Temporal and spatial variability of animal sound within a neotropical forest

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ABSTRACT

Soundscape ecology aims to use biological, geophysical and anthropogenic sound to understand natural-human landscape dynamics. The analysis of natural soundscapes with no human noise is a prerequisite to understand and quantify the effects of human activity on animal ecology linked to sound. Preserved tropical forests are the location of unique, highly diverse, and animal sound. However, although the acoustic behavior of several tropical species has been examined, very few analyses have attempted tropical sounds at a spatial scale able to incorporate landscape characters. Here we analyze the acoustic structure of a neotropical forest landscape in French Guiana. We used a four dimensional synchronous acoustic sampling (three spatial dimensions and the temporal dimension) by deploying an array of 24 microphones in the understory and canopy of the Nouragues Nature Reserve during a 43 day period and we undertook a detailed signal analysis to detect spatial and temporal animal acoustic heterogeneity. We identified a clear pattern of acoustic activity with four distinct periods of activity that differed by their spectral characteristics indicating acoustic heterogeneity along the 24-hour cycle but periodicity at a longer time scale. We revealed acoustic divergences between the understory and the canopy layers in terms of amplitude level and frequency content. We highlighted vertical (understory/canopy) and horizontal acoustic heterogeneities with a more diverse (frequency) patch in the north of the study area sampled and a more active (intensity) patch in the southeast of the study area. Our results show that the soundscape of a tropical forest, in the absence of human disturbance, is subtly structured in time and is heterogeneous in space. This structure is probably linked to endogenous factors that rule out the acoustic time activity of animal species, to the vertical stratification of singing communities or guilds, to horizontal variations in the distributions of species and to vegetation spatial heterogeneity. Our study emphasizes that tropical soundscapes need to be recorded and analyzed in considerable spatial and temporal detail to understand their dynamics without the presence of human produced noise. Our analysis also suggests that tropical forests are unique places for acoustic diversity, supporting the need for preservation from all perturbations including anthropic noise.

1. Introduction

A bridge between bioacoustics – the study of animal sound communication – and landscape ecology was recently built through the formalization and conceptualization of soundscape ecology, a new discipline for the life sciences (Farina et al., 2011a,b; Pijanowski et al., 2011a,b). Soundscape ecology mainly aims to analyze the interactions between ecological processes and all sounds arising from a landscape, namely the soundscape (Pijanowski et al., 2011b). Soundscape ecology naturally derives from pioneer work on natural or urban soundscapes (Schafer, 1977; Southworth, 1969; Truax, 1978) and follows recent work originally presented as "landscape bioacoustics" (Laiolo and Tella, 2006) or research establishing a clear linkage between the

landscape and the acoustic environment (Matsinos et al., 2008, Mazaris et al., 2009). Soundscape ecology tries to join bioacoustics and landscape ecology to understand the patterns and processes of soundscape heterogeneity and variation (Pijanowski et al., 2011b). One of main challenges of soundscape ecology is the identification of soundscape dynamics in time and space in reference to natural and/or anthropogenic sources of variation (Pijanowski et al., 2011b). To achieve this, several tools have been exploited or specifically developed as automated recorders (Acevedo and Villanueva-Rivera, 2006), signal analysis algorithms (Bormpoudakis et al., 2013; Gasc et al., 2013a,b; Kasten et al., 2012; Pieretti et al., 2010; Qi et al., 2008; Sueur et al., 2008a,b; Towsey et al., 2012; Villanueva-Rivera et al., 2011; Wimmer et al., 2013) and sound library management systems (Kasten et al., 2012; Villanueva-Rivera and Pijanowski, 2012).

As a recent discipline, soundscape ecology needs to firstly describe the patterns of the soundscape before trying to explain the processes

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structuring the soundscape. Until now, several studies have focused on the spatial and temporal pattern of temperate soundscapes revealing an important level of variability at a local scale in relation with biological processes, human activities and geophysical phenomena (Farina et al., 2011a, 2011b; Joo et al., 2011; Krause et al., 2011; Matsinos et al., 2008; Mazaris et al., 2009; Sueur et al., 2008a,b) but less studies have been conducted on tropical soundscapes (Pekin et al., 2012).

Most of these founder analyses investigated temperate soundscapes that were perturbed to different degrees by anthropogenic noise and land use. Such sound environments are of high interest to estimate the relative contribution of biophony (sounds produced by animal species), geophony (sounds originating from the geophysical environment) and anthropophony (sounds emanating from human activity), the three main components of a soundscape as defined by Krause (1998, 2008). However, it remains necessary to decipher the composition and dynamics of primary soundscapes to try to understand the natural processes beyond soundscape dynamics. Moreover, temperate soundscapes embrace rather low levels of acoustic diversity (Depraetere et al., 2012, Pijanowski et al., 2011a) while tropical acoustic soundscapes have been shown to reach very high levels of sound diversity (Diwakar et al., 2007; Riede, 1993, 1997). So far, these acoustics elements have been analyzed in the framework of bioacoustics focusing mainly on the behavior of specific taxa, as amphibians (Amézquita et al., 2011; Chek et al., 2003), birds (Luther, 2009; Planqué and Slabbekoorn, 2008), and insects (Diwakar and Balakrishnan, 2007a), even if some rare studies tried to include several taxa (Hammer and Barrett, 2001; Riede, 1997; Slabbekoorn, 2004; Sueur et al., 2008a). The complexity of tropical forest structure from the understory to the canopy offers different micro-habitats (Basset et al., 2003; Richards, 1996; Smith, 1973; Terborgh, 1985) that can be occupied by distinct vocalizing species. This potentially leads to a heterogeneous soundscape that can be complicated with different constraints on sound propagation in relation to habitat and micro-habitat structures (Marten et al., 1977; Morton, 1975; Richards and Wiley, 1980). However, to the best of our knowledge, there is a single study that has been conducted on the heterogeneity of a tropical soundscape (Pekin et al., 2012). In this study, the acoustic diversity could be spatially predicted by LIDAR (LIght Detection and Ranging) metrics describing the vertical structure of the forest, suggesting that acoustic diversity could be strongly linked to the vertical complexity of the canopy.

Soundscape dynamics such as periodicity, and horizontal and vertical heterogeneities are poorly known in tropical ecosystems before deforestation, therefore, there is an important need to record, describe, analyze and quantify them quickly. In this paper, we report the first description of a tropical soundscape sampled in four dimensions: the three spatial dimensions and the time dimension. We deployed 24 microphones that recorded synchronously the understory and the canopy soundscapes of a French Guiana tropical forest reserve. Using multivariate analysis of amplitude and frequency components of the soundscape associated with original spatial heterogeneity analysis transferred from population genetics, we found a clear diurnal cycle composed of four periods and important spatial differences along the horizontal and vertical axes of the forest. This indicates a high level of heterogeneity likely due to a high level of animal diversity and to a complex partitioning of the acoustic resource.

2. Methods

2.1. Study area

We deployed a four dimensional acoustic sampling scheme in a section of tropical forest managed by the French CNRS Nouragues Research Station (4°05′N; 54°40′W) within the Nouragues Nature Reserve (Fig. 1a). This 48 ha forest research station area is located in an inhabited region at the center of French Guiana, 100 km away from the main city Cayenne and 60 km away from the nearest village Regina.

