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ORIGINAL RESEARCH

Ecoacoustics in the rain: understanding acoustic indices under the most common geophonic source in tropical rainforests

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Abstract

Rainfall is one of the most predominant geophonic sources in nature, and the major climatic phenomenon influencing species biology in tropical ecosystems. Although its effects on acoustic indices have been studied, rainfall is recognized as a nuisance factor affecting their estimation. Consequently, files with rainfall sounds are typically removed from ecoacoustic analyses. In tropical rainforests, where rainfall is a common and unpredictable event, its influence on acoustic indices needs to be explicitly examined before implementing acoustic passive monitoring. Using mixed-effects models we assessed the effect of different rainfall conditions on the direction and magnitude of the values of eight commonly used acoustic indices. We obtained 18336 1-min recordings from 28 sampling sites in a montane forest on the northern Andes of Colombia between May-July 2018. We identified 2867 1-min recordings containing light to heavy rainfall. We found that both rainfall occurrence and its variation in intensity were associated with increases in ACI, ADI, H, and M index values, and decreases in AEI, BI, NDSI, and NP values. The estimated indices exhibited differential sensitivity to rainfall, with M, NDSI, and NP showing higher differences associated with increasing frequency and intensity of rainfall. Regardless the direction of change in index values caused by rainfall, we found that the magnitude of variation depended on the index. For instance, ACI and BI indices showed low sensitivity and can be considered as reliable acoustic metrics, even during heavy intensity rainfall. In contrast, M, NDSI, and NP might lead to misleading inferences, if rainfall events are not considered during calculation. We stress the importance of careful interpretation of biological inferences based on these sensitive indices and encourage an explicit assessment of rainfall, particularly in short-term acoustic surveys in highly pluvious regions where rainfall is a conspicuous component of the soundscape.

Introduction

Ecoacoustics is a discipline that considers animal and environmental sounds as a reliable proxy for complexity in all ecological levels from species to communities (Towsey et al. 2014; Sueur and Farina 2015; Farina 2019). To date, ecoacoustic approaches have been developed for a variety of applications, including: monitoring of biodiversity and animal populations (Depraetere et al. 2012; Kalan et al. 2015; Harris et al. 2016; Wrege et al. 2017), assessment of habitat and landscape condition (Fuller et al. 2015; Burivalova et al. 2018), and tracking of changes in natural ecosystems (Krause and Farina 2016; Deichmann et al. 2017). A vast amount of acoustic data can now be collected with relative ease, which has increased focus on ecoacoustic methods and consideration of sound as a functional ecological attribute (Gasc et al. 2015; Fairbrass et al. 2017). The need for extraction of meaningful information from massive data sets has advanced the development of acoustic indices as tools for standardized quantification of sounds. Hence, acoustic information offers increased understanding of natural systems in different ecological contexts (Sueur et al. 2014; Gasc et al. 2015; Gómez et al. 2018).

Acoustic indices are designed to summarize the heterogeneity of the sounds occuring in a specific site. These act as a description of diversity at community and landscape levels, using the amplitude, spectral and temporal dimensions of the soundscape (Sueur et al. 2014; Towsey et al. 2014; Sueur 2018). In the ecoacoustic context, the soundscape refers to the sounds emanating from a landscape, including (1) biophony, or the biotic sounds; (2) geophony, or non-biological sounds from geophysical sources (i.e. wind, rain, thunder); and (3) anthrophony, i.e. sounds caused by human activities (Pijanowski et al. 2011). The usefulness of acoustic indices as biodiversity estimators and their relationships with biotic sounds is a central focus in ecoacoustics. However, consistent links between biodiversity and acoustic indices values have proved elusive (e.g. Fuller et al. 2015; Machado et al. 2017; Mammides et al. 2017). In contrast, although abiotic sounds (geophony and anthrophony) can affect acoustic indices values (Depraetere et al. 2012; Fuller et al. 2015; Fairbrass et al. 2017), the direction and magnitude of such effects have received little research attention and are not yet well understood (Towsey et al. 2014; Gasc et al. 2015).

Rainfall is one of the most common, variable, and recognizable abiotic sounds in nature (Sueur and Farina 2015; Bedoya et al. 2017). As an acoustic event, rainfall generates a high intensity background noise. The acoustic energy of such sound is unevenly distributed across the frequency spectrum and is proportional to the rainfall intensity (Bedoya et al. 2017; Fig. 1). Most ecoacoustic studies tend to treat rainfall sound as a nuisance parameter, whose effects are controlled either through the use of low-frequency filters, or by removing recordings in which rainfall has been detected (e.g. Depraetere et al. 2012; Gasc et al. 2013; Duarte et al. 2015). Justifications for excluding files with rain from analyses include: (1) sounds produced by rainfall either change behavior of singing animals or mask sounds of all biological diversity (Farina and Pieretti 2017; Rankin and Axel 2017; Moreno-Gómez et al. 2019), and (2) heavy rainfall results in higher amplitude background noises, concealing a considerable proportion of the frequency spectrum and thus generating biases in the values of several acoustic indices (Depraetere et al. 2012; Gasc et al. 2013; Duarte et al. 2015).

Rainfall events and the quantification of their effects on acoustic indices have been rarely studied (Towsey et al. 2014; Gasc et al. 2015; Pieretti et al. 2015; Ferreira et al. 2018). As a result, the potential influence of rainfall is often ignored and, together with other geophonic sounds, rainfall has been treated as general background noise (Towsey et al. 2014; Gasc et al. 2015). Although excluding recordings is the most common method for reducing potential influence of rainfall, it can result in a large loss of data in short-term acoustic surveys or in areas where rainfall is a common phenomenon. Additionally, there is not a single, repeatable method to detect and eliminate audio files with rain. Conversely, the inclusion of a large number of recordings containing rainfall, without taking into account potential effects could yield misleading descriptions of acoustic patterns.

In recent years, acoustic indices have been widely used in ecological studies in highly pluvious tropical environments (e.g. Eldridge et al. 2018; Gómez et al. 2018; Jorge et al. 2018; Bradfer-Lawrence et al. 2019). Although rainfall occurs seasonally in these environments, it can also vary unpredictably at small spatial and temporal scales (Poveda et al. 2005; Rapp and Silma 2012). Before implementing ecoacoustic studies in these ecosystems, consideration should be given to the influence of rainfall on acoustic metrics. In this study, we evaluated the influence of rainfall on acoustic indices values, in a highly pluvious montane forest in the northern Andes in Colombia. In this region, rainfall is a common occurrence; therefore, a significant percentage of data would have to be excluded if recordings with rainfall were removed.

