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Changes in the acoustic structure and composition along a tropical elevational gradient

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Abstract

Elevational gradients influence the distribution and composition of animal species and can provide useful information for the development of conservation strategies in the context of climate change. Despite an increase in studies of species diversity along elevational gradients, there is still a lack of information about community responses to environmental gradients, in part because of the logistical limitations of sampling multiple taxa simultaneously. One solution is to use passive acoustic monitoring (PAM) to acquire and analyze information from different animal taxa simultaneously along an entire elevational gradient. To improve our understanding of how environmental gradients influence patterns of animal communities and to test the relationship between soundscapes and animal composition we investigated how variation in bird and anuran composition affect the acoustic structure and composition of the soundscapes along an elevation gradient. We used PAM deploying portable acoustic recorders along three elevational transects in the Luquillo Mountains (LM), Puerto Rico. We found that elevation plays a major role in structuring the acoustic community and that the soundscape composition reflected the same patterns of anuran and bird distribution and composition along the elevational gradient. This study shows how different animal taxa respond to environmental gradients and provide strong evidence for the use of soundscapes as a tool to describe and compare species distribution and composition across large spatial scales.

Introduction

The distribution of species diversity along elevational gradients has long been a topic of great interest for ecologists and biogeographers who have postulated important ecological concepts such as niche theory (Grinnell, 1917), life zones (Merriam and Stejneger, 1890) and community assembly (Whittaker, 1960). Ecological community characteristics, such as species occurrence, abundance, richness, composition and behavior are known to change along these gradients, often in very predictable manner (Lomolino, 2001; McCain and Grytnes, 2010). For instance, a recent meta-analysis examining diversity across 443 elevational gradients around the world found that overall diversity tends to be higher at middle elevations (Guo et al., 2013). A renewed interest in patterns of elevational diversity has recently emerged because of the increasing importance of human-driven processes, such as climate change, that are altering animal abundance and distribution, especially in mountains (Parmesan and Yohe, 2003). One of the most conspicuous signals of climate change, for example, is the upward shift of the elevational distributions of species, which can lead to disassembly of animal communities with possible impacts on the ecosystem function (Sheldon et al., 2011). Despite an increase in studies of species diversity along elevational gradients, there is still a lack of information about community responses to environmental gradients. The origin of this problem derives in part from logistical difficulties associated with sampling multiple taxonomic groups simultaneously. Nevertheless, the understanding of how environmental gradients influence the composition of animal communities may improve our conservation efforts in climate change scenarios.

Acoustic ecology, or ecoacoustic, can help us to study animal communities at large temporal and spatial scales by monitoring environmental sounds. Acoustic signals produced by animals are biological traits associated with animal reproduction, territory defense, and feeding (Bradbury and Vehrencamp, 1998; Marler and Slabbekoorn, 2004). These acoustic signals are species-specific (Alstrom and Ranft, 2003), and can function as a reliable proxy for animal occurrence, abundance, and species richness (Aide et al., 2017). Acoustic signals may also be produced by abiotic components of the landscapes *e.g.*, rain, thunder, running water and wind, which can provide additional information on environmental conditions. In addition, acoustic signals are also produced by human activities. The sound of aircrafts and cars can represent a considerable proportion of acoustic activity, particularly in urban environments. Aircraft sounds can be more evident in quiet areas than in cities where it is masked by the prominent road traffic. The combination of these sounds (*i.e.*, soundscape) can be used to characterize a particular site, and this combination often provides a unique signature of the habitat or landscape. For instance, unique patterns of temporal and spectral characteristics from ambient sounds were found at specific locations, both in tropical and temperate ecosystems (Bormpoudakis et al., 2013; Pieretti et al., 2015). The idea that each site has an acoustic signature is a basic concept in soundscape ecology (Pijanowski et al., 2011), and this provides an alternative approach for monitoring biodiversity at large spatial and temporal scales (Figure 1).

Recently, several studies compared spatial and temporal variation of the acoustic signals in a site to determine if soundscapes are indeed good indicators of the animal community. For instance, some acoustic indices have been successfully used to demonstrate differences in soundscapes between sites that vary in terms of species richness, functional diversity or phylogenetic diversity (Depraetere et al., 2012;