The climate is equatorial with a mean temperature of 26.3°, and a weak thermal amplitude of 2 °C. The mean annual rainfall is 3000 mm over 280 days per year (Grimaldi and Riéra, 2001). The annual cycle is constituted of a dry season from September to November, a rainy season from January to June, and a short dry season in March within the rainy season (Grimaldi and Riéra, 2001). Sunrise is at 06:15 am and sunset at 06:10 pm.
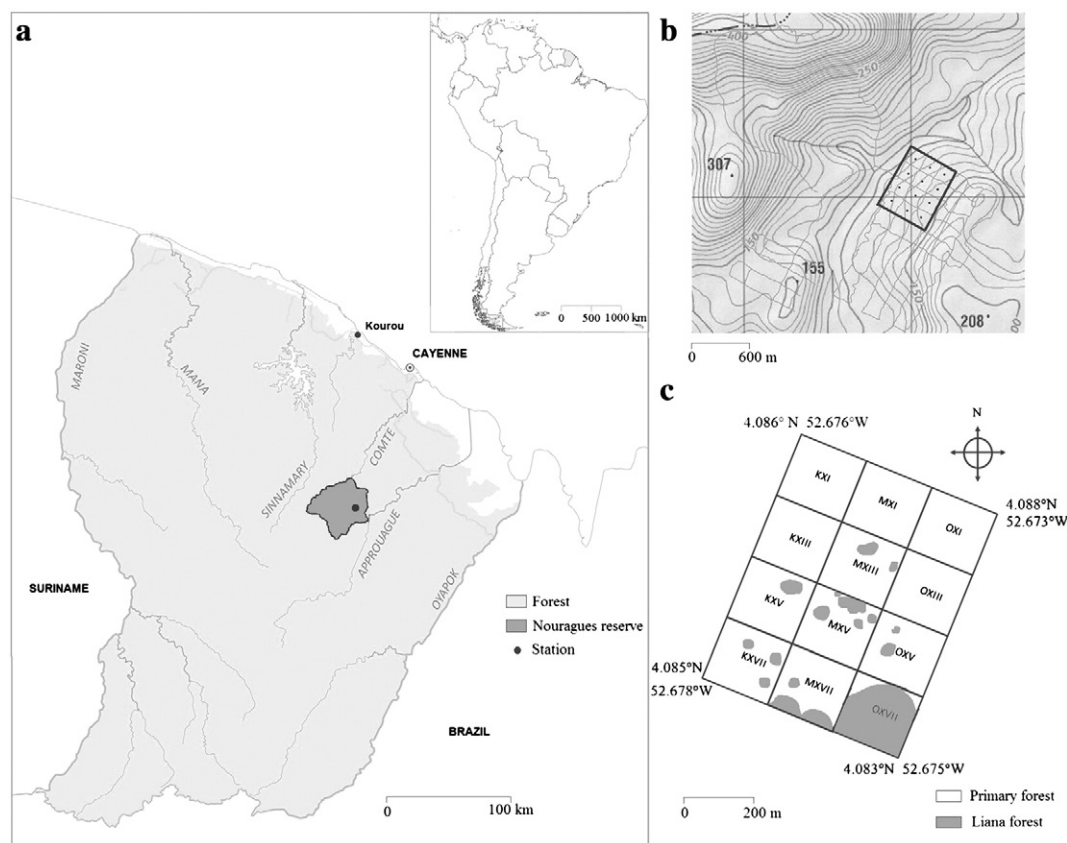
The Nouragues site has not undergone any anthropogenic perturbations since the Noraks, the native Amerindians, who disappeared during the eighteenth century (Charles-Dominique, 2001). The vegetation cover consists of a dense evergreen forest with trees typically reaching a height of 30 to 45 m. The exact study area is located on the main plateau, which has a clayey soil with a vertical drainage where trees can deeply root (Grimaldi and Riéra, 2001) (Fig. 1b). This area is covered with a high diversity of tree species including 550 species belonging to 63 families. The Caesalpinaceae is the most important family in terms of species richness, density and dominance, followed by the Sapotaceae and the Lecythidaceae (Poncy et al., 2001).

2.2. Sampling protocol

To regularly record the soundscape of the forest, we placed 24 microphones in the three spatial dimensions. These microphones covered two grids at two different heights (see details below). We used the two channels of 12 autonomous digital recording Song Meter 2 devices (Wildlife Acoustics, Massachusetts, USA, 2010) each equipped with weatherproof omni-directional microphones that have a flat frequency response in the range 0.02–20 kHz.

The recorders were spaced by using a regular array of linear trails previously named with a letter (K, M, O) or a Roman number (XI, XIII, XV, XVII). The trails drew a rectangular area divided into 12 squares with a side of 200 m in length. The recorders were settled at the crossing of trails (i.e. at the positions K-XI, K-XIII, K-X, K-XVII, M-XI, ..., O-XVII). For each recorder, one of the two microphones was positioned at a height of 1.50 m to record the acoustic activity of the understory and the other was positioned at a height of 20 m to record the acoustic activity of the canopy. Due to limited access to the canopy we could not run acoustic propagation experiments or model sound propagation around each microphone to estimate the area covered by each recording site. However, knowing that terrestrial animals produce sound with an intensity of circa 80 dB at 1 m *re.* 2×10^{-5} μPa (Sueur et al., 2012) and that the microphones have a sensitivity of -36 ± 4 dB, we could estimate that in a closed habitat, such as a tropical forest, each microphone would detect animal sound activity in a circle with a radius of about 100 m. We avoided overlap between adjacent microphones. However, comparison of recordings between understory and canopy microphones clearly showed a certain amount of acoustic overlap (see section 3).

We recorded the soundscape at the end of the dry season, from November 10th 2010 to December 22nd 2010. We recorded one minute every fifteen minutes, day and night. The recordings of each site were synchronized. This generated 99072 files (12 sites × 2 vertical levels × 4 recordings/h × 24 h × 43 days) for a total of 1634 h of recording. Due to a problem when programming the recording schedule, the recording time slot at 11:45 pm had to be removed from the analysis. In addition, 556 files (site M-XVII, from November 3rd 2010 to December 6th 2010) were also corrupted and had to be withdrawn. This led to a total of 98473 files. We processed all recordings at a sampling rate of 44.1 kHz and we stored the recordings in the form of Wildlife Acoustics Audio Compression (WAC) files, which we subsequently converted into Waveform AudioFile Format (WAV) with the software 'WAC to WAV Converter Utility' (v1.1, Wildlife Acoustics, 2009) for purposes of analysis. One of us (AR) listened to the recordings to exclude files corrupted with high background noise due to wind and heavy rain (geophony) or helicopter flights, the only source of human noise (anthropophony).

Fig. 1. Location of the study area. a. Location of the Nouragues Natural Reserve in French Guiana and location of French Guiana in South America (inset). b. Topographical position of the study area (CNRS Nouragues Research Station). c. Diagram of the sampling grid with a letter and a Roman number indicating the location of each pair of microphones at the cross of perpendicular trails.

2.3. Spectral analysis

We assessed acoustic differences between all pairwise recordings by estimating the dissimilarity of pairs of frequency spectra. Using the R package seewave (Sueur et al., 2008a,b), we obtained a frequency spectrum for each recording by (1) computing a short-time Fourier transform (STFT) with a 512 samples sliding but non-overlapping Hamming window, (2) averaging the columns of the resulting matrix (here it refers to its temporal dimension); and (3) scaling the amplitude averaged values by their integral. This procedure returned an average frequency spectrum with a frequency resolution of 86.13 Hz and a relative amplitude scale. We subsequently calculated a dissimilarity metric, named the D_f index (Sueur et al., 2008a,b), according to:

$$D_f = 0.5 \ \text{x} \ sum \ |S_1(f) - S_2(f)|$$

where $S_1(f)$ and $S_2(f)$ are the probability mass functions of the mean spectra of the two recordings to be compared.

We ran a distance-based multidimensional analysis in order to visualize whether the factors "Time" and "Site" could explain the acoustic variability, and which of these two factors was the most important in explaining the acoustic differences observed. We divided the "Time" factor into 24 categories corresponding to the 24 hours of the day. Each category was composed with the four recordings of each hour (e. g. 1:00 pm, 1:15 pm, 1:30 pm and 1:45 pm). We defined the "Site" factor with 24 categories corresponding to the 24 microphone locations (12 in the canopy and 12 in the understory). We computed the spectral metric D_f between all pairs of recording files leading to a first 10731*10731 dissimilarity matrix. We first applied a Principal Coordinate Analysis (PCoA) (Gower, 1966) on this distance matrix and we then applied a principal component analysis with respect to instrumental variables (PCAIV, Rao, 1964) on the coordinates returned by PCoA analysis. Each point projected in the resulting multidimensional space represented the acoustic position of one site, one recorder, at one hour. We ran all these multidimensional analyses with the R package ade4 (Dray and Dufour, 2007).

To estimate differences between adjacent recording spots, we transferred techniques used to detect genetic barriers between geographically distinct populations to detect acoustic barriers or differences between distinct recording sites. We used the Monmonier's algorithm (Monmonier, 1973), which detects boundaries by finding the path exhibiting the largest differences provided in a genetic distance matrix between neighboring populations localized with geographic coordinates. Here, we considered each microphone as a population localized with its latitude and longitude coordinates and we considered the distance matrix obtained with the spectral D_f index as the genetic distance matrix. We used the Barrier 2.2 software (Manni et al., 2004) that first created a Voronoi tessellation and a Delonay triangulation with the spatial coordinates of the microphones. This preliminary process defined the proximity web of axes where acoustic barriers could be drawn. Monmonier's algorithm was used to calculate the path of the decreasing acoustic distances and, lastly, the software projected the acoustic barriers onto a map where their thicknesses were correlated with acoustic dissimilarity between adjacent microphones. The Monmonnier's algorithm is not accompanied by a statistical procedure that tests barrier thickness. However, we defined the main barriers as those found in the last quartile (75–100%) of the barrier thickness distribution. This ensured an objective criterion of selection.