We employed a highly sensitive and automated algorithm to identify sound files with rainfall events, and to quantify their intensity (Bedoya et al. 2017). We compared acoustic indices between different rainfall intensity levels, and tested how the estimated rainfall frequency and intensity affect acoustic indices values. We hypothesize that indices based on amplitude parameters will exhibit greater numerical changes under rainfall conditions than indices measuring spectral complexity. We expect that soundscape changes during rainfall will be reflected through higher values of the ACI, ADI, BI, H, and M indices (see index description below) and lower values of the AEI, NDSI, and NP indices. Furthermore, we expect that indices will respond more strongly with increases in rainfall frequency and intensity.

Materials and Methods

Study area

Data collection was conducted at the eastern flank of the northern Cordillera Central in the Magdalena ecoregion in Colombia (Fig. 2). Sampling sites are part of area surrounding Jaguas hydroelectric power plant (06°26′ N,

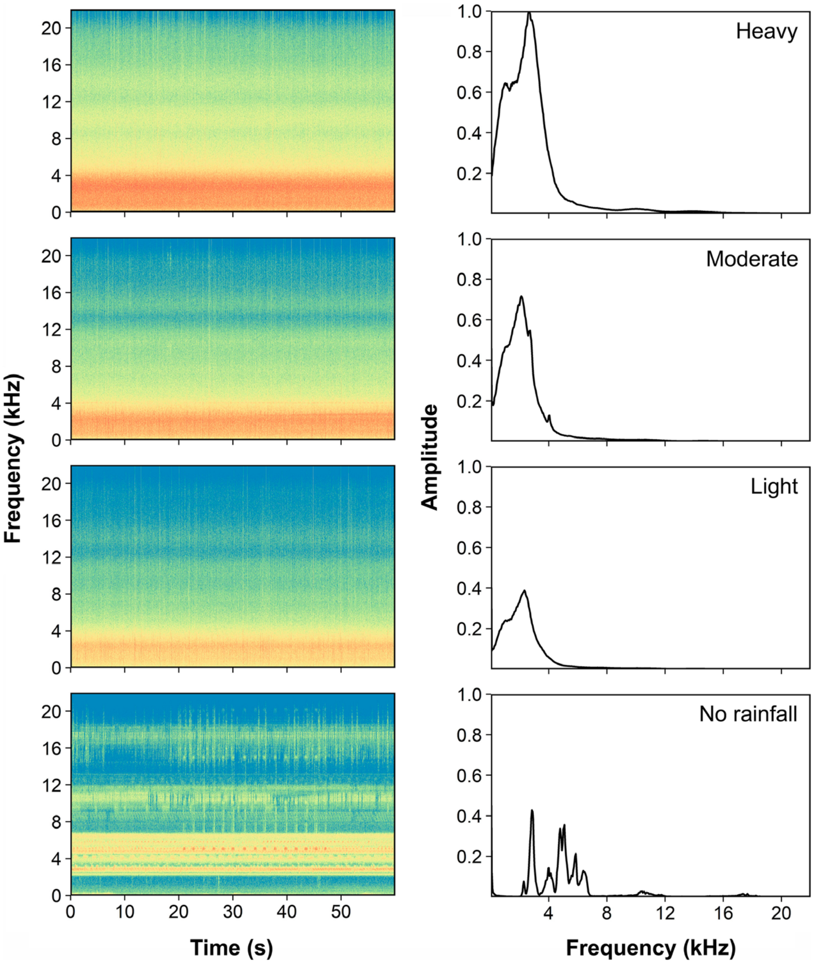

Figure 1. Spectrogram and mean frequency spectrum for 1-min recordings representing heavy, moderate, light, and no rainfall conditions. Amplitude gradient (dB) ranges from blue (minimum) to dark red (maximum). Spectrogram parameters: FFT, non-overlapping, hanning, and window size = 1024. Frequency spectrum parameters: non-overlapping, window size = 1024, hanning, and values scaled by its maximum.

075°05′ W; 06°21′ N, 074°59′ W), which comprises c.a. 50 km^2, including the San Lorenzo reservoir of 10.2 km^2, and spans an elevational gradient from 1000 to 1400 m.a.s.l. The area is characterized by an annual rainfall of 2000–4000 mm, and a bimodal rainfall regime with rainy seasons in March-May and September-November (Poveda et al. 2005). Vegetation is dominated by different successional stages of forest (70%), with the remaining areas composed mainly of a cropland/natural vegetation mosaic. This area supports highly diverse terrestrial vertebrate communities, including threatened and endemic species, and it is considered a paramount site for biodiversity conservation at a regional scale (Restrepo et al. 2017; Sánchez-Giraldo and Daza 2017; Sánchez-Giraldo and Daza 2019).

Acoustic data collection

Acoustic data were collected from 28 sampling sites between May and July 2018 (Fig. 2). This time period included the transition season when rainfall can occur frequently. Sampling sites were randomly selected with the Sampling Design Tool for ArcGIS (ESRI 2012), using the forest and non-forest mosaic habitats as strata, and a proportional allocation according to the extension of each cover (21 forest and 7 non-forest sites). In tropical systems, soundscapes can vary among habitat types (Rankin and Axel 2017; Gómez et al. 2018; Bradfer-Lawrence et al. 2019); therefore, we considered vegetation cover as a factor in the selection of the sampling sites and for the data analysis (see below). We used a minimum distance of 800 m between sites to ensure spatial independence and avoid overlap of acoustic signals among sites (Walls et al. 2014; Pieretti et al. 2015). Likewise, all sites were located at a minimum distance of 150 m from the edge of the reservoir in order to avoid recording sounds generated by raindrops colliding with the water surface.

Audio recordings were obtained using five autonomous recorders (SongMeter SM4; Wildlife Acoustics, Inc., Concord, Massachusetts) equipped with two omni-directional microphones (flat frequency response between 20 Hz and