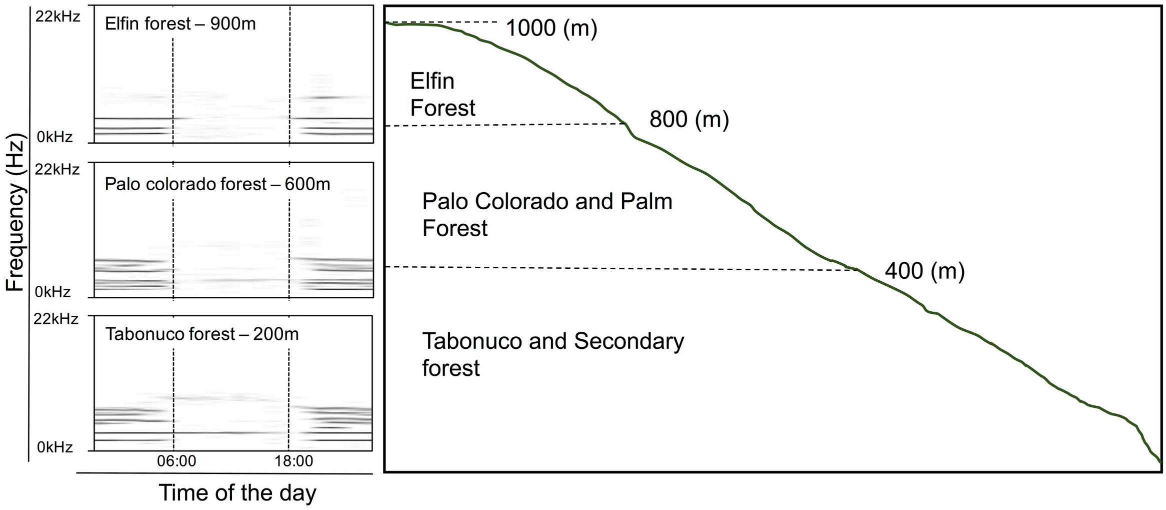

Figure 1. Variation of soundscapes along an elevational gradient.

A sample of soundscapes from three forests types at different elevations in the LM, Puerto Rico.

Gasc et al., 2013; Towsey et al., 2014). In Costa Rica, acoustic diversity was also correlated with the complexity of vertical forest structure (Pekin et al., 2012), an environmental feature known to influence animal communities (Verschuyl et al., 2008). In Italy, avian acoustic community were associated with different habitat types along an elevation gradient (Farina et al., 2015). In addition, soundscape acoustic richness was correlated with increasing distance from a gas exploration platform in Peru, which in turn was associated with an increase in avian species richness (Deichmann et al., 2017). These studies show how PAM and soundscape analyses can improve our understanding of animal communities, and enhance our ability to manage entire ecosystems. Nevertheless, it is still unclear how environmental gradients influence acoustic patterns of animal communities and more importantly how these changes in acoustic patterns are related with changes in species composition. To address these limitations, we aim to solve the following two questions: 1) How elevation influence bird, anuran and soundscape composition? 2) What is the relationship between animal community composition and soundscape structure? To our knowledge this is the first study to quantitatively compare the elevational variation of acoustic signals (Lomolino et al., 2015), an informative ecological trait.

Methods

Study area

The study was conducted in the LM in north-eastern Puerto Rico (Figure 2). Most of the LM are protected by the El Yunque National Forest (EYNF), also known as the Luquillo Experimental Forest, which is the largest protected area (115 km^2) with primary forest in Puerto Rico (Lugo, 1994) and

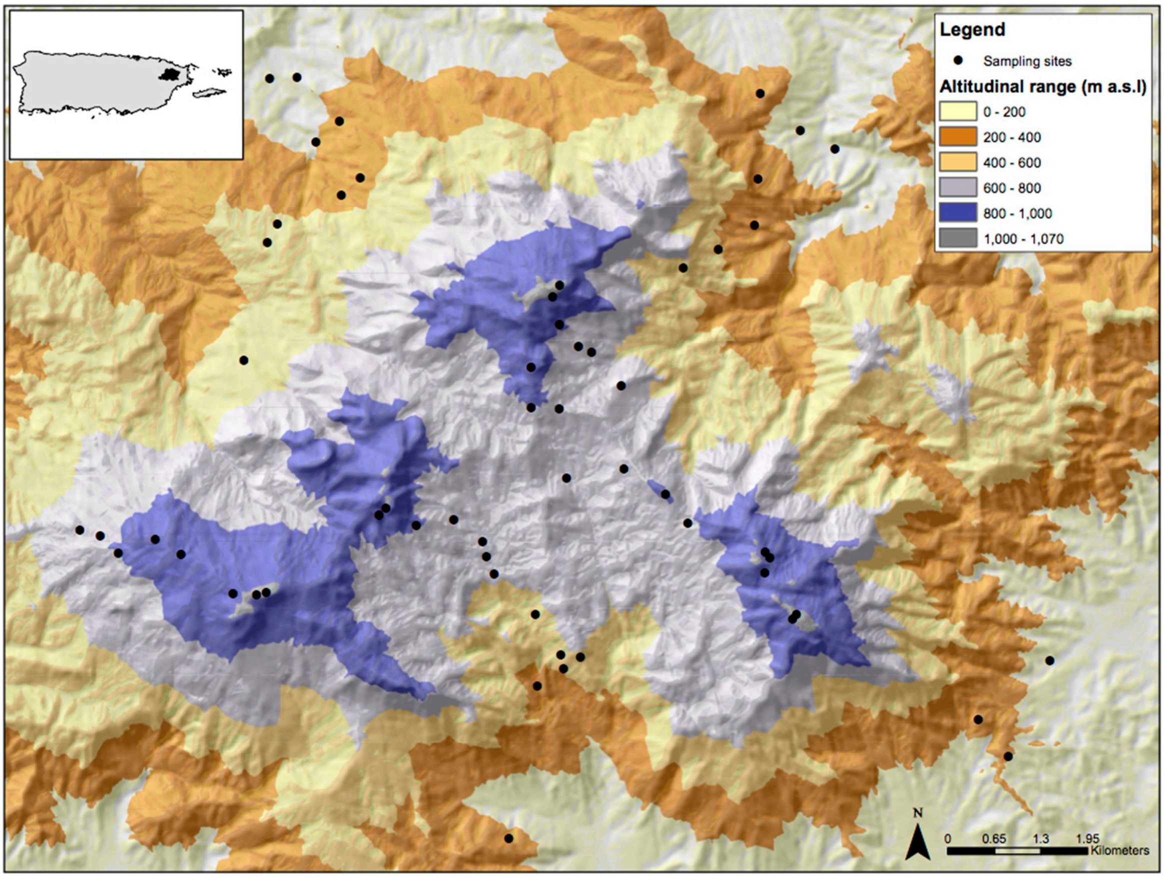

Figure 2. Map of LM and its location in NE Puerto Rico. Different colors represent different elevation bands (m a.s.l.).

