

Acoustic metrics predict habitat type and vegetation structure in the Amazon



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ABSTRACT

The rapidly developing field of ecoacoustics offers methods that can advance multi-taxa animal surveys at policy-relevant extents. While the field is promising, there remain foundational assumptions that need to be tested across different biomes before the methods can be applied widely. Here we test two of these assumptions in the Amazon: 1) that acoustic indices can be used to predict soundscapes of different habitat types, and 2) that acoustic indices are related to vegetation structure. We recorded soundscapes and collected vegetation data in 143 sites spanning six natural and two human-modified habitats in Viruá National Park, Roraima, Brazil. We grouped the eight habitats into three categories based on vegetative characteristics and flooding regime: open habitats, flooded-forests, and non-flooded forests. Thirteen acoustic indices were calculated from 92,283 one-minute recordings to describe the soundscapes of the habitats. We found that each habitat type had unique and predictable soundscapes. Random forest models were 74% accurate at predicting the eight habitats types and 87% accurate at predicting the three broader habitats categories. The most important acoustic indices to distinguish habitats were the third quartile and centroid. Canopy cover significantly affected 11 of 13 acoustic indices, and while other vegetation variables (e.g., shrub cover and number of trees) appeared in top models for some indices, their effects were not significant. The best indices linking soundscapes to vegetation structure were the acoustic evenness index and skewness, with canopy cover explaining 81% and 52% of the variance in these indices, respectively. These results expand our knowledge regarding which acoustic indices best connect changes in habitats to changes in soundscapes. These findings are particularly important for diverse ecosystems, like the Amazon, which are known to have complex soundscapes with sound-producing animals that are difficult to detect with traditional survey methods (e.g., visual transects). Ultimately, our results suggest that soundscapes are able to track changes in biodiversity levels across major habitat types of the Amazon.

1. Introduction

The rapidly developing field of ecoacoustics offers tools to extract information quickly from large audio datasets and serves as a cost-effective way to monitor biodiversity and environmental change (Krause and Farina, 2016; Farina et al., 2017; Pijanowski et al., 2011a; Rappaport et al., 2020). The field focuses on the investigation of natural and anthropogenic sounds (i.e., soundscapes) and their relationship with the environment over multiple spatial and temporal scales (Farina et al., 2017). Soundscapes have been used in a variety of studies on topics ranging from describing biotic homogenization (Burivalova et al., 2019) to the impacts of mining and wildfire on ecological communities (Duarte et al., 2015; Gasc et al., 2018). While ecoacoustic methods are promising for ecological monitoring, several lingering

knowledge gaps limit its widespread utility (Farina et al., 2017; Pijanowski et al., 2011b). For example, more studies are needed to determine the ability of acoustic indices to differentiate habitat types in different biomes (Farina et al., 2017; Pijanowski et al., 2011b). Another point that remains largely unaddressed is how acoustic indices relate to vegetative habitat structure (Farina et al., 2017; Pijanowski et al., 2011b). The need to fill these gaps in knowledge is particularly pressing for tropical areas, where ecoacoustic monitoring holds great potential for species conservation, yet whose soundscapes are largely understudied (Scarpelli et al., 2020).

An almost overwhelming 60 acoustic indices have been created to describe soundscapes and represent faunal richness (Buxton, et al., 2018; Sueur et al., 2014). Acoustic indices are calculated using different patterns of soundscapes such as pitch, saturation and amplitude

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(Buxton et al., 2018; Sueur et al., 2014). The theoretical underpinning of the application of acoustic indices for ecological monitoring is that acoustic diversity is positively associated with faunal species richness (Farina et al., 2017; Gage et al., 2001; Pijanowski et al., 2011ab). This positive relationship has been demonstrated through both empirical tests and computer simulations (Aide et al., 2017; Bradfer-Lawrence et al., 2020; Depraetere et al., 2012; Harris et al., 2016; Sueur et al., 2008a; Zhao et al., 2019), but in some cases no relationship was found (Gasc et al., 2015; Moreno-Gómez et al., 2019). As thousands of hours of soundscape recordings continue to accumulate globally, new indices continue to be developed that translate these data into ecological monitoring information, although often without sufficient tests for their ability to do so (Colonna et al., 2020; Gibb et al., 2019; Tunesu-Corral et al., 2020; Santiago et al., 2020).