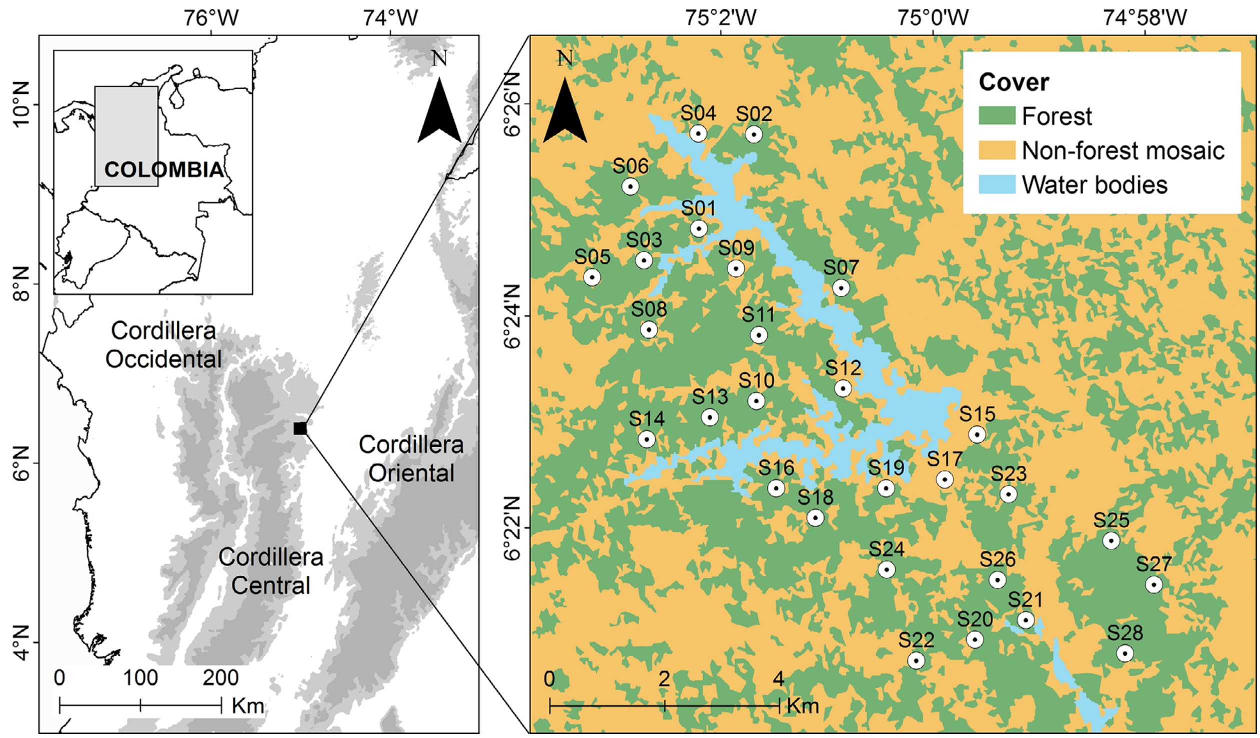

Figure 2. Study area on the eastern flank of the northern Cordillera Central in Colombia indicating sampling sites and vegetation cover around the Jaguas Hydroelectric Power Plant.

20 kHz). We collected recordings in groups of five sampling sites, installing a single recorder for between 5.0 and 9.6 consecutive days (mean = 7.1 days, SD = 1.4 days) at each site, before moving them to a new group (Table S1). Recorders were attached to trees at a distance of 1.5 m above ground, and programmed to collect 1-min recordings (as.*wav* files) every 15-min, using a sampling rate of 44.1 kHz, and 16 bit of resolution. This sampling scheme yielded 96 minutes of recordings per deployment day.

Rainfall detection and intensity

We used the method proposed by Bedoya et al. (2017) for detection and intensity estimation of 1-min recordings containing rainfall. Briefly, the algorithm automatically detects rainfall events and quantifies their intensity based on the estimation of the power spectral density (PSD) in the 600–1200 kHz frequency band. We modified the original algorithm in order to include an automatic threshold estimator to guarantee detection of light rainfall events, but the exclusion of extremely light ones which are acoustically similar to the breezes. The modification consisted in estimating the mean value of the PSD in the 600–1200 kHz frequency band for each 1-min recording at a specific site. Then, using a MatLab routine, we selected the values that fell between the 10th and 90th percentile. The automatic threshold for recordings containing rainfall was estimated as the average of this new distribution of mean PSD values. This operation was performed in order to reduce the effect of large amounts of silent recordings and rainfalls of violent intensity during the threshold estimation. Thresholds were also computed for each sampling site to avoid potential biases generated by differences in the recorder conditions or local rainfall regimes within sites. We manually reviewed all the recordings with PSD values close to the threshold value in order to validate rainfall occurrence. Because rainfall events occur in blocks (i.e. more than two consecutive files), we excluded singletons categorized as “rainfall” with extremely high values of PSD. The algorithm was programmed in MatLab version 2017a (MATLAB 2017).

We quantified rainfall intensity for each 1-min recording based on the mean PSD values and divided our entire dataset into four different intensity categories (i.e no rainfall, light, moderate, and heavy). Because recording sites had different background noise and experienced rainfall events of different maximum intensities, upper mean PSD boundaries among sites were not directly comparable. In order to address this, we selected the recordings with the highest mean PSD value per site (i.e. the recordings containing rainfall events with the highest intensities), and categorized aurally their intensity assigning discrete values from 0 (no rainfall) to 1 (violent rainfall). After this process was completed, maximum intensity levels in all 28 sites varied between 0.5 and 1. Then, mean PSD values from the recordings of each site were rescaled between zero (no rainfall) and the previously specified value for the site's maximum. Last, to define intermediate thresholds for the whole dataset, we followed Bedoya et al. (2017) and categorized rainfall intensity in each recording using an equivalent distribution of scaled mean PSD values (sPSD) as: no rainfall (sPSD = 0), light rainfall (0 < sPSD≤0.024), moderate rainfall (0.024 < sPSD≤0.145), and heavy rainfall (sPSD> 0.145).

Acoustic indices

We selected eight indices to quantify the acoustic heterogeneity at each sampling site: the acoustic complexity index (ACI) (Pieretti et al. 2011), the acoustic diversity index (ADI) (Villanueva-Rivera et al. 2011), the acoustic evenness index (AEI) (Villanueva-Rivera et al. 2011), the bioacoustic index (BI) (Boelman et al. 2007), the acoustic entropy index (H) (Sueur et al. 2008a), the median of amplitude envelope (M) (Depraetere et al. 2012), the normalized difference soundscape index (NDSI) (Kasten et al. 2012), and the number of peaks (NP) (Gasc et al. 2013). These indices are some of the most widely used estimators in passive acoustic monitoring, and have been tested under diverse habitat and environmental conditions at global scale (e.g. Sueur et al. 2014; Harris et al. 2016; Moreno-Gómez et al. 2019). We calculated all eight acoustic indices for each 1-min recording, and used an upper limit of 12 kHz in most of them. We chose this limit threshold because both the main acoustic activity in our system and the acoustic components of the rainfall are concentrated below this band (Fig. 1, S1; Bedoya et al. 2017). We acknowledge that our results are conditioned by the defined frequency limits as most of the tested acoustic indices are sensitive to the frequency range used in their estimation. We used the default settings when calculating the indices, including the bounds of 1–2 kHz and 2–8 kHz for anthrophony and biophony for the BI and the NDSI (Boelman et al. 2007; Kasten et al. 2012) (Table S2). All metrics were calculated in R v.3.5.1 (R Development Core Team 2016) using the packages *seewave v.2.1.4* and s*oundecology v.1.3.3* (Sueur et al. 2008b; Villanueva-Rivera and Pijanowski 2016).