spans an elevational range from 100 to 1,074 m. This protected site is ideal for investigating patterns of species diversity along an elevational gradient because: 1) There have been no or only minor direct effects of land-use change during the last 100 years in the LM; 2) The LM comprises three main peaks (Pico del Este – 1,051 m, Pico del Yunque – 1,050 m, Pico del Toro – 1,074 m) providing several elevational gradients; and 3) There is extensive research documenting abiotic and biotics changes along these elevational gradients. For instance, the LM elevational gradient has a positive relationship with rainfall, runoff, humidity, cloud cover and wind velocity (Briscoe, 1966; García-Martinó et al., 1996; Weaver and Gould, 2013) and a negative relationship with temperature, forest growth, and canopy height (Weaver and Murphy, 1990; Weaver, 2000; Wang et al., 2003; Weaver and Gould, 2013). Average temperature declines with elevation from ~26.5°C in the lowlands to ~20°C at the mountain top (Waide et al., 2013). Average annual rainfall ranges from 2,450 mm yr^{-1} at lower elevations to over 4,000 mm yr^{-1} at higher-elevation sites (Waide et al., 2013). There are four main forest types along the elevational gradient in EYNF: Tabonuco forest which is dominated by *Dacryodes excelsa* and occurs between 150 and 600 m a.s.l., Palo Colorado forest is dominated by *Cyrilla racemiflora*, and occurs between 600 and 950 m a.s.l, Elfin forest which is dominated by *Tabebuia rigida* and *Eugenia boriquensis* and occurs above 950 m a.s.l., and Sierra Palm forest, which is dominated by *Prestoea montana* and can occur anywhere along the elevational gradient. In addition to the four major forest types, EYNF has a considerable area in old secondary forest (>40 yr) that occurs mostly at low elevations near the border of the reserve. In addition, the distributions of animals are also strongly affected by this elevation gradient (Gould et al., 2006; Weaver and Gould, 2013; González et al., 2007; Gould et al., 2008; Willig et al., 2011; Brokaw et al., 2012; Campos-Cerqueira and Aide, 2016).

Surveys

The acoustic data were collected from 58 sampling sites in the LM along three elevational transects (85–1,047 m, ~20 sampling sites per elevational transect) between March and May of 2015 (Table S1). The elevational transects took advantage of roads and trails, but recorders were placed more than 200 m from any road. Each elevational transect started in the lowlands and reached one of the three main mountain peaks of the LM (East Peak, Pico del Toro, El Yunque Peak). Along each elevational transect, two recorders, separated by at least 200 m, were deployed at 100-m elevation interval in such way that recordings were collected simultaneously for an entire elevational gradient. Recorders collected data at each site for approximately one week (~1,000 recordings per site), and were then moved to another elevation transect.

ARBIMON portable recorders (LG smartphone enclosed in a waterproof case with an external connector linked to a Monoprice condenser microphone) running the ARBIMON Touch application (https://goo.gl/CbBavY) were used to collect the audio recording. Recorders were placed on trees at the height of 1.5 m and programmed to record 1 min of audio every 10 min for a total of 144, 1-min recordings per day at a sampling rate of 44.1 kHz. Microphones have a flat response between 50 Hz to 20 kHz and a sensitivity of –45 dB ± 2 dB.

All recordings were analyzed, permanently stored, and are available in the ARBIMON project (arbimon.sieve-analytics.com/project/elevation/dashboard) along with detail information about each site (*e.g.*, elevation, site coordinates, number of recordings and dates) (Table S1). We visually inspected all recordings and eliminated damaged recordings (*e.g.*, microphone malfunction). We did not remove recordings containing sounds from wind, rain, and river (running water) prior to the analyses since we were interested in characterizing the entire acoustic system of each site (Towsey et al., 2014). We also did not use a high pass filter in the recordings. There were no constant anthropogenic sounds in our recordings since recorders were deployed at least 200 m from any road and in a natural reserve. Occasional anthropogenic sounds were mostly restricted to aircraft noise.

Acoustic processing

To analyze the soundscapes for each site, we used the ARBIMON platform. The soundscape analysis tool allows the user to define the time scale of aggregation (*e.g.*, hour, month, or year), the frequency bin size, and the minimum threshold for the amplitude of a sound peak (*i.e.*, intensity). We aggregated recordings at the time scale of hour of day (24 hours), used a frequency bin size of 172 Hz, and an amplitude filtering threshold of 0.01. This resulted in a three dimensional (x = hour, y = acoustic frequency, z = proportion of all recordings in each time/frequency bin with a peak >0.01 amplitude) matrix of acoustic activity with a total of 3,072 time/frequency bins (24 hours × 128 frequency bins).