One area which needs further investigation is the ability of acoustic indices to distinguish soundscapes of different habitat types (e.g., anthropogenic versus natural). This area of research can improve biodiversity monitoring because if habitats have unique acoustic signatures we can use acoustic indices to monitor habitat change (Farina et al., 2017; Pijanowski et al., 2011b). Further, identifying the indices that correspond most closely with particular habitats across different ecosystems could reduce the computing burden of calculating several indices on large audio datasets (Bradfer-Lawrence et al., 2019; Buxton et al., 2018; Eldridge et al., 2018). To the best of our knowledge, only three studies have tested multiple acoustic indices to investigate habitat-specific soundscapes in terrestrial systems (Table 1). For example, Bormpoudakis et al. (2013) tested eight acoustic indices and found that the centroid index (CENT) performed best at distinguishing soundscapes of six habitat types in Greece, whereas Bradfer-Lawrence et al. (2019) tested seven acoustic indices across six habitats in Panama and found the acoustic complexity index (ACI) performed best. However, differences in sample sizes, acoustic indices used, and study regions limit the comparative and application value of these results in different ecosystems (Table 1).

A second area of research in ecoacoustics that requires further clarification is how vegetation structure influences acoustic indices (Farina and Pieretti, 2014; Farina et al., 2017; Pijanowski et al., 2011b). It is expected that habitats with greater vegetation structural complexity have higher species diversity leading to greater acoustic diversity (Farina and Pieretti, 2014; Fuller et al., 2015; Pijanowski et al., 2011b). Despite the centrality of this assumption, it has received limited empirical validation, likely due to the time-consuming task of collecting both vegetation structure and soundscape data (Table 1). This knowledge gap hinders our ability to build predictive models

linking changes in vegetation structure to acoustic diversity (Farina and Pieretti, 2014; Farina et al., 2017; Pijanowski et al., 2011b). In the few studies conducted on this topic, a relationship between vegetation structure and four acoustic indices [acoustic diversity index (ADI), acoustic evenness index (AEI), normalized difference soundscape index (NDSI), and total entropy (H)] was found across five habitats in Australia (Fuller et al., 2015; Ng et al., 2018), and between canopy cover and the bioacoustic index (BIO) in two habitats in Madagascar (Rankin and Axel, 2017). However, Tucker et al. (2014) suggested that landscape variables (e.g., patch size) were more important than vegetation structure in driving differences in one acoustic index (relative soundscape power; RSP) in Australia. Thus, it remains largely unknown if relationships between vegetation and soundscapes are a widespread phenomenon and which indices best connect vegetation structure to soundscapes.

Here, we investigate habitat-specific soundscapes and the relationships between vegetation structure and soundscapes in the Brazilian Amazon. We collected vegetation data and recorded soundscapes at 143 sites across eight habitat types (natural and anthropogenic) representing the majority of habitat types found in the Amazon. We used a total of 13 acoustic indices to describe the soundscapes. Our goals were to test if acoustic indices can predict habitat type, and to test how vegetation structure relates to acoustic indices. We then discuss the implications of our findings for biodiversity assessments.