Data analyses

We assessed the influence of rainfall sound on acoustic indices values in two ways. First, we quantified the differences in the indices under contrasting rainfall intensity levels (i.e., no rain, light, moderate and heavy). Second, we evaluated the relationship between the variation in the acoustic indices with the rainfall frequency and intensity. In both analyses, we fitted generalized linear (GLMER) or linear mixed-effects models in R using the package *glmmTMB v.1.0.1* (Brooks et al. 2017). We checked the full models for assumptions, including correlation of fixed-effects, homoscedasticity, and residual diagnostics using a simulation-based approach in the package *DHARMa v.0.2.7* (Hartig 2019). The selection of the best model for each acoustic index was based on the Akaike Information Criterion (AIC), selecting the model with the smallest AIC and considering all models with ΔAIC < 4 as equally plausible (Burnham and Anderson 2012). The selection among plausible models was made by model comparison using likelihood-ratio tests.

Rainfall intensity levels and acoustic indices

Models were fit using the indices values from 1-min recordings as the response variable, and rainfall intensity level and vegetation cover (forest and non-forest mosaic) as fixed effects. We modeled sites as a random effect, and incorporated an autoregressive covariance structure (corAR1) for the time (hour) to account for potential temporal autocorrelation (e.g. Fuller et al. 2015). We used GLMERs to fit AEI, H, M, and NDSI with a beta error structure; ACI with gamma structure and log link function; ADI data with Gaussian structure and log link function; and NP with Poisson structure and logit link function. Prior to the analyses, we transformed NDSI data according to the formula (NDSI+1)/2 (Fairbrass et al. 2017). The BI data were normally distributed and modeled with linear mixed-effect models. We fitted a common set of six models for each acoustic index, which included the full model, individual fixed effects models, model without temporal covariance structure, model with only random effects, and model with only fixed effects and without temporal covariance structure (Table S3).

Influence of rainfall frequency and intensity on the acoustic index values

For each acoustic index, we modeled the relationship between deviations in its estimation derived of rainfall occurrence with the frequency and the intensity of the rainfall. In this analysis, acoustic indices were averaged per hour over all sampling days in each site, resulting in a vector of 24 hourly values per site per acoustic index. Previous ecoacoustic studies have used hourly average values, as these may adequately represent the acoustic characteristics of a specific site (Gasc et al. 2013; Fuller et al. 2015). Hourly means were estimated in two different ways: (1) using the entire data set (i.e. complete), and (2) using a data set in which recordings containing rainfall were excluded (i.e. no rainfall). To quantify the relative deviation of the acoustic indices values estimated from complete and no rainfall datasets, we calculated the relative difference between mean values of both groups for each acoustic index at specific 1-hour intervals using the percent deviation (*pd*): $[(\text{mean}_{\text{complete}} - \text{mean}_{\text{no rainfall}})/\text{mean}_{\text{no rainfall}}] \times 100$ (Bennett and Briggs 2008).

Rainfall frequency was defined as the proportion of 1-min recordings in each hour that included rainfall (number of 1-min recordings containing rainfall/ total of 1-min recordings). We created a rainfall intensity index, which reflected the variation of rainfall intensity in recordings. This was defined as the hourly ratio between the weighted sum of the number of 1-min recordings containing rainfall and the total number of 1-min recordings. We calculated the weighted sum by multiplying the number of 1-min recordings in each rainfall intensity level by specific weights: *1/3* for light rainfall level, *2/3* for moderate, and *1* for heavy. The rainfall intensity index ranges between 0 and 1, where 1 indicates the occurrence of recordings containing only rainfall of heavy intensity. In this way, we finally obtained for each sampling site 24 temporal values of rainfall frequency, rainfall intensity index, and percent deviation for each of the acoustic metrics used.

We modeled the relationship between the percent deviation and both rainfall frequency and intensity index. In each case, a mixed model was fit with the percent deviation as response variable, the rainfall parameter (frequency or intensity) and the type of vegetation cover as fixed effects, and included the sampling site as random effect. Because rainfall parameters were highly co-linear ($r > 0.9$) we separately modelled their relationship with the percent deviation of indices. We excluded 1-hour intervals in which the rainfall frequency and intensity index were zero. We fit GLMERs to model the percent deviation of ADI, ACI, BI, H, and M with a gamma error structure and log link function, and NDSI with a beta structure. In the cases of AEI and NP, we modeled the percent deviation with linear mixed-effect models. We scaled the percent deviation to a positive range of values using the formula $(pd/100) + 1$, which facilitated the use of non-Gaussian error structures. We fitted five models for the percent deviation of each index: the full model, individual fixed effects models, model with only fixed effects, and model with only random effect (Table S4, S5).

Results

We collected a total of 18336 minutes of recordings from all the sampled sites, excluding aberrant recordings caused by microphone failures. The number of recordings per site ranged from 408 to 908 (mean = 654.9, SD = 143.7), representing a combined length of 305.6 h (Table S1). Recorders installed at sites S02, S24, and S28 had operating problems and recorded intermittently over several days; therefore, the final number of collected recordings was lower than originally intended according to the sampled days (Table S1).

We identified 2867 1-min recordings containing rainfall (range: 18–194 per site), where 1914 were categorized as light rainfall, 694 as moderate, and 259 as heavy. Thus, recordings with rainfall sound represented between 3.3 and 26.3 % of the total number of recordings at each sampling site (mean = 15.2%, SD = 7.2%) (Table S1). Among sites, there was a high variation in hourly rainfall frequency over the day. Rainfall frequency (i.e. proportion of recordings per hour with rainfall) ranged from 0 to 0.82, with maximum values above 0.50 in 58% of the sites, and only four sites had maximum values below 0.20 (Fig. 3). The distribution of rainfall frequency showed a marked diel pattern throughout the study period, with rainfall mainly occurring between 19:00 and 05:00 h (Fig. 3).

Rainfall intensity levels and acoustic indices

All acoustic indices showed significant differences associated with rainfall occurrence and changes in intensity (Table 1, Table S3). ACI, ADI, H, and M indices exhibited positive differences, with higher values in rainfall recordings, irrespective of rainfall intensity (Table 1). Conversely, AEI, BI, NDSI, and NP indices showed the opposite pattern, with lower index values in recordings containing rainfall (Table 1). For the indices ADI, AEI, H, M, and NP, we found significant differences associated with the habitat type, with index values being lower in the non-forest mosaic cover, except those of AEI (Table 1, S3). The best fitted models for all the tested indices included the autoregressive covariance structure, where the estimated correlation values were above 0.85 in most of them (Table 1, Table S3).