To calculate the amplitude, we used the meanspec (f = 44,100, wl = 256, wn = "hanning") and fpeaks (threshold = 0.1, freq = 172) function from the seewave package in R (Sueur et al., 2008a). The value of each peak was normalized using the maximum amplitude value within all recordings in the soundscape (*i.e.*, site), and thus values ranged from 0 to 1. The number of frequency peaks was determined by counting the number of recordings with a peak within each of the 128 frequency bins that were equal or greater than the amplitude threshold. To control for the different number of recordings in each site and each time interval (*i.e.*, hour), we divided the number of recordings with a peak in each time/frequency class by the total number of recordings collected during each hourly interval.

The presence and absence of frog and bird species at each specific site was determined by listening to a subset of recordings from each site and then a visually inspecting the spectrograms of all remaining recordings. To detect birds, the first author (MCC) listened to all recordings from 05:30 to 10:00 hr, and then, one recording every hour (*e.g.*, 11:00 hr, 12:00 hr, 13:00 hr) until 18:00 hr on the first survey day for each sampling site (*n* = 35, 1-min recordings/site) for a total of 2,100 validated recordings, and 2) with a preliminary bird list from the first survey day from each location, MCC visually scanned all spectrograms of recordings from 05:30 to 18:00 hr for all subsequent days, thus an additional ~41,000 1 minute recordings were evaluated. During this process, MCC listened to every recording that included an unidentified vocalization for the site. Vocalizations that could not be identified by MCC were reviewed by two Puerto Rico avifauna experts. To detect frogs, the first author used a similar approach, but focused on recordings between 18:00 and 06:00 hr.

To evaluate the effect of the elevational gradient on soundscapes and on the distribution of anurans and birds we created an ordination using a non-metric multidimensional scaling (NMDS) and the Bray-Curtis dissimilarity with the *MetaMDS* function in the *Vegan* package (Oksanen, 2015). Ordination of soundscapes were derived from the relative frequency of the 3,072 time/frequency bins, whereas ordination for anuran and bird species were based on presence/absence data. We removed time/frequency bins that were not detected at any site. To plot the ordination results, we applied the *ordisurf* function from the *Vegan* package in R (Oksanen, 2015). This function fits an environmental surface using thin late splines in two dimensions following a generalized additive model (GAM) with a selection of smoothness. We chose the restricted maximum likelihood (REML) method for smooth selection. The results of the GAM models are used to predict and plot the surface, providing a visual reference of the environmental gradient to the location of each time/frequency bin as also for each anuran and bird species. The function *envfit* was used to access the importance of elevation on the ordination based on a permutation test with 9,999 iterations.

In addition to the ordination analysis we also ran a classification to determine if groups existed along the elevational gradient, both for the soundscapes data and for the anuran and bird distribution data. For the classification, we create hierarchical clusters using Bray-Curtis distance among sites using the average distance for clustering method from the *Vegan* package. To determine the optimal number of clusters we used the average silhouette method (Rousseeuw, 1987) from the R Package *Cluster*. The classification into different groups was further inspected using boxplots. In addition, we used PERMANOVA (Anderson, 2001) with the functions *adonis* and *betadisper* with 9,999 permutations to test for significant difference of means between the groups created in the cluster analyses and homogeneity within each group (beta diversity), respectively. To summarize the community composition in each group detected by cluster analyses, both for the soundscapes data and the anuran and bird distribution data, we used the function *indval* from the *labdsv* package in R. The function *indval* combines species occurrence frequencies in groups and mean abundance to find species that are significantly concentrated into specific groups. Anuran and bird species were classified as a significant indicator only if the probability of finding higher indicator value in random permutations was < 0.005. In contrast, given the large numbers of time/frequency bins, we chose to decrease this threshold to 0.001 in the soundscape data set. Once we identified the acoustic species indicators of each cluster, we selected the corresponding regions of the soundscape in which the acoustic species occurred and inspected the recordings associated with that region to determine which animal species were responsible for that particular acoustic activity.

Results

Soundscape composition

Soundscape composition was best visualized by an NMDS with two dimensions (stress = 0.15) and showed a clear change in the composition of time/frequency bins along the elevation gradient (Figure 3A). A significant effect of elevation on the ordination of the time/frequency bins was found by both the *ordisurf* (REML = 352.17, df = 7.6, R2 = 0.90, $p < 0.001$), and *envfit* function (R2 = 0.89, $p < 0.001$).

Cluster analyses identified two groups: the first group encompasses the majority of sites below 700 meters (low elevation sites), and the second group encompasses the majority of sites above 700 meters (high elevation sites) (Figure 4A). Overlap between the two groups occurred mostly among sites at 600 and 700 meters (Figure 5A). The two groups accounted for 13% of the variation in the data ($p < 0.001$). The low variation explained by the difference between the two groups may be attributed to the overall high heterogeneity of species composition (F = 10.71, $p = 0.001$) or high beta diversity. This result means that there is a core acoustic community common to both groups, but sites at the extremes of the elevation profile are probably responsible for increasing beta diversity.