2.4. Amplitude analysis

We estimated the variation in space and time of the soundscape amplitude. The amplitude of each file was measured using the root-

mean-square (RMS) of the absolute value of the wave of each recording. We decomposed the time series of amplitude variation along days using a moving average and an additive model with three components (trend component, seasonal component and error or random component). We estimated the periodicity of these time series with an auto-correlation function (Shumway and Stoffer, 2006). The auto-correlation function consisted of correlating the original time series with itself after a specific time lag. The auto-correlation shows local maxima when the time lag corresponds to a periodic event. Time series decomposition and auto-correlation was estimated on raw recordings (i.e. without removing recordings, including helicopter or rain noise). Results are reported for a single site but were representative of all others sites.

We also calculated the median of the acoustic amplitude for each time of the day (factor "Time") and we used this median as a variable. The values were log transformed to reach normality. Variation between recording sites (factor "Site") and between the understory and canopy was visualized using boxplot representations. We tested the differences between the sound amplitudes monitored in the understory and the canopy with a parametric two-sided t-test for paired samples with unequal variances. We corrected the p-value with a Bonferroni correction for multiple tests ($n = 12$). We mapped linear sound amplitude spatial variation using a circle with a radius and a background color scaled with the median of the relative amplitude level recorded at each recording spot. This led to a plot representing twelve amplitude medians. We assessed the statistical distribution of these amplitude medians with a kernel density estimation and we also calculated the median and the median absolute deviation of the medians to give an estimation of the amplitude of the soundscape. We did not attempt to use any spatial models because the spatial resolution was too low, with only 12 sampling points, to allow reliable predictions.

3. Results

3.1. Spectral analysis

We estimated the variation in time and space of the soundscape of the tropical forest by running distance-based multidimensional analyses on a spectral dissimilarity matrix obtained between pairs of recordings. The "Time" factor revealed a structure along the day-night cycle on the first two axes of the multidimensional analysis which explained 3.2% of the variability (Fig. 2). We could identify four distinct periods: (1) a long transition morning period from 1:00 am to 9:00 am;

(2) a day period from 9:00 am to 6:00 pm; (3) a short transition evening period from 6:00 pm to 7:00 pm; and (4) a night period from 7:00 pm to 1:00 am. The "Site" factor did not show any particular structure along the understory and canopy arrays respectively but showed a difference between the understory and canopy positions as indicated by the two first axes of the multidimensional analysis which explained 1.3% of the variability (Fig. 3). We therefore identified a coherent spatial structure along the vertical axis but not along the horizontal axes of the 3D arrays of microphones.

To investigate more specifically the horizontal pattern, we obtained Monmonier maps that indicated relative spectral differences between adjacent recording sites (Fig. 4). These maps showed important acoustic barriers in the northern part of the studied area revealing contrasting soundscapes. In particular the K-XI recording site was always acoustically very different at both the understory and canopy levels from its neighboring recording sites (K-XIII, M-XI), except during the day period (9:00 am–6:00 pm). The recording site M-XI also appeared acoustically distinct from the three neighboring recording sites (K-XI, O-XI, M-XIII). M-XIII was acoustically different from its surrounding recording sites (K-XIII, M-XI, M-XV, O-XIII) during the day period (9:00 am–6:00 pm). Except for the recording site K-XVII, which differed from recording sites K-XV and M-XVII during the day period (9:00 am–6:00 pm), the southern part of the maps did not show significant acoustic barriers, denoting a homogeneous soundscape.

3.2. Amplitude analysis

We decomposed the times series of amplitude variation with an additive model (Fig. 5a). The trend component of the model showed a regular pattern (Fig. 5b) when the error or random component was made of accidental events (Fig. 5c). The auto-correlation analysis clearly showed that the regular pattern of the trend component followed a 24 hour cycle (Fig. 5d). The trend component alternated low and high amplitude levels. In particular, the microphones placed in the understory showed a small amplitude peak between 6:00 am and 7:00 am, an amplitude trough between 10:00 am and 2:00 pm, and high levels between 6:00 pm and 7:00 pm. The microphones settled in the canopy revealed low values between 10:00 am and 2:00 pm and high values between 8:00 pm and 9:00 pm and during all the night. There was then a +2 h lag between the understory and the canopy at twilight hours. The accidental events revealed by the random component were
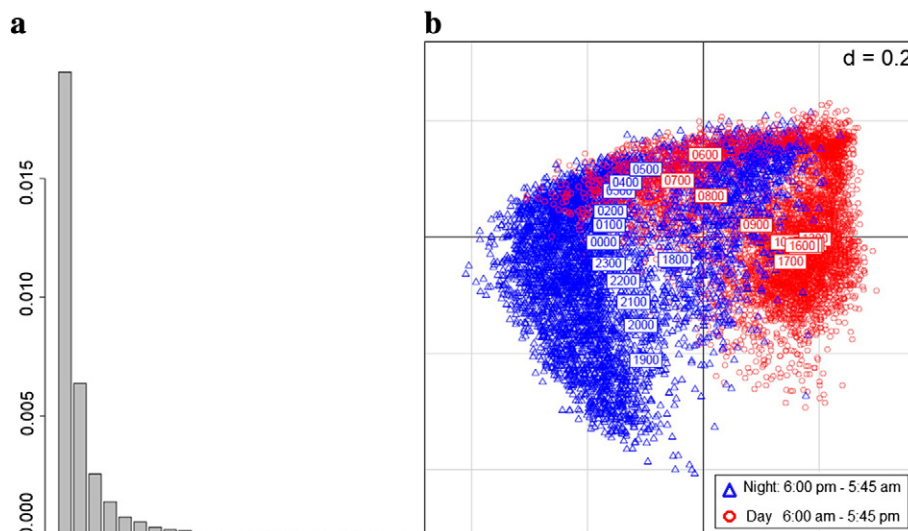

Fig. 2. Multidimensional analysis of the acoustic dissimilarity matrix obtained with the spectral dissimilarity index D_f. a. Bar plot of the eigenvalues. b. Projection along the axes 1 and 2 with the "Time" factor as an explanatory variable. Day hours, from 6 am to 5:45 pm, are depicted with a red circle and night hours, from 6:00 pm to 5:45 am are depicted with a blue triangle.
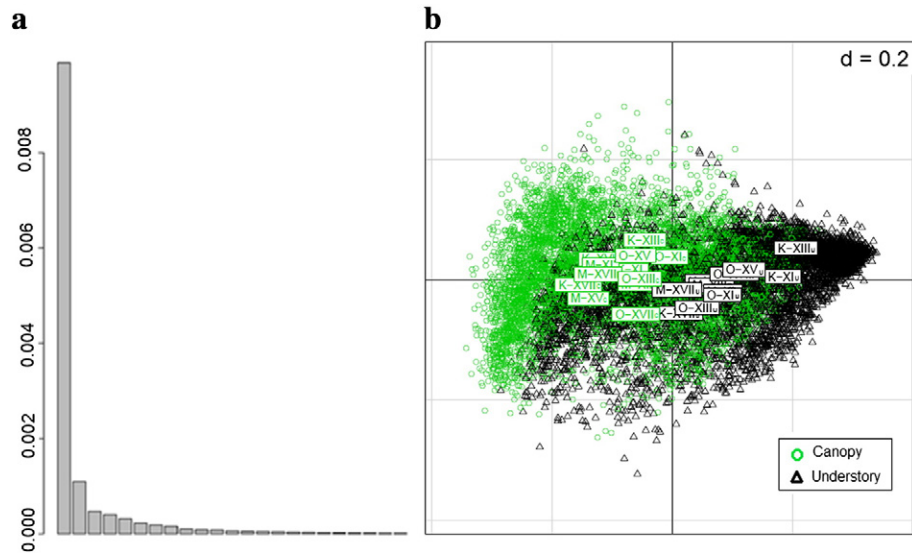
Fig. 3. Multidimensional analysis on the acoustic dissimilarity matrix obtained with the spectral dissimilarity index D_f. a. Bar plot of the eigenvalues. b. Projection along the axes 1 and 2 with the "Site" factor as an explanatory variable. Recordings achieved in the understory and in the canopy are depicted with a black triangle and a green circle respectively.

mainly due to helicopter flights, heavy rain and loud howler monkey (*Alouatta seniculus*) choruses.

We found that the amplitude of the understory soundscape was mainly lower than the amplitude of the canopy soundscape (Fig. 6). During the morning period, this difference was significant for all record-ing sites except M-XVII. During the day period, this difference was less clear as it was not significant for K-XVII and the difference was inversed, i.e. the understory soundscape was louder than the canopy soundscape, for M-XIII, M-XVII, O-XI, O-XIII and O-XVII. During the evening period, we found that half of the recording sites had a quieter understory soundscape than the canopy soundscape. During the night period, we observed that the understory was always significantly quieter than the canopy. The differences along the vertical axis were therefore more pronounced during night than during the other periods of the 24-hour cycle.