In both habitat types, values of ADI, AEI, H, M, and NP indices showed a similar trend in response to rainfall intensity levels (Fig. 4). The M index showed the greatest differences associated with changes in rainfall intensity, where the estimated mean differed about 41% between no rainfall and light rainfall intensity (Fig. 4). For AEI and NP, estimated differences between the no rainfall level and the light and heavy levels were over 20%. In ADI, BI, H, and NDSI, the minimum and maximum differences between no rainfall and the other intensity levels were above 5–9% and 15–25% respectively. The lowest differences were found in the ACI estimates, with differences between 2.4–5% respectively (Fig. 4).

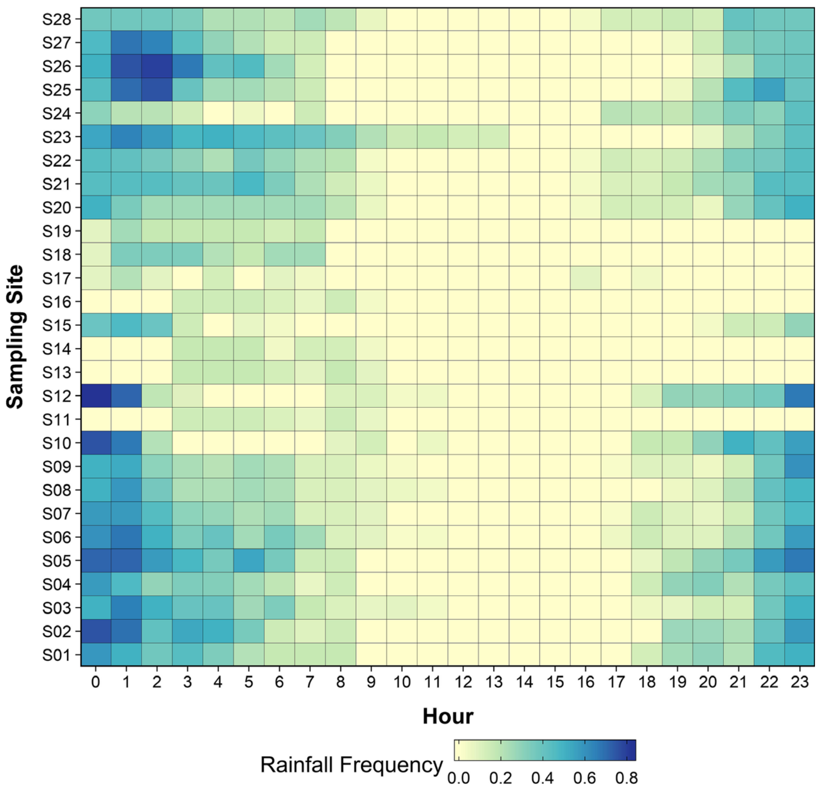

Figure 3. Hourly rainfall frequency (see methods) extracted from 1-min recordings across sampling sites.

Influence of rainfall frequency and intensity on acoustic index values

Percent deviations of acoustic indices exhibited similar relationships with both rainfall frequency and rainfall intensity index (Table 2, 3). These relationships were not affected by the habitat type (Table S4, S5). ACI, ADI, H, and M had higher values in rainfall recordings, with significant, positive deviations associated with rainfall frequency and rainfall intensity index, whereas for AEI, BI, NDSI and NP equivalent associations were negative (Table 2, 3). Additionally, the predicted percent deviations for all indices were higher for the variation in rainfall intensity index than for the rainfall frequency (Fig. 5, S2). Among the tested indices, M had the largest deviations with rainfall, reaching deviations about 75% for the maximum values of frequency and intensity (Fig. 5, Fig. S2). For the AEI, NDSI and NP indices, maximum estimated deviations associated with rainfall frequency and intensity index were 19–27% and 26–37%, respectively. The smallest deviations occurred in the ACI and BI indices, where the maximum deviations were below 5% for both rainfall measurements (Fig. 5, Fig. S2).

Discussion

We found that both the occurrence of rainfall and its intensity correlate with variations in the values of the eight examined acoustic indices. The trends exhibited by the acoustic indices outline the main effects of the rainfall on the soundscape patterns in a pluvious montane forest. M increased in value with rainfall intensity and was the most sensitive index to rainfall conditions. This was a consequence of higher amplitude levels of the acoustic signal during rainfall events, and an increase in the background noise is the most evident manifestation of pluviosity in audio recordings (Bedoya et al. 2017). The positive trend of ACI is the result of an increase in rain intensity, clearly derived from higher amplitudes, but its lower sensitivity indicates signals of constant intensity during rainfall events. Likewise, positive trend of ADI, and negative of AEI are also a direct effect of an increase in signal amplitude, and consequently on rainfall levels. The core of these index is based on the product of power values in a pre-selected set of frequency bands of the spectrogram, and they reflect the increase in the number of occupied frequency bands during rainfall events (Pekin et al. 2012; Bradfer-Lawerence et al. 2019). Reduction in the index values of NDSI and NP are associated to the spectral heterogeneity from rainfall and indicates that amplitude changes from rainfall sounds are more evident in low frequency bands. Even light intensity rainfall generates a significant power increase in the low frequency spectrum (Bedoya et al. 2017). This increases the power of the anthrophony band (1–2 kHz), and consequently, the ratio used for the NDSI estimation so that most values will

Table 1. Mixed-effects models describing the relationship between acoustic indices and rainfall intensity levels (no rainfall, light, moderate, and heavy) and vegetation cover (forest and non-forest mosaic).