The time/frequency bins that characterize the low elevation cluster were formed by two main groups of frequencies during the night (17:00 to 05:00) and two groups during the day (06:00 to 18:00) (Figure 6; Table 1). During the night, the cluster from low elevation sites consisted of:

A) three time/frequency bins from 516 to 1,032 Hz, which consisted of background noise of river and some vocalizations of *Megascops nudipes*;

B) three time/frequency bins ranging from 2,408 to 2,924 Hz, which consisted mostly of the "qui" note from the common coqui frog (*Eleutherodactylus coqui*);

C) 15 time/frequency bins ranging from 4,128 to 6,708 Hz, which consisted mostly of unidentified insect species and the vocalization of the Grass coqui frog (*Eleutherodactylus brittoni*).

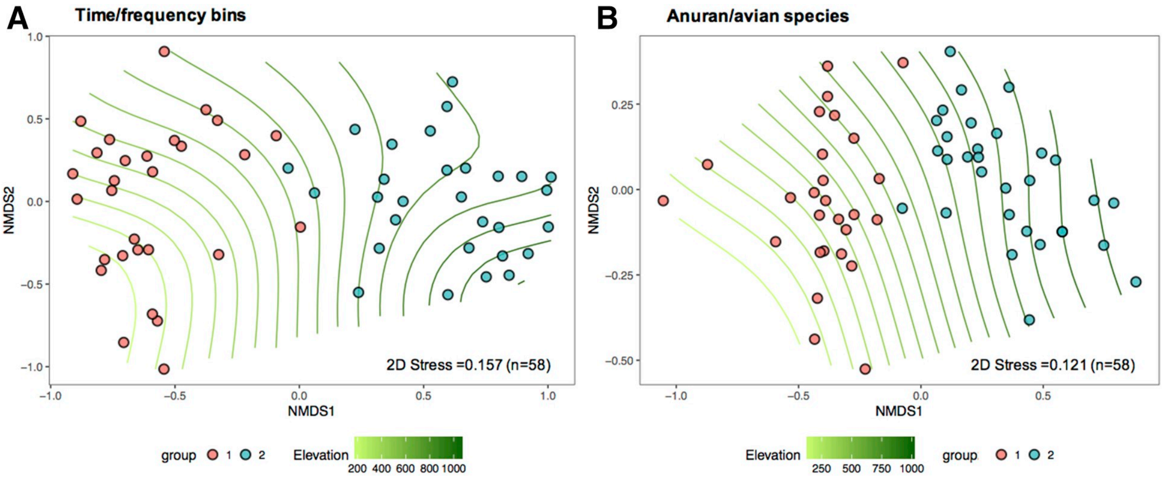

Figure 3. Plot of sampling sites based on time/frequency bins (A) and anuran/avian species (B) in ordination space overlaid on a fitted environmental surface (elevation contour lines).

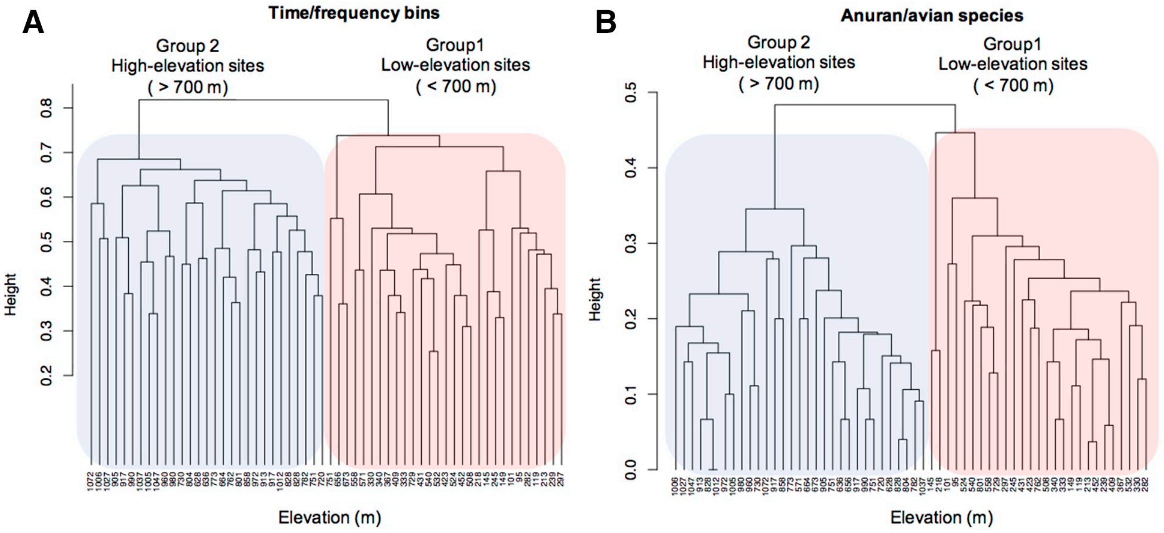

Figure 4. Dendrograms resulting from hierarchical clustering based on Bray-Curtis dissimilarity (values indicated on the left axis of dendrogram) using a group average method.

