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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 $\times$ 2 vertical levels $\times$ 4 recordings/h $\times$ 24 h $\times$ 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).