections which take into account species probabilities of detection (Boulinier et al., 1998). Research is needed to apply such corrections.

The *AR* index gave results expected when inventorying diversity in different woodland habitats. During the morning at the time of bird dawn chorus, it correctly revealed a higher acoustic diversity in the young forest (sampling site B) than in the mature forest (sampling site A) and at the forest edge (sampling site C). These differences were probably linked to the number of vegetation strata and tree density of each forest habitat (Blondel et al., 1973; Tellería et al., 1992; Urban and Smith, 1989). During the evening, the forest edge had a higher acoustic diversity than the young forest. This pattern could be explained by the occurrence at sunset of amphibians calling from ponds nearby the cornfield. The *D* index indicated that the young forest was significantly different from the two other sites during the morning. This supports the presence of a community in the young forest that significantly differs from the communities recorded in the mature forest and at the forest-cropland ecotone. However, these differences vanish in the evening when the acoustic activity is lower: the acoustic communities are similar probably due to the activity of shared species. The *D* index provides complementary information to that of the *AR* index but it might be more relevant when the acoustic community is particularly active.

In addition to spatial structures, our results highlight expected temporal characteristics of acoustic diversity. A temporal profile of diversity changes clearly appeared. This diversity profile was particularly obvious when comparing data collected during the morning and the evening. Diversity was particularly high just before sunrise. This intense singing period is known as the “dawn chorus” (Brown and Handford, 2003; Staicer et al., 1996). In the evening, diversity decreases regularly around sunset, before eventually becoming very low at nightfall. The *AR* index correctly captures this pattern: acoustic α diversity increased around the morning chorus then decreased around sunset. Regarding the index *D* that assesses β diversity, the decrease in acoustic α diversity through day was associated with lower dissimilarity among acoustic communities. This might be explained by the fact that, when specific diversity is low, mainly common species adapted to all

habitats are expected to be present, such as the carrion crow (*Corvus corone*), the blackcap (*Sylvia atricapilla*), the song thrush (*Turdus philomelos*) or the common blackbird (*Turdus merula*). In closed habitat near to the edge, both common and edge species occur. At the borders of forestland and fields, skylarks (*Alauda arvensis*), rooks (*Corvus frugilegus*), common linnets (*Carduelis cannabina*) and yellowhammers (*Emberiza citrinella*) are found, which are typical of open habitats.

Recently, another acoustic index based on a measure of acoustic complexity (Acoustic Complexity Index or *ACI*) has been developed to infer the singing activity of a bird community (Pieretti et al., 2011). Both *ACI* and *AR* indices are therefore based on a shared principle of complexity measure. However the *ACI* has been proved to be correlated to the number of vocalisations recorded but it has not been elaborated to estimate neither α nor β diversity. *ACI* and *AR* can be then considered as complementary indices and could be used together with the *D* index to obtain a multidimensional estimation of the acoustic community. The *ACI* has been reported to be resistant to continuous noise produced by plane traffic but sensitive to accidental noise such as wind, rain and irregular machine traffic. As discussed above, similar effects due to irregular background noise can affect the *AR* index. The solution was here to statistically identify the days where bad weather conditions affect *AR* values and to remove them from the sample. Hence, reducing noise impact on the recordings will certainly be the main next challenge for assessment biodiversity studies.

To conclude, a simple acoustic analysis of an animal community can be used as a rapid assessment of local animal diversity. The results obtained with the acoustic approach are in agreement with those obtained with traditional methods. The information provided by the indices has the potential to highlight temporal and structural characteristics of each habitat and is thus likely to allow the establishment of animal conservation priorities.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.ecolind.2011.05.006](https://doi.org/10.1016/j.ecolind.2011.05.006).

References

- Acevedo, M.A., Villanueva-Rivera, L.J., 2006. Using automated digital recording systems as effective tools for the monitoring of birds and amphibians. *Wildlife Society Bulletin* 34, 211–214.
- Bardeli, R., Wolff, D., Kurth, F., Koch, M., Frommolt, K.H., 2010. Detecting bird sounds in a complex acoustic environment and application to bioacoustic monitoring. *Pattern Recognition Letters* 31, 1524–1534.
- Bas, Y., Devictor, V., Moussus, J.P., Jiguet, F., 2008. Accounting for weather and time-of-day parameters when analysing count data from monitoring programs. *Biodiversity and Conservation* 17, 3403–3416.
- Basset, Y., Novotny, V., Miller, S.E., Pyle, R., 2000. Quantifying biodiversity: experience with parataxonomists and digital photography in Papua New Guinea and Guyana. *BioScience* 50, 899–908.
- Blondel, J., Ferry, C., Frochet, B., 1973. Avifaune et végétation, essai d'analyse de la diversité. *Alauda* 41, 63–84.

- Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E., Pollock, K.H., 1998. Estimating species richness: the importance of heterogeneity in species detectability. *Ecology* 79, 1018–1028.
- Brandes, T.S., 2005. Acoustic Monitoring Protocol. Tropical Ecology Assessment and Monitoring (TEAM) Initiative Set of Biodiversity Monitoring Protocols, Center for Applied Biodiversity Science, Conservation International. <http://www.teamnetwork.org/files/protocols/amphibian/TEAMAcoustic-PT-EN-2.1.pdf>.
- Brandes, T.S., 2008. Automated sound recording and analysis techniques for bird surveys and conservation. *Bird Conservation International* 18, S163–S173.
- Brandes, T.S., Naskrecki, P., Figueroa, H.K., 2006. Using image processing to detect and classify narrow-band cricket and frog calls. *Journal of the Acoustical Society of America* 120, 2950–2957.
- Bridges, A.S., Dorcas, M.E., 2000. Temporal variation in anuran calling behavior: implications for surveys and monitoring programs. *Copeia* 2000, 587–592.
- Brown, T.J., Handford, P., 2003. Why birds sing at dawn: the role of consistent song transmission. *Ibis* 145, 120–129.
- Brown, J.C., Hodgins-Davis, A., Miller, P.J., 2006. Classification of vocalizations of killer whales using dynamic time warping. *Journal of the Acoustical Society of America* 119, 40–46.
- Buckland, S.T., Magurran, A.E., Green, R.E., Fewster, R.M., 2005. Monitoring change in biodiversity through composite indices. *Philosophical Transactions of the Royal Society B—Biological Sciences* 360, 243–254.
- Chen, Z., Maher, R.C., 2006. Semi-automatic classification of bird vocalizations using spectral peak tracks. *Journal of the Acoustical Society of America* 120, 2974–2984.
- Cleveland, W.S., 1981. LOWESS: a program for smoothing scatterplots by robust locally weighted regression. *American Statistician* 35, 54–154.
- R Development Core Team, 2010. The R Project for Statistical Computing. <http://www.r-project.org/> (accessed 02.05.10.).
- Devictor, V., Julliard, R., Couvet, D., Jiguet, F., 2008. Birds are tracking climate warning, but not fast enough. *Proceedings of the Royal Society, Biological Sciences B* 275, 2743–2748.
- Diserud, O.H., Odegaard, F., 2007. A multiple-site similarity measure. *Biology Letters* 3, 20–22.
- Diwakar, S., Balakrishnan, R., 2007a. The assemblage of acoustically communicating crickets of a tropical evergreen forest in southern India: call diversity and diel calling patterns. *Bioacoustics* 16, 113–135.
- Diwakar, S., Balakrishnan, R., 2007b. Vertical stratification in an acoustically communicating ensiferan assemblage of a tropical evergreen forest in southern India. *Journal of Tropical Ecology* 23, 479–486.
- Diwakar, S., Jain, M., Balakrishnan, R., 2007. Psychoacoustic sampling as a reliable, non-invasive method to monitor orthopteran species diversity in tropical forests. *Biodiversity and Conservation* 16, 4081–4093.
- Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* 22, 1–20.
- Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* 61, 1–10.
- Fuller, R.J., Crick, H.Q.P., 1992. Broad-scale patterns in geographical and habitat distribution of migrant and resident passerines in Britain and Ireland. *Ibis* 134, 14–20.
- Gotelli, N.J., Graves, G.R., 1996. *Null Models in Ecology*. Smithsonian Institution Press, Washington, DC.
- Hammer, O., Barrett, N., 2001. Techniques for studying the spatio-temporal distribution of animal vocalizations in tropical wet forests. *Bioacoustics* 12, 21–35.
- Herzog, S.K., Kessler, M., Cahill, T.M., 2002. Estimating species richness of tropical bird communities from rapid assessment data. *Auk* 119, 749–769.
- Hill, D., Fasham, M., Tucker, G., Shewry, M., Shaw, P., 2005. *Handbook of Biodiversity Methods: Survey, Evaluation and Monitoring*. Cambridge University Press, Cambridge.
- Laiolo, P., 2010. The emerging significance of bioacoustics in animal species conservation. *Biological Conservation* 143, 1635–1645.
- Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, T.B., Watt, A.D., 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391, 72–75.
- MacArthur, R.H., 1965. Patterns of species diversity. *Biological Reviews* 40, 510–533.
- Magurran, A., 2004. *Measuring Biological Diversity*. Blackwell, Oxford.
- Margalef, R., 1958. Information theory in ecology. *General Systematics* 3, 36–71.
- May, R.M., 1975. Patterns of species abundance and diversity. In: Cody, M.L., Diamond, J.M. (Eds.), *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, pp. 81–120.