When mapping the amplitude median by time periods for both understory and canopy strata, we revealed a higher amplitude in the southern part of the area (trails XV and XVII) with a particularly high amplitude in the square made of the recording sites K-XV, K-XVII, M-XV and M-XVIII at any time of the 24-hour cycle (Fig. 7). This square was therefore louder, suggesting either a higher density of vocalizing animals or the presence of species that vocalize more loudly. We could also identify the recording site O-XIII in the understory in the evening and the recording site M-XI in the canopy during the day as two other important sound sources. The density distribution of the amplitude medians showed a low and sharp profile during the morning and day periods at both understory and canopy levels (understory morning: 363 ± 97; canopy morning: 576 ± 148; understory day: 277 ± 83; canopy day: 243 ± 107; median $\pm$ median absolute deviation). The distribution of the amplitude medians showed a high and wide profile during the evening and night periods, in particular in the canopy stra-tum (understory evening: 631 ± 276; canopy evening: 1249 ± 472; understory night: 551 ± 228; canopy night: 1146 ± 433).

4. Discussion

Tropical forests are renowned for holding the highest levels of plant and animal species richness (Basset et al., 2012; Giam et al., 2012; Myers et al., 2000). However accelerated wood exploitation, agricultural ex-tension and urbanization threaten this unique diversity and generate landscapes with complex natural-human dynamics (Lawton et al.,

1998; Whitmore, 1997; Wright, 2005). Tropical forest soundscapes undoubtedly generate rich natural sound environments with a complex mix of amphibian, mammal, bird and arthropod sounds (Riede, 1993, 1997). Soundscape ecology has been recently introduced as a new way to analyze variation over space and time reflecting important landscape processes and human activities (Pijanowski et al., 2011a,b). A soundscape analysis of an intact tropical forest area should then enlighten the animal dynamics of a natural landscape before the en-trance of human noise. To estimate the structure of an unaltered tropical soundscape, we deployed for the first time a large and long acoustic sampling in the Nouragues Nature Reserve, a preserved area localized in the middle of the Guiana forest. This remote sensing of the forest soundscape revealed different crossed levels of temporal and spatial heterogeneities.

4.1. Temporal heterogeneity

We first found that the spectral content and the amplitude level of the soundscape fluctuated with time. A multidimensional analysis based on frequency dissimilarities did not return obvious breaks along time but a rather circular continuum of variability with four main overlapping periods and a more pronounced difference between day and night. In terms of amplitude, we could also clearly identify a 24-hour cycle with a low peak at dawn, a high peak at dusk and higher amplitudes during the night than during the day. Finally, in our study the soundscape of the tropical forest was heterogeneous along the night–day cycle but homogeneous at an over-day scale.

The difference between the day and the night soundscapes was expected as singing species follow diel patterns due to endogenous or exogenous constraints (Henwood and Fabrick, 1979; McNamara et al., 1987). In particular, birds and cicadas mainly sing during the day, while amphibians, mammals, crickets and katydids are mostly active during the night. Such patterns have been frequently reported at a species level but rarely at community or landscape levels (Ellinger and Hödl, 2003; Gasc et al., 2013a,b; Riede, 1997). The transition between the night and day soundscapes was obvious with amplitude rises at dawn and dusk and spectral differences. However, if it was clear that birds and howler monkeys were more active at dawn and Orthoptera at dusk (AG and JS observation), we did not find very intense, brief, strictly limited in time, and finely structured dawn–dusk choruses as reported at other tropical sites (Riede, 1997; Schwartz, 1994; Sueur,
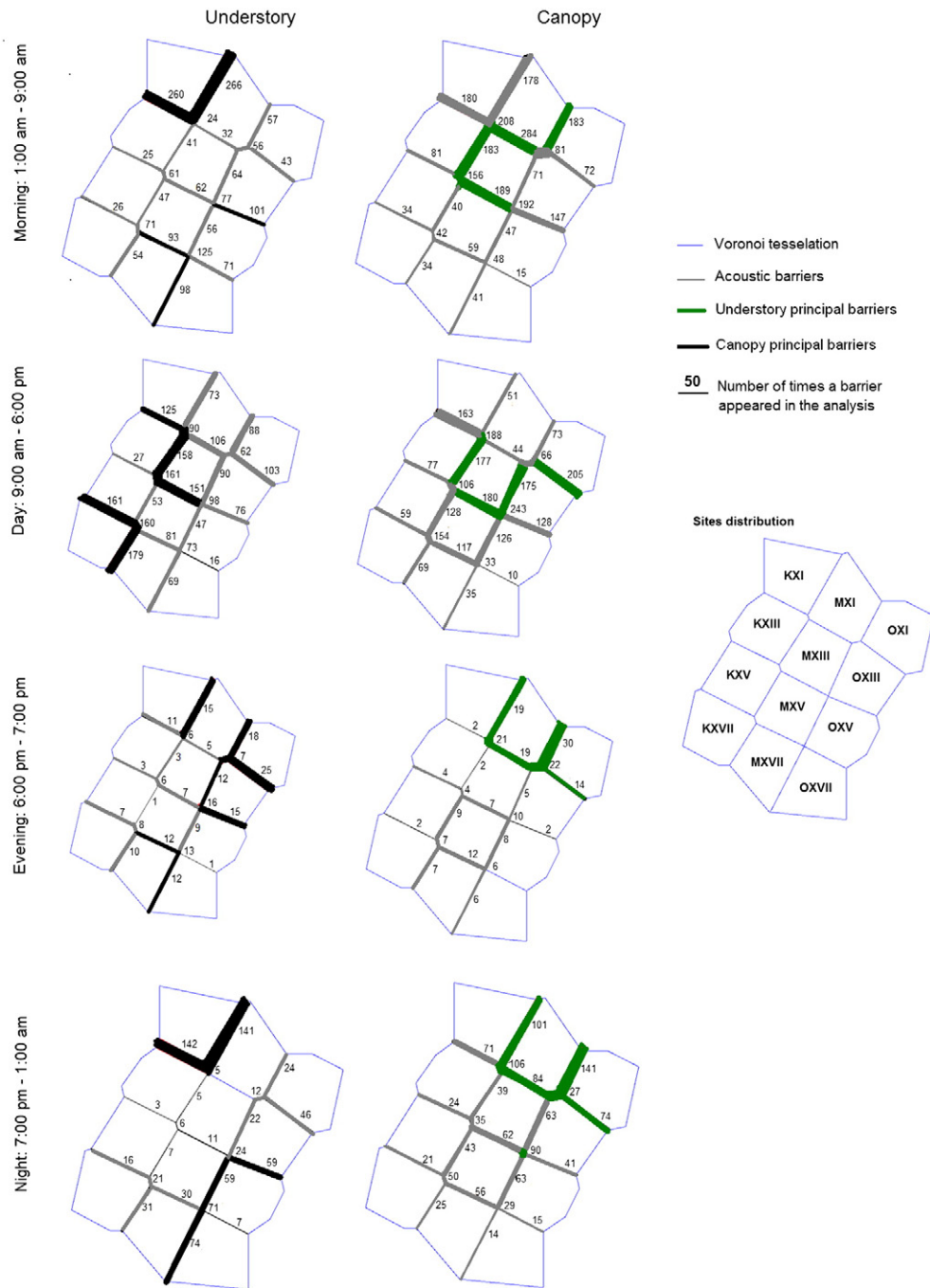
Fig. 4. Acoustic barriers between the different adjacent areas obtained with the Monmonier algorithm applied to the spectral dissimilarity D_f index. Understory and canopy main barriers are indicated with a black or green bold line.

2002; Young, 1981). This might be due to the fact that cicadas and amphibians, which are the main components of dawn–dusk choruses, were not breeding in high number at this period of the year.

Our sampling did not cover a year as we intentionally recorded the soundscape during the dry season to avoid losing important noise due to rainfalls. Extension of the sampling through the rainy season would certainly have revealed heterogeneity over days and seasons due to the sound produced by cicadas, which emerge intensively at first rains (Wolda, 1989; Young, 1972) and to the extremely intense vocalizations of amphibians emanating from explosive breeding after heavy rainfalls (Gottsberger and Gruber, 2004; Savage, 2002). The soundscape of the rainy season remains therefore to be described and we can predict that seasons will lead to an additional level in soundscape dynamics.