2. Methods

2.1. Study sites

We conducted this research in and around Viruá National Park (VNP), Roraima, Brazil, in the north of the Brazilian Amazon (Fig. S1). VNP was established in 1998 and is 240,000 ha (ICMBio, 2014). The climate in VNP is warm and wet with mean annual temperature of 26 °C and mean annual precipitation of ~ 2,000 mm (ICMBio, 2014). Rainfall is mostly concentrated from May to September (ICMBio, 2014). VNP is regulated by floods that create a vegetation mosaic ranging from dense forests to grasslands, and representing most major habitats found across the Amazon biome (ICMBio, 2014). These habitats share common species, but also harbor unique fauna and flora (Table S1). Based on vegetation characteristics and flooding regime, the eight habitats surveyed can be grouped as open habitats (burned campina, campina, and pastures), flooded forests (igapó, islands, and várzea), and non-flooded forests (campinarana and terra-firme). In summary, open habitats have lower species richness than forested habitats, and campiranana, igapó,

Table 1

Acoustic indices used to investigate habitat-specific soundscapes and the effect of vegetation structure on indices at different countries in comparison to this study that investigated both topics. Total recording hours and the number of sites surveyed are indicated. Abbreviations: ACI = Acoustic complexity index, ADI = Acoustic diversity index, AEI = Acoustic evenness index, BIO = Bioacoustics index, CENT = Centroid, D = Acoustic dissimilarity index, DF = Dominant frequency, ESM = Entropy spectral maxima, ESV = Entropy spectral variance, FLAT = Spectral flatness, FQ = First quartile, H = Total entropy, KURT = Kurtosis, M = Mean amplitude, MID = mid-band activity, NDSI = Normalized difference soundscape index, NP = Number of peaks, RSP = Relative soundscape power, SD = Standard deviation, SKEW = Skewness, TQ = Third quartile, ZCR = Zero-crossing Rate, 1/F = Spearman correlation to 1/f noise.

| Topic | Study | Acoustic indices | Country | Hours | Sites |
|------------------------------|---------------------------------|--|------------|--------|-------|
| Habitat-specific soundscapes | This study | ACI, AEI, BIO, CENT, DF, FLAT, FQ, H, KURT, NDSI, SD, SKEW, TQ | Brazil | 1,538 | 143 |
| | Bormpoudakis et al., (2013) | CENT, FLAT, H, KURT, SD, SKEW, ZCR, 1/F | Greece | 2 | 32 |
| | Bradfer-Lawrence et al., (2019) | ACI, ADI, AEI, BIO, H, M, NDSI | Panama | 26,000 | 117 |
| Vegetation structure effects | Gómez et al., (2018) | ACI, ADI, AEI, BIO, ESM, ESV, H, M, MID, NDSI, NP | Colombia | 905 | 8 |
| | Bradfer-Lawrence et al., (2020) | ACI, ADI, AEI, BIO, H, M, NDSI | Panama | 84 | 43 |
| | Farina and Pieretti (2014) | ACI | Italy | 520 | 20 |
| | Fuller et al., (2015) | ACI, ADI, AEI, BIO, H, NDSI | Australia | 465 | 19 |
| | Myers et al., (2019) | ACI, ADI, BIO | Greece | 132 | 22 |
| | Ng et al., (2018) | ACI, ADI, AEI, BIO, D, H, NDSI, RSP | Australia | 378 | 9 |
| | Pekin et al., (2012) | ADI | Costa Rica | 14 | 14 |
| | Rankin and Axel (2017) | BIO | Madagascar | 3,504 | 6 |
| | Tucker et al., (2014) | RSP | Australia | 272 | 10 |

and island forests are not as diverse as terra-firme and várzea forests (see Table S2 for additional information on habitats and Figs. S2–S9 for photos).

2.2. Passive acoustic monitoring and index extraction

We used ARBIMON acoustic recorders (Campos-Cerqueira & Aide, 2016) to collect acoustic data from November 2016 to February 2017 in the eight habitat types. We deployed recorders at 20 replicate sites in each habitat, with the exception of pastures, which were limited to six replicates because they comprised a small area in the VNP; and terra-firme, which had 17 replicates because of recorder malfunctions. This resulted in a total of 143 sites surveyed. Recorders were spaced over 500 m apart to minimize overlap in detections across recorders. Previous field tests conducted with ARBIMON recorders indicate that calls of the majority of bird and frog species can be detected up to ~100 m (Campos-Cerqueira et al., 2019). We attached recorders to trees or fixed poles at the height of 1.5 m. Acoustic devices were programmed to record 1 min of audio every 10 min for six days in each sampling site (sample rate = 44.1 kHz; resolution = 16 bit; format = WAV). After six days, the 20 recorders were moved to a different habitat type and the method repeated (see Table S2 for sampling periods).