- Mennill, D.J., Burt, J.M., Fristrup, K.M., Vehrencamp, S.L., 2006. Accuracy of an acoustic location system for monitoring the position of duetting songbirds in tropical forest. *Journal of the Acoustical Society of America* 119, 2832–2839.
- Météo France, 2009. Prévision météo de météo France—Climat en France. http://france.meteofrance.com/france/climat.france?CLIMAT_PORTLET.path=climatstation%2F78621001 (accessed 26.05.10.).
- Moussus, J.P., Jiguet, F., Clavel, J., Julliard, R., 2009. A method to estimate phenological variation using data from large-scale abundance monitoring programmes. *Bird Study* 56, 198–212.
- Obrist, M.K., Pavan, G., Sueur, J., Riede, K., Llusia, D., Márquez, R., 2010. Bioacoustics approaches in biodiversity inventories. In: Eymann, J., Degreaf, J., Häuser, C., Monje, J.C., Samyn, Y., Vandenspiegel, Y.D. (Eds.), *Manual on Field Recording Techniques and Protocols for All Taxa Biodiversity Inventories and Monitoring*. ABC Taxa, vol. 8, pp. 18–48.
- Parker III, T.A., 1991. On the use of tape recorders in avifaunal surveys. *Auk* 108, 443–444.
- Pavoine, S., Dufour, A.B., Chessel, D., 2004. From dissimilarities among species to dissimilarities among communities: a double principal coordinate analysis. *Journal of Theoretical Biology* 228, 523–537.
- Penman, T., Lemckert, F.L., Mahony, M., 2005. A cost-benefit analysis of automated call recorders. *Applied Herpetology* 2, 389–400.
- Petchey, O.L., Gaston, K., 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* 9, 741–758.
- Petraborg, W.H., Wellein, E.G., Gunvalson, V.E., 1953. Roadside drumming counts a spring census method for ruffed grouse. *Journal of Wildlife Management* 17, 292–295.
- Pieretti, N., Farina, A., Morri, D., 2011. A new methodology to infer the singing activity of an avian community: The Acoustic Complexity Index (ACI). *Ecological Indicators* 11, 868–873.
- Pijanowski, B.C., Villanueva-rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H., Pieretti, N., 2011. Soundscape ecology: the science of sound in the landscape. *Bioscience* 61, 203–216.
- Purvis, A., Hector, A., 2000. Getting the measure of biodiversity. *Nature* 405, 212–219.
- Qi, J., Gage, S.H., Joo, W., Napoletano, B., Biswas, S., 2008. Soundscape characteristics of an environment. A new ecological indicator of ecosystem health. In: Wei, J. (Ed.), *Wetland and Water Resource Modeling and Assessment*. CRC Press, Boca Raton, pp. 201–211.
- Rao, C.R., 1964. The use and interpretation of principal component analysis in applied research. *Sankhya A* 26, 329–359.
- Rempel, R.S., Hobson, K.A., Holborn, G., Van Wilgenburg, S.L., Elliott, J., 2005. Bioacoustic monitoring of forest songbirds: interpreter variability and effects of configuration and digital processing methods in the laboratory. *Journal of Field Ornithology* 76, 1–11.
- Riede, K., 1993. Monitoring biodiversity: analysis of Amazonian rainforest sounds. *Ambio* 22, 546–548.
- Riede, K., 1997. Bioacoustic monitoring of insect communities in a Bornean rain forest canopy. In: Stork, N.E., Adis, J.A. (Eds.), *Canopy Arthropods*. Chapman & Hall, London, pp. 442–452.
- Staicer, C.A., Spector, D.A., Horn, A.G., 1996. The dawn chorus and other diel patterns in acoustic signaling. In: Kroodsma, D.E., Miller, E.H. (Eds.), *Ecology and Evolution of Acoustic Communication in Birds*. Ithaca: Cornell University Press, New York, pp. 426–453.
- Sueur, J., Aubin, T., Simonis, C., 2008a. Seewave: a free modular tool for sound analysis and synthesis. *Bioacoustics* 18, 213–226.
- Sueur, J., Pavoine, S., Hamerlynck, O., Duval, S., 2008b. Rapid acoustic survey for biodiversity appraisal. *PLoS ONE* 3, 1–9.
- Sutherland, W.J. (Ed.), 1996. *Ecological Census Techniques, A Handbook*. Cambridge University Press, Cambridge.
- Tellería, J.L., Santos, T., Sánchez, A., Galarza, A., 1992. Habitat structure predicts bird diversity distribution in Iberian forests better than climate. *Bird Study* 39, 63–68.
- Urban, D.L., Smith, T.M., 1989. Microhabitat pattern and the structure of forest bird communities. *American Naturalist* 133, 811–829.
- Villanueva-Rivera, L.J., 2007. Digital recorders increase detection of *Eleutherodactylus* frogs. *Herpetological Review* 38, 59–63.
- Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon* 21, 213–251.
- Wildlife Acoustics, 2009. *Wildlife Acoustics, Inc.—Bioacoustics Software and Field Recording Equipment*. <http://www.wildlifeacoustics.com/> (accessed 26.05.10.).