Index	Effect	Estimate	SE	Z-value	*P*-value	Corr
ACI	Intercept	6.830	0.004	1719.100	<0.0001	0.67
	Light	0.048	0.001	60.600	<0.0001	
	Moderate	0.040	0.001	32.300	<0.0001	
	Heavy	0.024	0.002	12.200	<0.0001	
ADI	Intercept	0.553	0.032	17.060	<0.0001	0.86
	Light	0.054	0.004	13.060	<0.0001	
	Moderate	0.147	0.006	24.800	<0.0001	
	Heavy	0.155	0.009	17.820	<0.0001	
	Non forest	−0.160	0.065	−2.470	0.014	
AEI	Intercept	−0.403	0.110	−3.670	0.002	0.88
	Light	−0.424	0.015	−28.830	<0.0001	
	Moderate	−1.230	0.025	−49.030	<0.0001	
	Heavy	−1.469	0.043	−34.360	<0.0001	
	Non forest	0.537	0.219	2.460	0.014	
BI	Intercept	22.040	0.501	43.96	<0.0001	0.90
	Light	−1.272	0.106	−11.96	<0.0001	
	Moderate	−1.708	0.164	−10.4	<0.0001	
	Heavy	−3.819	0.258	−14.8	<0.0001	
H	Intercept	1.242	0.076	16.320	<0.0001	0.88
	Light	0.481	0.009	54.200	<0.0001	
	Moderate	0.875	0.015	56.700	<0.0001	
	Heavy	0.866	0.026	33.930	<0.0001	
	Non forest	−0.392	0.152	−2.580	0.010	
M	Intercept	−2.876	0.056	−51.560	<0.0001	0.89
	Light	0.363	0.014	26.810	<0.0001	
	Moderate	0.794	0.018	44.530	<0.0001	
	Heavy	1.479	0.022	66.160	<0.0001	
	Non forest	−0.282	0.111	−2.530	0.012	
NDSI	Intercept	3.466	0.084	41.060	<0.0001	0.87
	Light	−1.445	0.022	−65.160	<0.0001	
	Moderate	−2.337	0.030	−77.490	<0.0001	
	Heavy	−2.605	0.044	−59.230	<0.0001	
NP	Intercept	1.520	0.072	21.167	<0.0001	0.90
	Light	−0.251	0.014	−17.796	<0.0001	
	Moderate	−0.630	0.025	−24.782	<0.0001	
	Heavy	−0.691	0.039	−17.546	<0.0001	
	Non forest	−0.404	0.142	−2.838	0.005	

Estimates of fixed effects and standard errors from conditional model, and their significance are indicated. Corr: correlation estimated from covariance structure AR1. Acoustic complexity index (ACI), Acoustic diversity index (ADI), Acoustic evenness index (AEI), Bioacoustic index (BI), Acoustic entropy index (H), Median of amplitude envelope (M), Normalized difference soundscape index (NDSI), and Number of peaks (NP).

fall (Kasten et al. 2012). Trend of NP index is linked to both the increase in amplitude in the low frequency region, and to the concomitant reduction in the frequency band where biophony is manifested (<8kHz) (Fig. 1, Fig. S3), which offers insights about possible effects of rainfall on the biophonic components of the soundscape.

Our results agree with previous studies where the influence of geophonic sources on acoustic indices has been assessed. Higher ACI values are associated with recordings containing rainfall, or noise from other adverse weather conditions (Depraetere et al. 2012; Ferroudj et al. 2014; Pieretti et al. 2015; Farina et al. 2016). Similarly, ADI, H, and M exhibit positive responses to geophonic sources and increase their values under high levels of background noise or dominant broadband signals (Sueur et al. 2014; Gasc et al. 2015; Fairbrass et al. 2017). Our findings match those from simulations studies, which show that ACI, H and M are sensitive to background noise (Gasc et al. 2015). In addition, the trends found for AEI and ADI estimates are congruent with the documented responses of each index to other geophonic sources, in which lower and higher values respectively are produced by windy conditions (Bradfer-Lawerence et al. 2019).

The negative response to rainfall found in the BI and NDSI indices contrasts with previous studies in other systems. Studies conducted in urban environments have found a positive relationship between BI and NDSI indices and an increase in geophonic sounds (Fairbrass et al. 2017). Discrepancies in BI and NDSI values between these two environments can be explained by differences of the acoustic components within the band defined as biophony (2–8 kHz), on which the estimation of both indices is directly dependent (Boelman et al. 2007; Kasten et al. 2012), and their response to geophonic sources. In natural environments, biotic components are predominant in the 2–8 kHz frequency band, and are impaired by noise from rainfall or wind (Brumm and Slabbekoorn 2005). Conversely, in urban areas the 2–8 kHz band is dominated by anthropogenic components (e.g. Fairbrass et al. 2017), whose acoustic activity is less affected by geophonic sources.

This is the first study assessing the influence of rainfall on the NP index. Similar to BI and NDSI indices, we also found contrasting results in NP estimates. It has been previously stated that the performance of the NP index is more dependent on animal sounds than the ambient noise, and simulation analyses have indicated a low sensitivity of the index to the addition of background noise (Gasc et al. 2013; Sueur et al. 2014; Deichman et al. 2017). Nonetheless, the response of the NP index to non-animal sounds such as rainfall, is previously undocumented, and is one of the most remarkable findings in our study. Therefore, the reported low sensitivity of NP to ambient noise should be reconsidered, since rainfall sounds affect the estimation of this index values.

Low NP values under rainfall conditions may be the result of decreased biophony, as NP is usually correlated with the number of singing species in the landscape. The acoustic activity of singing organisms in tropical systems is generally concentrated between 1.5 and 7.5 kHz (Bedoya et al. 2014; Pearse et al. 2018; Furumo and Aide