Acoustic data collection resulted in 96,726 one-minute recordings (1612 h). For each one-minute recording, we calculated 13 acoustic indices to summarize the soundscapes of the eight habitats studied (Table 2). Two broad types of indices were used: indices that rely on statistical features of recordings (as described in Bormpoudakis et al., 2013; Mitrović et al., 2010); and signal complexity indices specifically developed for biodiversity assessments and landscape investigation (Sueur et al., 2014). We selected indices that were previously used to describe habitats in peer-reviewed publications (Bormpoudakis et al., 2013; Bradfer-Lawrence et al., 2019) and that could be calculated through open-source software.

Calculations were performed in the R Environment (R Core Team, 2019). The function “specprop” from Seewave package (Sueur et al., 2008b) was used to calculate the centroid (CENT), dominant frequency (DF), first quartile (FQ), kurtosis (KURT), skewness (SKEW), spectral flatness (FLAT), standard deviation (SD), and the third quartile (TQ) with default parameters of the package. The Soundecology package (Villanueva-Rivera and Pijanowski, 2018) was used to calculate the acoustic complexity index (ACI; Pieretti et al., 2011), acoustic evenness index (AEI; Villanueva-Rivera et al., 2011), bioacoustic index (BIO;

Boelman et al., 2007), total entropy (Sueur et al., 2008a), and the normalized difference soundscape index (NDSI; Kasten et al., 2012). Minimum frequency for ACI calculation was set to 500 Hz and maximum frequency to 12 kHz because the package did not have default values for this index, and this range encompasses most of birds’, amphibians’, and non-flying-mammals’ sounds while also reducing possible microphone self-noise interference (Bradfer-Lawrence et al., 2019). All other parameters used in the indices’ calculations were set to default values provided in the package.

We inspected index calculations for outliers that could be linked to file corruption, rain, or wind, and removed recordings containing these anomalies because they affected indices values disproportionately as observed in other studies (Bradfer-Lawrence et al., 2019; Depraetere et al., 2012; Pieretti et al., 2015). This removal of 4443 files resulted in 92,283 one-minute recordings (1538 h) for subsequent analysis. Our sites lacked significant anthropogenic sounds due their remoteness, but studies in more urbanized locations should inspect recordings for this source of sound because they may also affect indices values disproportionately (Fairbrass et al., 2017).

2.3. Vegetation structure survey

Vegetation structure data were collected within a 20-m radius plot from each acoustic recorder location (143 sites) after the devices were moved to a different habitat type to avoid interference with the recordings (similar to Rankin and Axel, 2017). We took two measurements of percent canopy cover facing north and then south with a densiometer at two points (5 m and 10 m from recorder’s original location) in each cardinal direction for a total of eight locations and 16 measurements per plot. We measured canopy height by visually estimating the height of the two largest trees in each plot. Two field assistants along one of the researchers took independent measurements of tree height to reduce possible bias in the field. We took two measurements (spaced 1 m apart) of litter depth at two points (5 m and 10 m from recorder original location) in each cardinal direction for a total of eight locations and 16 measurements per site. We measured diameter at breast height (DBH) of trees in four subplots 4 m from the recorder location and stretching for 10 m in length and 8 m wide in each cardinal direction. We counted all trees with DBH > 1 cm and divided them in small (DBH > 1 cm to < 10 cm) and large (DBH > 10 cm) classes for subsequent analysis. Finally, we used a 20-m tape to take two measurements of shrub cover per site (along north and south directions

Table 2
Description of the eight statistical indices and five complexity indices used in this study.