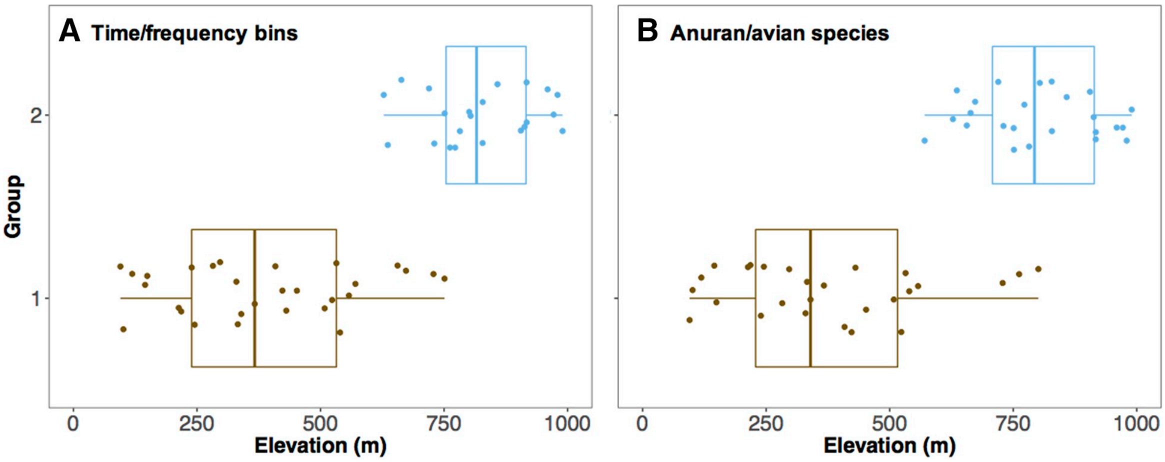

Figure 5. Boxplot showing the distribution of data in each group according to results of cluster analyses.

During the day, groups of frequencies from low elevation sites consisted of:

A) two time/frequency bins ranging from 1,548 to 1,892 Hz, which consisted of the "co" note of *E. coqui*;

B) four time/frequency bins ranging from 2,408 to 3,096 Hz, which consisted mostly of avian vocalizations of the black-whiskered vireo (*Vireo altiloquus*);

C) three time/frequency bins ranging from 8,256–9,632 Hz, which consisted mostly of vocalization of the Bananaquit bird (*Coereba flaveola*).

In contrast, species that best indicate the high elevation cluster was formed by four groups mostly predominant during the night and all of them derived from frog species:

A) two time/frequency bins ranging from 1,204 to 1,376 Hz, which consisted primarily of the "co" note of *E. coqui*;

B) three time/frequency bins ranging from 1,892–2,408 Hz, which consisted mostly of the "qui" notes from *E. coqui* and *E. portoricensis*;

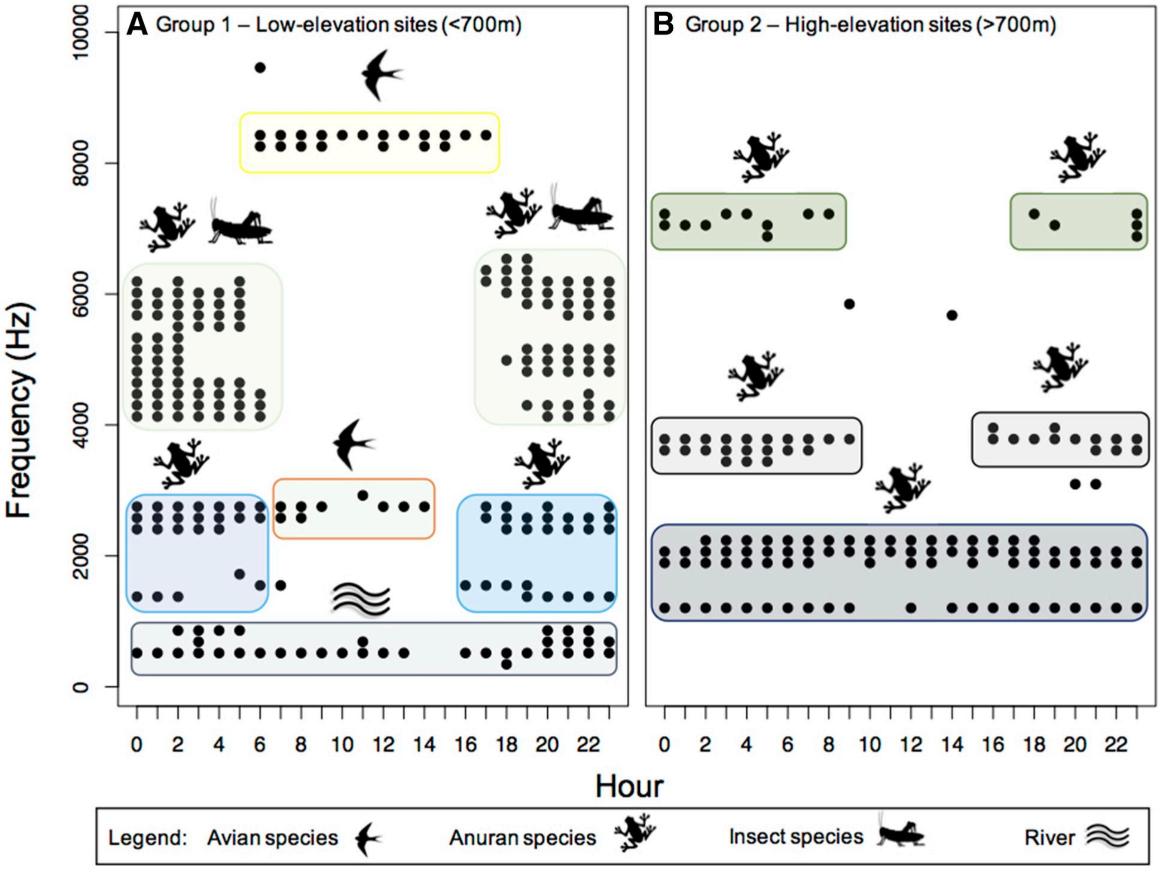

Figure 6. Plot of time/frequency bins that best indicate the two groups created by cluster analyses.