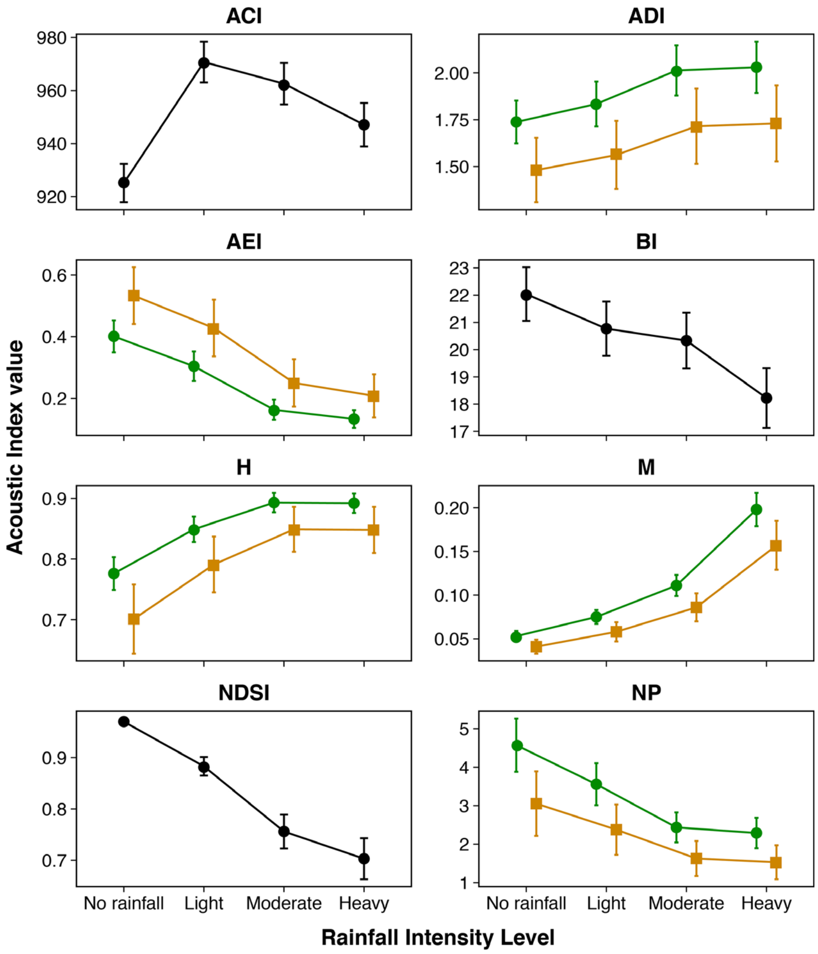

Figure 4. Association between acoustic index values and rainfall intensity level. Dots and bars indicate the mean and 0.95 confidence interval respectively. Values predicted from fixed effects of conditional models including non-effect (black circles) or effect of the habitat type: forest (green circles) and non-forest mosaic (orange squares). Abbreviations of acoustic indices as in Table 1.

2019). Moderate and heavy rainfalls may reduce biophony, mostly due to impairing the animal acoustic signals as a consequence of the increased background noise (Brumm and Slabbekoorn 2005; Farina and Pieretti 2017; Rankin and Axel 2017). In our study, the analysis of recordings with different rainfall intensity levels at the same sampling site shows that peaks between 3 and 8 kHz tend to decrease in activity during rainfall events (Fig. S3). On the other hand, activity in the 0–3 kHz frequency band either remains constant or increases (Fig. S3). The reduced acoustic activity in the biophony frequency range suggests rainfall either interrupts or masks acoustic signals from vocalizing organisms. Because vocal activity of several species is either maintained or stimulated during low intensity rainfalls (e.g. Brauer et al. 2016; Pérez-Granados et al., 2019), future work will focus on determining the causes of the reduction of acoustic activity during rainfall events. Such reduction could be an intrinsic behavioral response of singing animals or a physical constraint that masks the sounds and complicates the detection of biophonic signals.

Our results show that the sensitivity of an index to rainfall sounds is derived directly from its dependence on signal amplitude and the frequency band used during its estimation. Thus, the most sensitive indices are either those whose values are based on specific amplitude measurements or are focused on the frequency band in which rainfall sounds occur. ACI and BI have low sensitivity to rainfall interference, and are consequently reliable estimators of acoustic patterns under conditions of high rainfall frequency and intensity. Although ACI is affected by amplitude changes, the way it is calculated within audiofiles (i.e. small temporal bins) makes the index relatively insensitive to sounds with constant intensity, e.g. rainfall, even when high sounds possess high amplitude (i.e. high intensity rainfalls). The main steps in the index computation implies the subtraction of adjacent intensity values in the same frequency bin of the time-frequency representation (spectrogram) (Pieretti et al. 2011). This heavily reduces the influence of rainfall in the ACI, if the rainfall event remains constant during the index estimation. Since most ecoacoustic studies use recordings of 1-min length,

Table 2. Mixed-effects models describing the relationship between the percent deviation of acoustic indices and rainfall frequency (Rainfall frequency). Estimates of fixed effects and standard errors from conditional model, and their significance are indicated. Abbreviations of acoustic indices as in Table 1.

Index	Effect	Estimate	SE	Z-value	*P*-value
ACI	Intercept	0.003	0.001	2.212	0.027
	Rainfall frequency	0.034	0.002	17.591	<0.0001
ADI	Intercept	0.006	0.007	0.934	0.350
	Rainfall frequency	0.091	0.014	6.366	<0.0001
AEI	Intercept	0.989	0.011	90.170	<0.0001
	Rainfall frequency	−0.236	0.024	−10.040	<0.0001
BI	Intercept	−0.004	0.008	−0.551	0.518
	Rainfall frequency	−0.049	0.016	−3.121	0.0018
H	Intercept	0.004	0.005	0.841	0.401
	Rainfall frequency	0.120	0.008	15.188	<0.0001
M	Intercept	0.029	0.019	1.556	0.120
	Rainfall frequency	0.753	0.046	16.392	<0.0001
NDSI	Intercept	4.306	0.097	44.200	<0.0001
	Rainfall frequency	−3.482	0.148	−23.500	<0.0001
NP	Intercept	1.013	0.008	124.350	<0.0001
	Rainfall frequency	−0.347	0.019	−18.320	<0.0001

Table 3. Mixed-effects models describing the relationship between the percent deviation of acoustic indices and rainfall intensity index (Rainfall intensity).

Index	Effect	Estimate	SE	Z-value	*P*-value
ACI	Intercept	0.005	0.001	4.141	<0.0001
	Rainfall intensity	0.053	0.004	13.302	<0.0001
ADI	Intercept	0.010	0.006	1.621	0.105
	Rainfall intensity	0.158	0.026	6.059	<0.0001
AEI	Intercept	0.986	0.010	97.960	<0.0001
	Rainfall intensity	−0.464	0.042	−11.060	<0.0001
BI	Intercept	0.003	0.008	0.346	0.729
	Rainfall intensity	−0.159	0.027	−5.770	<0.0001
H	Intercept	0.010	0.005	2.132	0.033
	Rainfall intensity	0.200	0.015	13.268	<0.0001
M	Intercept	0.033	0.018	1.806	0.071
	Rain intensity	1.534	0.075	20.532	<0.0001
NDSI	Intercept	4.285	0.096	44.520	<0.0001
	Rainfall intensity	−6.779	0.236	−28.770	<0.0001
NP	Intercept	1.012	0.008	130.490	<0.0001
	Rainfall intensity	−0.237	0.010	−23.870	<0.0001

Estimates of fixed effects and standard errors from conditional model, and their significance are indicated. Abbreviations of acoustic indices as in Table 1

this is a feasible scenario. This also explains why the ACI values tend to decrease with the rainfall intensity level (Fig. 4); as the frequency of rain drops increases, the spectrogram becomes more uniform and adjacent intensity values get cancelled out during the subtraction operation. In the case of BI, the index is a function of both the signal amplitude and the number of frequency bands, but its formulation excludes the frequency band (i.e. 0–2 kHz) in which the spectral content of the rainfall sound is concentrated (Boelman et al. 2007; Bedoya et al. 2017).