4.2. Spatial heterogeneity

In addition to a temporal variation, we also revealed a three dimensional spatial variation. A previous work established a link between forest vertical structure and soundscape structure by confronting LIDAR (LIght Detection and Ranging) and acoustic data gathered above ground over six days (Pekin et al., 2012). Here, we could settle for the first time an array of microphones at 1.5 and 20 m respectively sensing
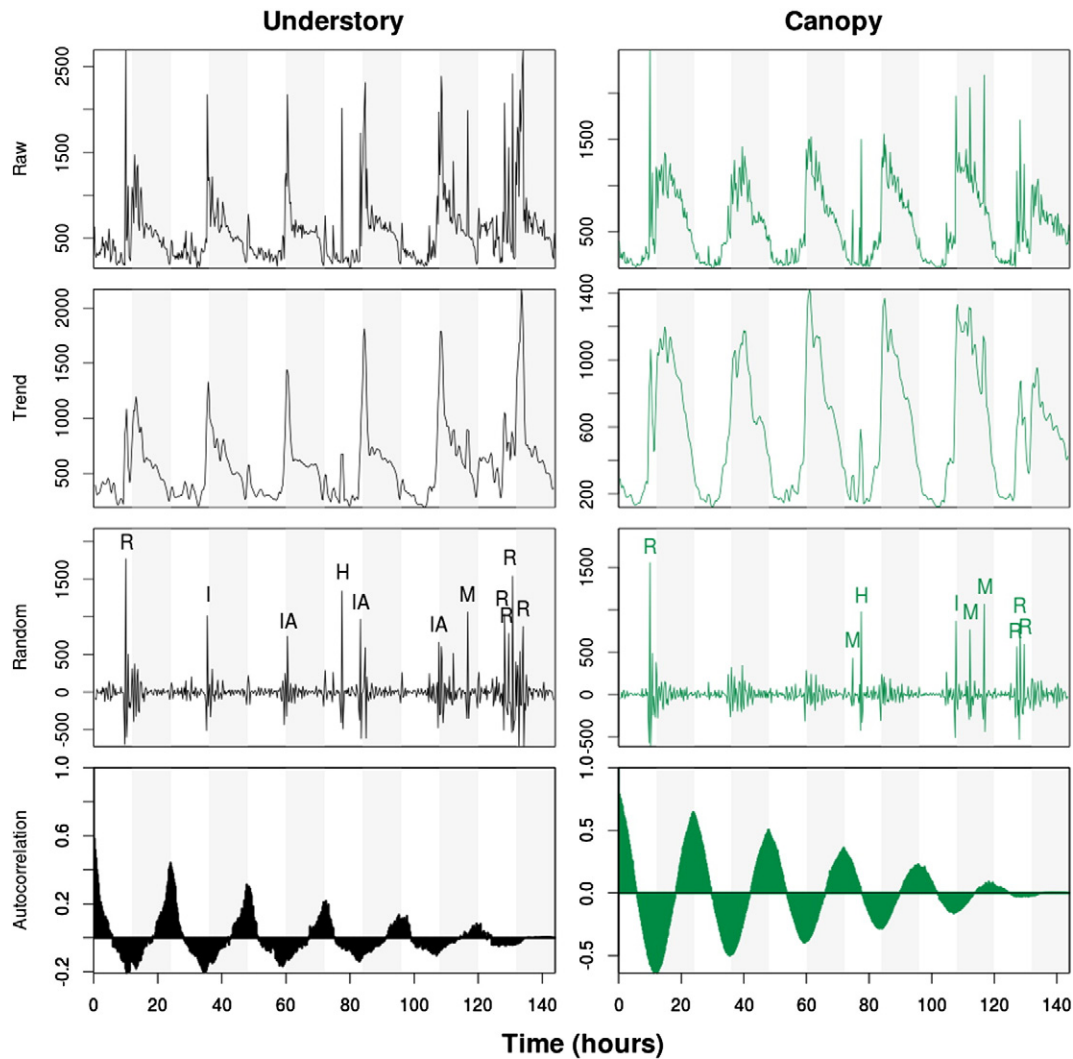
Fig. 5. Decomposition and autocorrelation analysis of the sound amplitude recorded at the site O-XIII from November 13th at 6:00 am to November 18th 2010 at 23:30 am for both understory and canopy levels. a. Raw data. b. Amplitude trend component of the additive decomposition revealing a 24 hour cycle. c. Random component of the decomposition indicating the occurrence of exceptional events such as howler monkeys choruses (M), heavy rains (R), helicopter flight (H), insect chorus (I) or amphibian chorus (A). d. Autocorrelation function of the observed amplitude data clearly confirming a 24 hour cycle.

both understory and canopy soundscapes over a long period. We detected amplitude and spectral differences between the understory and canopy soundscapes even if the acoustic volume covered by the microphones of each pair certainly overlapped in part.

The spectral analysis indicated differences between the understory and the canopy suggesting distinct soundscapes due to the occurrence of different species confirming pioneer observations conducted in a Bornean lowland forest (Riede, 1997). These differences were more important during the night than during other periods probably because of a higher diversity in species vocalizing during the night. Similar results were found for temperate bird communities. The differences between the communities were higher at dawn chorus time when species diversity was at its maximum (Depraetere et al., 2012). The understory and canopy differences might be explained with the acoustic adaptation hypothesis that stipulates that the evolution of acoustic properties of animal songs is shaped by selection dependent on habitat or micro-habitat structure (Marten et al., 1977; Morton, 1975). However, this hypothesis still remains debated (Boncaraglio and Saino, 2007; Ey and Fischer, 2009) and is difficult to test in such complex habitat and soundscape. Several studies have reported a vertical stratification of acoustic guilds with species singing only in the first vertical layers of the forest and others inhabiting only the canopy, considering

birds (Luther, 2009; Pearson, 1971), anurans (Hödl, 1977; Lüddecke et al., 2000), bats (Bernard, 2001), cicadas (Sueur, 2002) or katydids and crickets (Diwakar and Balakrishnan, 2007b; Jain and Balakrishnan, 2012; Schmidt et al., 2013). Such microhabitat selection induces different communities and therefore soundscapes. This vertical heterogeneity interfered with the temporal heterogeneity as a +2 h lag was observed between the amplitude of the canopy and understory soundscapes. This time shift might be the result of different micro-climatic and ambient light conditions between the low and high forest strata as described at the Nouragues (Bongers et al., 2001) and at other tropical sites (Barker, 1996; Madigosky, 2004).

The canopy soundscape appeared louder than the understory soundscape. This amplitude difference could be due to: (i) better sound propagation conditions in the canopy; (ii) the occurrence of louder species in the canopy; and/or (iii) a higher number of active individuals in the canopy. All three hypotheses are very difficult to test as they require full access to the canopy, which is in addition a complex acoustic environment due to the occurrence of acoustic boundaries, interfering objects, temperature gradients and wind gradients that counteract and vary with time (Richards and Wiley, 1980). However, propagation experiments in Panama did not show significant differences at heights of 2 m and 12 m corresponding to the understory and low canopy
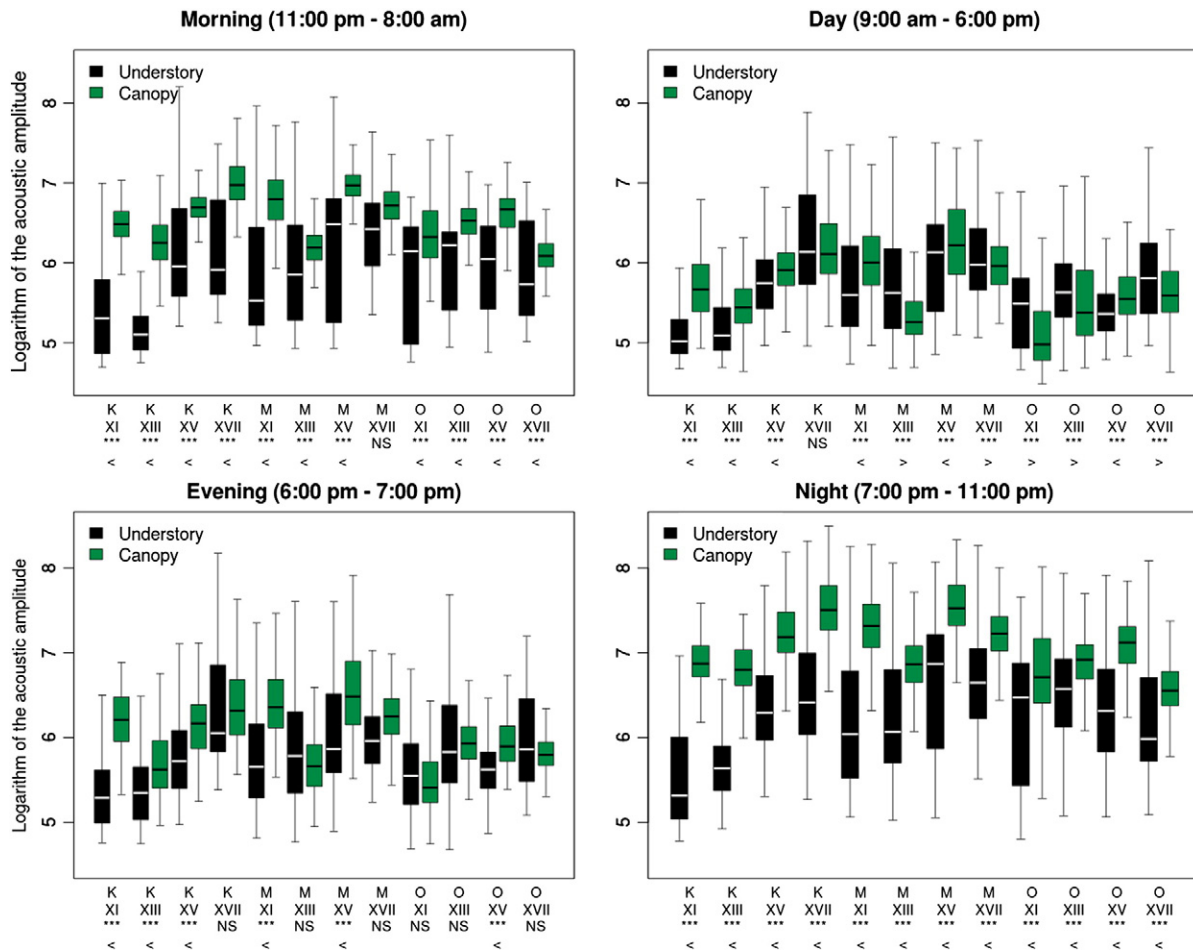
Fig. 6. Boxplot of the acoustic amplitude recorded in the understory and in the canopy at each recording site and during the four time periods identified on the multidimensional analysis (see Fig. 2). For each understory/canopy pair of recording a two-sided t-test for paired samples with unequal variances was computed. The significance of the test is indicated with either NS for non significant or *** for a Bonferroni corrected p value lower than 0.001. The sign '<' (respectively '>') indicates that the understory amplitude level was lower (respectively higher) than the canopy amplitude level when the t-test was significant.