| Index type and name | Description |
|---|---|
| Statistical indices | |
| Centroid (CENT) | Mean frequency of the spectrum. |
| Dominant frequency (DF) | The frequency with the most energy in the spectrum. |
| First quartile (FQ) | Median frequency of the lower half of the spectrum. |
| Kurtosis (KURT) | Measures tailedness of signals in the spectrum. High values indicate outliers. |
| Skewness (SKEW) | Measures symmetry of signals in the spectrum. High values indicate that signals are skewed towards the high or low end of the spectrum. |
| Spectral flatness (FLAT) | Ratio between geometric and arithmetic mean amplitudes. Noisy signals will tend towards one and pure tones to zero. |
| Standard deviation (SD) | Spectral distribution of sounds. |
| Third quartile (TQ) | Median frequency of the upper half of the spectrum. |
| Complexity indices | |
| Acoustic Complexity Index (ACI) | Based on differences in amplitude between one time step and the next within a frequency band. Filters out constant sounds (e.g., insect chorus), this may lead to low values in rich soundscapes. |
| Acoustic Evenness Index (AEI) | Based on applying the Gini index to a specific number of frequency bands with signals above an amplitude threshold. High values indicate sound intensity is restricted to few frequencies. |
| Bioacoustic Index (BIO) | Based on the amplitude of a signal relative to the quietest frequency band within the 2–8 kHz range. High values indicate a great difference between loudest and quietest bands. |
| Total entropy (H) | Based on applying the Shannon index to a specific number of frequency bands and time steps. High values indicate sound intensity is distributed through many frequencies and time steps. |
| Normalized Difference Soundscape Index (NDSI) | Ratio between anthropogenic (1–2 kHz) and biological (2–11 kHz) sounds. High values indicate more biological sounds in the upper frequencies. |

from the recorder location) using the line-intercept method (Floyd and Anderson, 1987). For each vegetation structure variable, we used the mean value per site for subsequent analysis. Similar methods have been used in other studies to determine vegetation structure (Hill et al., 2019; Rankin and Axel, 2017; Smith et al., 2018).

2.4. Statistics

All statistical tests and model diagnostics were run in the R environment (R Core Team, 2019). To test for the existence of habitat-specific soundscapes, we used a random forest (RF) modeling approach (Cutler et al., 2007) with the 13 acoustic indices calculated from the recordings. We used RF because this approach allowed us to summarize the importance of individual indices in the classification (as in Bormpoudakis et al., 2013; Bradfer-Lawrence et al., 2019). We built two RF models, one classifying soundscapes of the eight different habitats and another classifying soundscapes of the three broader habitat types (open habitats, flooded forests, and non-flooded forests). In the first RF model, we separated the data into training (80%) and testing (20%) datasets. With the training dataset and the R package RandomForestSRC (Ishwaran et al., 2008), we built a random forest classifier with default values. We used the 13 acoustic indices from each one-minute recording to build the classifier to tentatively assign each one-minute recording to one of the eight habitats. We then used the “predict” function in the Caret package (Kuhn, 2008) to measure the accuracy of our model to predict the testing dataset. In the second RF model, we used the same approach as the first RF model; the only difference was that recordings were assigned to the three broader habitats instead of the eight finer-scale habitat types.

After visualizing the soundscapes and noticing distinct diel patterns

among the different habitats for each index (Fig. 1), we decided to separate day and night data to better understand the RF outputs. We averaged each one-minute recording made in the same time across all replicates within a habitat and assigned each recording to day (0600–1800 h) or night (1800–0600 h). We ran a permutational multivariate analysis of variance (PERMANOVA) with the Vegan package (Oksanen et al., 2019) to test if diurnal soundscapes were different from nocturnal soundscapes across habitats.