Table 1. Summary of frequency bins and their corresponding soundscape component that characterize clusters from low and high elevations.

Low elevation		High elevation	
Frequency bins	Composition	Frequency bins	Composition
516–1,032 Hz/night	River	1,204–1,376 Hz/night	*E. coqui*
	Megascops nudipes		
2,408–2,924 Hz/night	*E. coqui*	1,892–2,408 Hz/night	*E. coqui*
			E. portoricensis
4,128–6,708 Hz/night	Insects	3,096–3,956 Hz/night	*E. unicolor*
	E. brittoni		
1,548–1,892 Hz/day	*E. coqui*	6,880–7,224 Hz/night	*E. gryllus*
2,408–3,096 Hz/day	*Vireo altiloquus*		
8,256–9,632 Hz/day	*Coereba flaveola*		

C) five time/frequency bins ranging from 3,096 to 3,956 Hz, which consisted primarily of the vocalization of *E. unicolor*;

D) three time/frequency bins ranging from 6,880 to 7,224 Hz, which consisted mostly of vocalization of *E. gryllus*.

Anuran and bird composition

Anuran and bird composition was best visualized by an NMDS with two dimensions (stress = 0.12) and showed a clear change in species composition along the elevational gradient (Figure 3B). A significant effect of elevation on the ordination of the time/frequency bins was found by both the *ordisurf* (REML = 361.01, df = 5.8, R2 = 0.84, $p < 0.001$) as also by the *envifit* function (R2 = 0.82, $p < 0.001$).

Cluster analyses identified two groups: the first group encompassed the majority of sites below 700 meters (low elevation sites), and the second group encompassed the majority of locations above 700 meters (high elevation sites) (Figure 4B). Overlap between the two groups occurred mostly among sites at 600 and 700 meters (Figure 5B). The two groups accounted for 38% of the variation in the data ($p < 0.001$) and there was high homogeneity between groups (F = 12, $p = 0.72$).

The indicator species that characterized the low elevation cluster included one anuran species (*E. brittoni*), and five bird species (*Coccyzus vieilloti*, *Megascops nudipes*, *Geotrygon montana*, *Icterus portoricensis*, *Turdus plumbeus*, and *Vireo altiloquus*). In contrast, the best indicators species in the high elevation cluster were three anuran species (*E. gryllus*, *E. unicolor*, *E. portoricensis*) and one bird species (*Setophaga angelae*).

Thirty-three bird species were detected in the recordings comprising 33% of the avifauna of the LM, and a maximum of 16 species was detected at two single sites (200 and 600 m) (Campos-Cerqueira et al., 2017). In contrast, we were able to detect all 12 anuran species that occur in the LM, and a maximum of seven species was detected at single site (800 m) (Campos-Cerqueira and Aide, 2017).

Discussion

Elevational gradients offer a reliable framework for understanding how biotic and abiotic factors influence biodiversity and can serve as a baseline for comparison of changes in species composition, population decline, range shifts and extinction risk (Parmesan, 2006; McCain and Grytnes, 2010; Campos-Cerqueira and Aide, 2017). However, despite an increased interest in elevational gradients, there are still few studies that consider the acoustic character of the environment (Lomolino et al., 2015), an important biological trait. Our study is the first to document how acoustic data offers biological information about the community structure and composition of vocal organisms along an elevational gradient. We found that elevation plays an important role in structuring the acoustic community and that the soundscape composition reflected the patterns of anuran and bird distribution and composition along the elevational gradient.

One possible limitation of our study is that we did not measured the propagation loss at each sampling site, which could lead to different detection range of the audio recorders along the elevational gradient. All sampling sites were in the same montane tropical forest, the best protected and preserved forest of Puerto Rico (*e.g.*, same land use type), and all recordings were collected in a relatively short period of time. In addition, the entire elevation gradient was sampled simultaneously using the same equipment which could help to minimize any potential bias related to environmental factors affecting the detection range of the audio recorders. Furthermore, given that our soundscapes comparisons agree with anuran and bird distribution that were obtained by modeling the elevation as a function of detection probability (Campos-Cerqueira et al., 2017; Campos-Cerqueira and Aide, 2017) we believe that any effect of differences in sampling area were minimal.