ADI, AEI, and H have intermediate sensitivity, and in conditions of low to moderate rainfall their values may still result as expected. ADI and AEI are based on spectral content and susceptible to the frequency range and number of frequency bands. As a result, their estimation is more dependent on the distribution of sound occupancy across the entire frequency spectrum than on a specific amplitude measurement (Villanueva-Rivera et al. 2011). On the other hand, H is based on amplitude envelope and power spectrum distribution of the signal, and its formulation is designed to quantify the amplitude distribution in both temporal and spectral domains rather than focusing on a central or maximum measure of amplitude (Sueur et al. 2008a). Lastly, M, NDSI, and NP are indices with high rainfall sensitivity, from which acoustic inferences could be potentially misleading if rainfall effects are not considered. Indices M and NP depends on specific measurements of amplitude and not on the entire amplitude of the signal, i.e. the median of amplitude envelope, and the maximum values of the mean frequency spectrum (Depraetere et al. 2012; Gasc et al. 2013). NDSI is also computed using amplitude-based measurements (i.e. PSD), and its sensitivity is primarily due to the fact that the anthrophony -one of the two components in its formulation- shares similar frequency range with the rainfall sounds (1–2 kHz) (Kasten et al. 2012; Bedoya et al. 2017). In study regions such as ours, where there are strong diel peaks in rainfall occurrence, these three indices are not recommended for comparing acoustic patterns.

The proposed categorization of index sensitivity depends on the recording schedule (i.e. 1-min recording per 15 min). In tropical habitats, patterns in acoustic indices values may depend on the recording scheme (Pieretti et al. 2015; Bradfer-Lawrence et al. 2019). Recent research indicates that continuous recordings capture the complete acoustic variability of a site when compared to subsamples recorded on a schedule, even when effects of geophonic sources are not considered (Bradfer-Lawrence et al. 2019). This implies that the effect of rainfall could be neglected for the estimation of acoustic indices from large sound files (i.e. 120 h; Bradfer-Lawrence et al. 2019). However, in highly pluvious environments, a short-term continuous recording scheme (e.g. 120 h = five days) may include entire rainy days, which in turn influence acoustic indices values. Therefore, acoustic monitoring based on continuous recordings will likely also benefit from an explicit estimation of rainfall patterns and the quantification of their effects (Bedoya et al. 2017; Metcalf et al. 2020, this study). We suggest

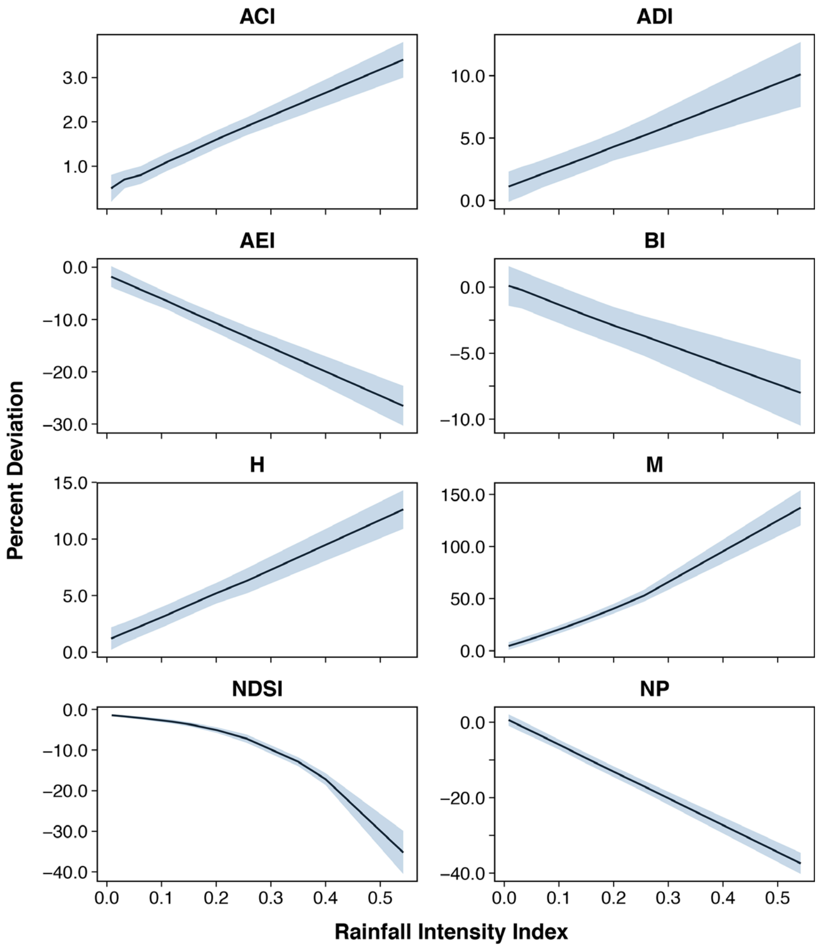

Figure 5. Relationship between percent deviation of acoustic indices and the rainfall intensity index. The shaded area indicates the 0.95 confidence interval. Values are estimated from fixed effects of conditional models. Abbreviations of acoustic indices as in Table 1.

future research on this topic to focus on the interaction between rainfall sounds and sampling schemes, and its effects on the estimation of acoustic indices.

Acoustic indices are used as indicators of diversity and disturbance in multiple ecological levels (Gasc et al. 2013, 2018; Sueur et al. 2014). Alterations in acoustic indices values associated with rainfall sound might directly affect inferences about ecosystem functioning; particularly in regions where rainfall is a common event. Hence, we advise careful interpretation of biological patterns based on the acoustic indices analyzed here, as most are sensitive to rainfall sounds. We hope our work underpins future research on the topic, and aids the understanding of the relationship between acoustic indices and the rainfall sound in pluvious tropical environments.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Average spectrogram depicting the daily acoustic pattern in sites with forest and non-forest mosaic covers.
Figure S2. Relationship between percent deviation of acoustic indices and rainfall frequency. The shaded area indicates the 0.95 confidence interval.
Figure S3. Mean frequency spectrum for 1-min recordings representing heavy, moderate, light, and no rainfall intensity levels in S01 (left), S04 (center), and S20 (right) sites.
Table S1. Summary of sampling sites and acoustic data collection in the protected area of Jaguas Hydroelectric Power Plant, May-Jul 2019.
Table S2. Summary of parameters used in the estimation of acoustic indices.
Table S3. Mixed-effects models evaluated to describe the relationship between acoustic indices and rainfall intensity level (Rainfall) and vegetation cover (Cover).
Table S4. Mixed-effects models evaluated to describe the relationship between the percent deviation of acoustic indices with rainfall frequency (Rainfall frequency) and vegetation cover (Cover).
Table S5. Mixed-effects models evaluated to describe the relationship between the percent deviation of acoustic indices with rainfall intensity index (Rainfall intensity) and vegetation cover (Cover).