To determine whether acoustic indices relate to vegetation structure, we first calculated the mean value of each acoustic index per site (143 total), averaged across the six days of data collection (as in Fuller et al., 2015; Ng et al., 2018). Using the package nlme (Pinheiro et al., 2019), we built linear mixed models (LMMs) with each of the 13 acoustic indices as dependent variables, six vegetation structure variables (canopy cover, canopy height, litter depth, number of large trees, number of small trees, and shrub cover) as independent fixed effects, and habitat type as a random effect. Independent fixed effects were scaled (“scale” function in base R) to make their parameter estimates comparable within models. We performed model selection using the corrected Akaike information criteria (AICc; Burnham and Anderson, 2004). We selected the top four performing models based on $\Delta AICc$ and considered models to be similar if $\Delta AICc < 2$ (Burnham and Anderson, 2004). With the package car (Fox and Weisberg, 2019), we checked for multicollinearity of predictors and removed canopy height from the analysis. Residuals of the models were checked for linearity, homoscedasticity, independence, and normality with the package SjPlot (Lüdtke, 2020). We consider a fixed effect to be significant at an alpha level of < 0.05 . With the package R2glmm (Jaeger, 2017), we calculated the marginal and conditional R2 values (Nakagawa and Schielzeth, 2013) to estimate the proportion of variance explained by