levels (Marten et al., 1977). Similar transmission tests in Venezuela did not reveal advantageous acoustic conditions at the canopy level (Ellinger and Hödl, 2003). A recent study undertaken in India with Ensiferan insects showed that the canopy was not the best place for signal transmission but that the mid and upper understory (2 m and 4 m) less degraded the signals produced (Jain and Balakrishnan, 2012). All these data suggest that the canopy does not constitute a more favorable acoustic environment, which could explain higher amplitude levels. The second hypothesis regarding loudness has never been investigated, as the sound pressure level of a series of species, which are difficult to approach in the canopy, requires documentation. The third hypothesis would be supported by a high level of species richness and species density of animals, in particular arthropods, in the canopy (Allen, 1996; Basset et al., 2003; Nadkarni, 1994; Shaw, 2004) potentially leading to a higher acoustic intensity in the canopy than close to ground.

Tropical spatial community structure and dynamics reveal a high level of horizontal heterogeneity within tropical landscapes (Carson and Schnitzer, 2008). In particular, tree species diversity was found to be highly heterogeneous at the Nouragues Research Station (Poncy et al., 2001) and branch falls, tree falls and canopy gaps induced complex habitat and spatial landscape dynamics locally (Meer van der and Bongers, 2001). We could detect here another layer of horizontal heterogeneity as both frequency and amplitude acoustic analyses revealed significant variation along the horizontal plane. In particular, the north part showed the most important spectral barriers between adjacent plots and the patch in the southeast part was characterized by the highest amplitude values. The ecological processes beyond

these horizontal patterns are difficult to identify but there are several candidate factors that could shape soundscape dynamics: (1) vegetation heterogeneity might induce different sound propagation environments more or less suitable for an efficient signal transfer; (2) the quality of habitats and micro-habitats within the forest landscape in terms of food resources might act as source-and-sink systems (Pulliam, 1988) and lead to an excess or a deficit of singing individuals; (3) specific movement patterns of each species (stationary vs. different degrees of mobility) within their habitat might induce specific spatial and temporal dynamics of the sound sources; and (4) the social and mating systems of each species might a generate specific spatial pattern with individual calling isolated, in dynamic leks or in pseudo or fully synchronized choruses.

5. Conclusion

Acoustic recording is a new remote sensing technique that can provide complementary information on landscape structure, animal ecology processes, and the local animal diversity state. We could detect temporal and spatial heterogeneity in a small tropical forest area. However, this study, together with a previous study (Pekin et al., 2012), should be considered as a very first attempt to characterize the acoustic complexity of tropical soundscapes. The heterogeneity and dynamics of a tropical soundscape are probably the result of a complex net of interacting processes that are still to be clearly identified. To understand the diversity and variation of a tropical soundscape might be as difficult as deciphering tropical forest animal and plant patterns that have
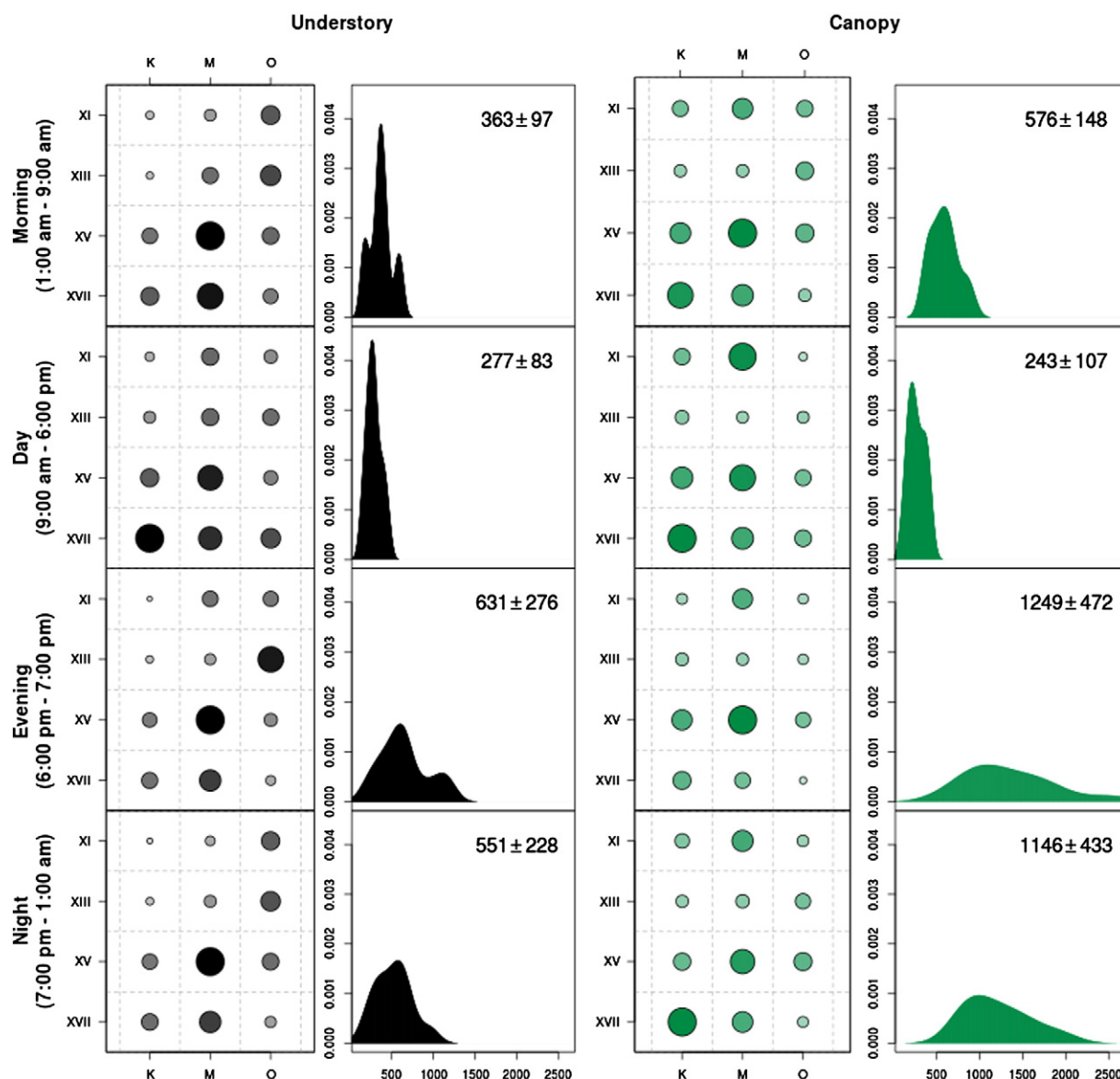
Fig. 7. Amplitude variation in space in the understory and in the canopy during the four time periods identified on the multidimensional analysis (see Fig. 2). For each recording site a circle shows the relative amplitude scaled between 0 and 1. A small white circle indicates a low amplitude level when a large black or green circle indicates a high amplitude value. The density profiles indicate the distribution of the raw values before to be scaled between 0 and 1. For each density plot the median ± median absolute deviation is given as an inset.

now been studied for decades. Soundscape ecology is a promising discipline for the study of tropical animal sound but this should not discredit the species-specific approach. Here, we definitely need to go down to an analysis of species-level acoustic ecology to better understand the patterns that emerge at a landscape scale. In other words, both behavioral and ecological approaches, led by bioacoustics and soundscape ecology respectively, are necessary. Finally, our study emphasizes that tropical forests contain a very important and complex acoustic diversity that can be impaired with the rise of anthropic noise. Acoustic diversity is a very valuable part of biodiversity that should be considered together with classical biodiversity facets, like species richness or functional diversity, for tropical habitat preservation.