The change in acoustic composition detected via ordination and cluster analyses reflects our current knowledge about anuran and bird distributions along the elevational gradient (Campos-Cerqueira and

Aide, 2017; Campos-Cerqueira et al., 2017) and reveals that anurans are the main driver of the natural soundscape in the LM. The acoustic species that contributed to the low elevation grouping consisted of anuran and bird species (*E. brittoni* and *Vireo altiloquus*) that have higher occupancy ($\Psi > 0.50$) below 600 meters, whereas acoustic species that contributed to the high elevation grouping consisted of anuran species that have higher occupancy above 600 meters (*E. gryllus*, *E. unicolor*, *E. portoricensis*). Although the common coqui (*E. coqui*) appears as indicator species in both groups, the call of this species changes with elevation; high elevation sites have larger individuals and slower and lower frequency calls (Narins and Smith, 1986). Our soundscape data reflects this change in call characteristics along the elevational gradient, differentiating the common coqui vocalization into two distinct time/frequency bins. Interestingly, the widespread Bananaquit (*Coereba flaveola*), which occurred in all sites, was selected as an indicator species for the low elevation cluster. This apparent contradiction may be explained by changes in the species vocal behavior. Analyses of occupancy models (Campos-Cerqueira et al., 2017) show that although this species occurs across the entire elevational gradient, the detection probability decrease with elevation, a pattern that implies fewer vocalizations at high elevation sites.

Although anuran species are the main drivers of the natural soundscape in the LM, the analysis of the acoustic community reveals that birds, insects, and geological sounds also contribute to characterize the elevational gradient (Figure 6), highlighting the importance of studies at community and landscape levels. While insects have been systematically ignored in many biodiversity inventories, they can be the largest component of acoustic communities and thus may influence the evolution of avian and anuran acoustic signals. Different insect species were detected as indicator species in low elevation sites, demonstrating the effect of the elevation gradient on the distribution of invertebrates, thus supporting previous recommendations that insects should be incorporated in acoustic monitoring studies. In addition, sound produced by running water was also an indicator of sites at low elevations indicating a disproportional influence of geological factors shaping the acoustic community along the elevation gradient.

A comparison between fauna (anuran/bird species) composition and soundscape (time/frequency bins) composition revealed similar patterns along the elevational gradient. Both data sets indicate a significant effect of elevation and clustered the data into two groups corresponding to sites at low (<700 m) and high elevations (>700 m). Among the indicator species that contributed to the grouping of sites at high elevation *E. gryllus*, *E. unicolor* and *E. portoricensis* appear in both fauna and soundscape data sets whereas *E. brittoni*, *Megascops nudipes* and *Vireo altiloquus* appear as indicator species at low elevation sites in both data sets. The absence of the Bananaquit (*Coereba flaveola*) and the common coqui (*E. coqui*) as indicator species in the fauna dataset can be explained by the fact that both species occur at all sampling sites. The absence of *Coccyzus vieilloti*, *Geotrygon montana*, *Icterus portoricensis*, *Turdus plumbeus* and *Setophaga angelae* as indicator species in the soundscape ordination may be related to temporal sparse calling behavior of these species in contrast with the almost continuously vocal behavior of the Bananaquit and Black-whisked vireo for example.

One advantage of using PAM for studying elevational gradients of diversity is the ability to overcome sampling issues, such as differences in sampling effort and the spatial and temporal scale of the study (McCain and Grytnes, 2010). For example, relatively few studies span the full extent of available elevational gradients (Rahbek, 2005) and traditional sampling techniques rarely survey the entire elevational gradient simultaneously, adding a temporal sampling effect that must be accounted statistically. In addition, PAM surveys several animal taxa simultaneously, collecting data 24 hours for several days, without observer bias, and all recordings can be permanently stored functioning as "museum specimens." Our study demonstrates the applicability of PAM in acquiring biological information along the entire elevation gradient for different taxonomic groups simultaneously and provides a quantitative comparison between soundscapes and animal composition and distribution along an elevational gradient in a tropical mountain. Because elevational distribution affects species extinction risk (Gage et al., 2004; Sekercioglu et al., 2008), studies that provide a detailed quantitative description of changes in animal distribution and composition along elevational gradients are invaluable for improving predictions on species vulnerability to climate and land-use changes.

As more evidence emerges, demonstrating the relationship among soundscapes, animal community and habitat condition, the use of acoustic recording should become a more common tool for monitoring and managing ecosystems. For instance, acoustic indices were able to correctly differentiate sites with different logging histories in Costa Rica (Ström, 2013), sites with different levels of disturbance in Tanzania (Sueur et al., 2008b), sites with broad land cover types along a urban-rural gradient in Michigan (Joo et al., 2011), and sites with different patch size and patch connectivity in Australia (Tucker et al., 2014). Our study, along with these pioneering studies, show how PAM and soundscape analyses can provide a cost-effective way to rapidly assess the status of a landscape and to describe and compare animal communities across large spatial scales. From a conservation perspective, this is the first study to provide a quantitative assessment of soundscapes and fauna distribution and composition along an elevational gradient, which can now be used to improve conservation management. We argue that soundscape analyses can be utilized as a first exploratory analysis of the fauna community and that the structure, diversity and composition of frequency/time bins should be treated as another aspect of the biodiversity.

Supporting material

S1. Summary of acoustic data collection in the Luquillo Mountains, Puerto Rico. (DOCX)

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Competing interests

Marconi Campos and Mitch Aide are employees at Sieve Analytics Inc. Sieve Analytics is the company that host the ARBIMON platform.

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