References

Acevedo, M.A., Villanueva-Rivera, L.J., 2006. Using automated digital recording systems as effective tools for the monitoring of birds and amphibians. Wildl. Soc. Bull. 34, 211–214.

Allen, W.H., 1996. Traveling across the Treetops. Bioscience 46, 796–799.

Amézquita, A., Flechas, S.V., Lima, A.P., Gasser, H., Hödl, W., 2011. Acoustic interference and recognition space within a complex assemblage of dendrobatid frogs. Proc. Natl. Acad. Sci. 108, 17058–17063.

Barker, M.G., 1996. Vertical profiles in a Brunei rain forest: I. Microclimate associated with a canopy tree. J. Trop. For. Sci. 8, 505–519.

Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L., 2003. Arthropods of tropical forests. Spatio-temporal dynamics and resource use in the canopy. Cambridge University Press, Cambridge, UK.

Basset, Y., Cizek, L., Cuénoud, P., Didham, R.K., Guilhaumon, F., Missa, O., Novotny, V., Ødegaard, F., Roslin, T., Schmidl, J., Tishechkin, A.K., Winchester, N.N., Roubik, D.W.,

Aberlenc, H.-P., Bail, J., Barrios, H., Bridle, J.R., Castaño-Meneses, G., Corbara, B., Curletti, G., Duarte da Rocha, W., De Bakker, D., Delabie, J.H.C., Dejean, A., Fagan, L.L., Floren, A., Kitching, R.L., Medianero, E., Miller, S.E., de Oliveira, E.G., Orivel, J., Pollet, M., Rapp, M., Ribeiro, S.P., Roisin, Y., Schmidt, J.B., Sørensen, L., Leponce, M., 2012. Arthropod diversity in a tropical forest. Science 338, 1481–1484.

Bernard, E., 2001. Vertical stratification of bat communities in primary forests of Central Amazon, Brazil. J. Trop. Ecol. 17, 115–126.

Boncaraglio, G., Saino, N., 2007. Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis, Functional Ecology 21, 134–142.

Bongers, F., Meer van der, P.J., Théry, M., 2001. Scales of ambient light variation. In: Bongers, F., Charles-Dominique, P., Forget, P.M., Théry, M. (Eds.), Nouragues. Dynamics and plant-animal interactions in a neotropical rainforest. Kluwer Academic Publishers, Netherlands, pp. 19–29.

Bormpoudakis, D., Sueur, J., Pantis, D.J., 2013. Spatial heterogeneity of ambient sound at the habitat type level: ecological implications and applications. Landsc. Ecol. 28, 495–506.

Carson, W.P., Schnitzer, S.A., 2008. Tropical Forest Community Ecology. Wiley-Blackwell, Oxford, UK.

Charles-Dominique, P., 2001. Scales of ambient light variation. In: Bongers, F., Charles-Dominique, P., Forget, P.M., Théry, M. (Eds.), Nouragues. Dynamics and Plant–Animal Interactions in a Neotropical Rainforest. Kluwer Academic Publishers, Netherlands, pp. 1–9.

Chek, A.A., Bogart, J.P., Loughheed, S.C., 2003. Mating signal partitioning in multi-species assemblages: a null model test using frogs. Ecol. Lett. 6, 235–247.

Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S., Sueur, J., 2012. Monitoring animal diversity using acoustic indices: implementation in a temperate woodland. Ecol. Indic. 13, 46–54.

Diwakar, S., Balakrishnan, R., 2007a. The assemblage of acoustically communicating crickets of a tropical evergreen forest in southern India: call diversity and diel calling pattern. Bioacoustics 16, 113–135.

Diwakar, S., Balakrishnan, R., 2007b. Vertical stratification in an acoustically communication Ensiferan assemblage of a tropical evergreen forest in southern India. J. Trop. Ecol. 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. Biodivers. Conserv. 16, 4081–4093.

Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Softw. 22, 1–20.

Ellinger, N., Hödl, W., 2003. Habitat acoustics of a neotropical lowland rainforest. Bioacoustics 13, 297–321.

Ey, E., Fischer, J., 2009. The "acoustic adaptation hypothesis" – a review of the evidence from birds, anurans and mammals. Bioacoustics 19, 21–48.

Farina, A., Lattanzi, E., Malavasi, R., Pieretti, N., Piccioli, L., 2011a. Avian soundscapes and cognitive landscapes: theory, application and ecological perspectives. Landsc. Ecol. 26, 1257–1267.

Farina, A., Pieretti, N., Piccioli, L., 2011b. The soundscape methodology for long-term bird monitoring: a Mediterranean Europe case-study. Ecol. Inform. 6, 354–363.

Gasc, A., Sueur, J., Jiguet, F., Devictor, V., Grandcolas, P., Burrow, C., Depraetere, M., Pavoine, S., 2013a. Assessing biodiversity with sound: Do acoustic diversity indices reflect phylogenetic and functional diversities of bird communities? Ecol. Indic. 25, 279–287.

Gasc, A., Sueur, J., Pavoine, S., Pellens, R., Grandcolas, P., 2013b. Biodiversity sampling using a global acoustic approach: contrasting sites with micro-endemics in New Caledonia. PLoS ONE 8 (5), e65311.

Giam, X., Scheffers, B.R., Sodhi, N.S., Wilcove, D.S., Ceballos, G., Ehrlich, P.R., 2012. Reservoirs of richness: least disturbed tropical forests are centres of undescribed species diversity. Proc. R. Soc. B 279, 67–76.

Gottsberger, B., Gruber, E., 2004. Temporal partitioning of reproductive activity in a neotropical anuran community. J. Trop. Ecol. 20, 271–280.

Gower, C., 1966. Some distance properties of latent root and vector methods used in multivariate analysis. Biometrika 53, 325–338.

Grimaldi, M., Riéra, B., 2001. Scales of ambient light variation. In: Bongers, F., Charles-Dominique, P., Forget, P.M., Théry, M. (Eds.), Nouragues. Dynamics and Plant–Animal Interactions in a Neotropical Rainforest. Kluwer Academic Publishers, Netherlands, pp. 9–18.

Hammer, O., Barrett, N., 2001. Techniques for studying the spatiotemporal distribution of animal vocalization in tropical wet forests. Bioacoustics 12, 21–35.

Henwood, K., Fabrick, A., 1979. A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. Am. Nat. 114, 260–274.

Hödl, W., 1977. Call differences and calling site segregation in anuran species from Central Amazonian floating meadows. Oecologia 28, 351–363.

Jain, M., Balakrishnan, R., 2012. Does acoustic adaptation drive vertical stratification? A test in a tropical cricket assemblage. Behav. Ecol. 23, 343–354.

Joo, W., Gage, S.H., Kasten, E.P., 2011. Analysis and interpretation of variability in soundscapes along an urban rural gradient. Landsc. Urban Plan. 103, 259–276.

Kasten, E.P., Gage, S.H., Fox, J., Joo, W., 2012. The remote environmental assessment laboratory's acoustic library: an archive for studying soundscape ecology. Ecol. Inform. 12, 50–67.

Krause, B., 1998. Into a Wild Sanctuary: A Life in Music and Natural Sound. Heyday Books, Berkeley, USA.

Krause, B., 2008. Anatomy of the soundscape: evolving perspectives. J. Audio Eng. Soc. 56, 73–80.

Krause, B., Gage, S., Joo, W., 2011. Measuring and interpreting the temporal variability in the soundscape at four places in Sequoia National Park. Landsc. Ecol. 26, 1247–1256.

Laiolo, P., Tella, J.L., 2006. Landscape bioacoustics allow detection of the effects of habitat patchiness on population structure. Ecology 87, 1203–12014.

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, D.S., Watt, A.D., 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391, 72–75.

Lüddecke, H., Amézquita, A., Bernal, X., Guzmàn, F., 2000. Partitioning of vocal activity in a neotropical highland-frog community. Stud. Neotropical Fauna Environ. 35, 185–194.

Luther, D., 2009. The influence of the acoustic community on songs of birds in a neotropical rain forest. Behav. Ecol. 20, 864–871.

Madigosky, S.R., 2004. Tropical microclimatic considerations. In: Lowman, M.D., Rinker, H.B. (Eds.), Forest canopies. Elsevier Academic Press, Burlington, USA, pp. 24–48.

Manni, F., Guérard, E., Heyer, E., 2004. Geographic patterns of genetic, morphologic, linguistic variation: how barriers can be detected by using Monmonier's algorithm. Hum. Biol. 76, 173–190.

Marten, K., Quine, D., Marler, P., 1977. Sound transmission and its significance for animal vocalization. II. Tropical forest habitats. Behav. Ecol. Sociobiol. 2, 291–302.

Matsinos, Y.G., Mazaris, A.D., Papadimitriou, K.D., Mniestris, A., Hatzigiannidis, G., Maioglou, D., Pantis, J.D., 2008. Spatio-temporal variability in human and natural sounds in a rural landscape. Landsc. Ecol. 23, 945–959.

Mazaris, A., Kallimanis, A., Chatzigianidis, G., Papadimitiou, K., Pantis, J.D., 2009. Spatio-temporal analysis of an acoustic environment: interactions between landscape features and sounds. Landsc. Ecol. 24, 817–831.

McNamara, J.M., Mace, R.H., Houston, A.I., 1987. Optimal daily routines of singing and foraging in a bird singing to attract a mate. Behav. Ecol. Sociobiol. 20, 399–405.

Meer van der, P.J., Bongers, F., 2001. Tree-falls and canopy gaps: patterns of natural disturbance. In: Bongers, F., Charles-Dominique, P., Forget, P.M., Théry, M. (Eds.), Nouragues. Dynamics and Plant–Animal Interactions in a Neotropical Rainforest. Kluwer Academic Publishers, Netherlands, pp. 243–250.

Monmonier, M., 1973. Maximum-difference barriers: an alternative numerical regionalization method. Geogr. Anal. 3, 245–261.

Morton, E.S., 1975. Ecological sources of selection on avian sounds. Am. Nat. 109, 17–34.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca da, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Nadkarni, N.M., 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. Am. Zool. 34, 70–78.

Pearson, D.L., 1971. Vertical stratification of birds in a tropical dry forest. Condor 73, 46–55.

Pekin, B.K., Jung, J., Villanueva-Rivera, L.J., Pijanowski, B.C., Ahumada, J.A., 2012. Modeling acoustic diversity using soundscape recordings and LIDAR-derived metrics of vertical forest structure in a neotropical rainforest. Landsc. Ecol. 27, 1513–1522.

Pieretti, N., Farina, A., Morri, F.D., 2010. A new methodology to infer the singing activity of an avian community: the Acoustic Complexity Index (ACI). Ecol. Indic. 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., 2011a. Sounscape ecology: the science of sound in the landscape. Bioscience 61, 203–216.

Pijanowski, B.C., Farina, A., Gage, S.H., Dumyahn, S., Krause, B.L., 2011b. What is soundscape ecology? An introduction and overview of an emerging new science. Landsc. Ecol. 26, 1213–1232.

Planqué, R., Slabbekoorn, H., 2008. Spectral overlap in songs and temporal avoidance in a Peruvian bird assemblage. Ethology 114, 62–271.

Poncy, O., Sabatier, D., Prévost, M.F., Hardy, I., 2001. The lowland high rainforest: structure and tree species diversity. In: Bongers, F., Charles-Dominique, P., Forget, P.M., Théry, M. (Eds.), Nouragues. Dynamics and Plant–Animal Interactions in a Neotropical Rainforest. Kluwer Academic Publishers, Netherlands, pp. 31–46.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. Am. Nat. 132, 652–661.

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, Canada, pp. 201–211.

Rao, C.R., 1964. The use and interpretation of principal component analysis in applied research. Sankhya A 26, 329–359.

Richards, P.W., 1996. The tropical rain forest. Cambridge University Press, Cambridge, UK.

Richards, D.G., Wiley, R.H., 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest—implications for animal communication. Am. Nat. 115, 381–399.

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 rainforest canopy. In: Stork, N.E., Adis, J.A., Dinham, R.K. (Eds.), Canopy and Arthropods. Chapman and Hall, London, UK, pp. 442–452.

Savage, J.M., 2002. The Amphibians and Reptiles of Costa Rica, A Herpetofauna Between Two Continents, Between Two Seas. The University of Chicago Press, Chicago, USA.

Schafer, R.M., 1977. Tuning of the World. Alfred Knopf, New York, USA.

Schmidt, A.K., Römer, H., Riede, K., 2013. Spectral niche segregation and community organization in a tropical cricket assemblage. Behav. Ecol. 24, 470–480.

Schwartz, J.J., 1994. Male advertisement and female choice in frogs: recent findings and new approaches to the study of communication in a dynamic acoustic environment. Am. Zool. 34, 616–624.

Shaw, D.C., 2004. Vertical organization of canopy biota. In: Lowman, M.D., Rinker, H.B. (Eds.), Forest Canopies. Elsevier Academic Press, Burlington, USA, pp. 73–101.

Shumway, R.H., Stoffer, D.S., 2006. Time Series Analysis and Its Applications with R Examples. Springer, New York, USA.

Slabbekoorn, H., 2004. Habitat-dependent ambient noise: consistent spectral profiles in two African forest types. J. Acoust. Soc. Am. 116, 3727–3733.

Smith, A.P., 1973. Stratification of temperate and tropical forests. Am. Nat. 107, 671–682.

Southworth, M., 1969. The sonic environment of cities. Environ. Behav. 1, 49–70.

Sueur, J., 2002. Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera: Cicadomorpha: Cicadidae). Biol. J. Linn. Soc. 75, 379–394.

Sueur, J., Pavoine, S., Hamerlynck, O., Duvail, S., 2008a. Rapid acoustic survey for biodiversity appraisal. PLoS ONE 3 (12), e4065.

Sueur, J., Aubin, T., Simonis, C., 2008b. Seewave: a free modular tool for sound analysis and synthesis. Bioacoustics 18, 213–226.

Sueur, J., Gasc, A., Grancolas, P., Pavoine, S., 2012. Global estimation of animal diversity using automatic acoustic sensors. In: Le Gaillard, J.F., Guarini, J.M., Gaill, F. (Eds.), Sensors for Ecology: Towards Integrated Knowledge of Ecosystems. CNRS Institut Ecologie et Environnement, Paris, France, pp. 99–117.

Terborgh, J., 1985. The vertical component of plant species diversity in temperate and tropical forests. Am. Nat. 126, 760–777.

Towsey, M., Planitz, B., Nantes, A., Wimmer, J., Roe, P., 2012. A toolbox for animal call recognition. Bioacoustics 21, 107–125.

Truax, B., 1978. The World Soundscape Project's Handbook for Acoustic Ecology. ARC Publications, Vancouver, USA.

Villanueva-Rivera, L.J., Pijanowski, B.C., 2012. Pumilio: a web-based management system for ecological recordings. Bulletin of the Ecology Society of America 93, 71–81.

Villanueva-Rivera, L., Pijanowski, B., Doucette, J., Pekin, B., 2011. A primer of acoustic analysis for landscape ecologists. Landsc. Ecol. 26, 1233–1246.

Whitmore, T.C., 1997. Tropical forest disturbance, disappearance and species loss. In: Laurance, W.F., Bierregaard, R.O. (Eds.), Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago, USA, pp. 3–12.

Wimmer, J., Towsey, M., Planitz, B., Williamson, I., Roe, P., 2013. Analysing environmental acoustic data through collaboration and automation. Futur. Gener. Comput. Syst. 29, 560–568.

Wolda, H., 1989. Seasonal cues in tropical organisms. Rainfall? Not necessarily! Oecologia 80, 437–442.

Wright, S.J., 2005. Tropical forests in a changing environment. Trends Ecol. Evol. 20, 553–560.

Young, A.M., 1972. Cicada ecology in a Costa Rican tropical rain forest. Biotropica 4, 152–159.

Young, A.M., 1981. Temporal selection for communicatory optimization: the dawn dusk chorus as an adaptation in tropical cicadas. Am. Nat. 117, 826–829.