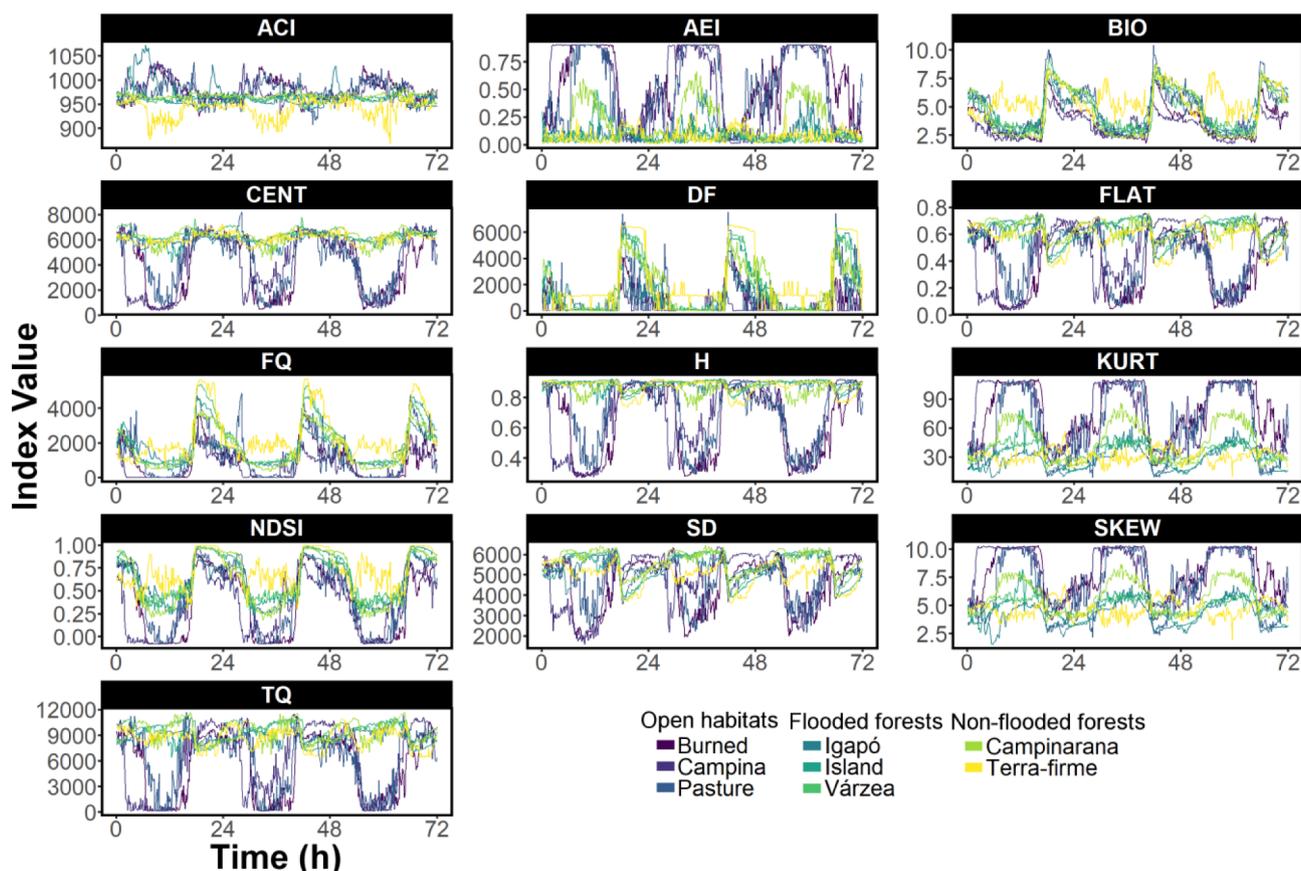


Fig. 1. Temporal trends of 13 acoustic indices across the eight habitats studied. Values of indices are the mean values calculated across all replicates within a habitat for each one-minute recording. Graph starts at 0100 h. For simplicity only three days of data are showed because patterns were consistent across the six-day sampling period.

Table 3

Confusion matrices from random forest classification of eight different habitats (first classification) and three broad habitat types (second classification) using 13 acoustic indices calculated from 73,827 one-minute recordings made in the Viruá National Park, Roraima, Brazil. Accuracy was measured by predicting the testing dataset (18,456 one-minute recordings). Abbreviations: B = burned campina, C = campina, Ca = campinarana, Ig = igapó, Is = island, P = pasture, T = terra-firme, V = várzea, O = open habitats (B + C + P), F = flooded forests (Ig + Is + V), NF = non-flooded forests (Ca + T).

| | | Actual | | | | | | | | | |
|-----------------------|----------------------|--------|-------|------|------|------|------|------|------|---------------------------------------|---------------------------------------|
| Predicted | First classification | | B | C | Ca | Ig | Is | P | T | V | Classification error |
| | B | 7724 | 1782 | 641 | 35 | 118 | 171 | 74 | 66 | 0.27 | |
| | C | 2108 | 7341 | 571 | 135 | 106 | 251 | 106 | 168 | 0.31 | |
| | Ca | 537 | 549 | 7408 | 272 | 297 | 20 | 194 | 219 | 0.21 | |
| | Ig | 65 | 220 | 466 | 7813 | 313 | 27 | 263 | 423 | 0.18 | |
| | Is | 175 | 265 | 450 | 498 | 7413 | 16 | 342 | 1394 | 0.29 | |
| | P | 505 | 637 | 172 | 154 | 98 | 1486 | 153 | 124 | 0.55 | |
| | T | 112 | 220 | 222 | 404 | 459 | 16 | 6790 | 635 | 0.23 | |
| | V | 70 | 120 | 241 | 453 | 1230 | 10 | 530 | 7953 | 0.24 | |
| | | | | | | | | | | | Total error = 0.26 Accuracy = 0.74 |
| Second classification | | O | F | NF | | | | | | Classification error | |
| O | 22207 | 1318 | 1200 | | | | | | 0.10 | | |
| F | 940 | 28299 | 1510 | | | | | | 0.07 | | |
| NF | 1879 | 3087 | 13387 | | | | | | 0.26 | | |
| | | | | | | | | | | Total error = 0.13 Accuracy = 0.87 | |

fixed and random effects.

3. Results

3.1. Habitat-specific soundscape patterns

The first RF classifier separated all 13 acoustic indices in the training dataset into the eight habitat classes. Internal error of the classifier was 26% and the model accuracy when predicting on the testing dataset was 74%. The habitat with the lowest internal error was igapó (18%), and the habitat with the highest internal error was the pasture (55%). Soundscapes from pastures were usually misclassified as the other two open habitats (Table 3). The most important acoustic indices to distinguish habitat types were TQ and CENT; if these variables were removed, the accuracy of the model would proportionally drop 0.15 and 0.14, respectively. SD, NDSI, ACI, KURT, and SKEW also performed well in the classification. The least important acoustic indices were DF and FLAT (Fig. 2).

The second RF classifier built to distinguish the soundscapes of three broader habitat types performed better than the first one. It had a lower

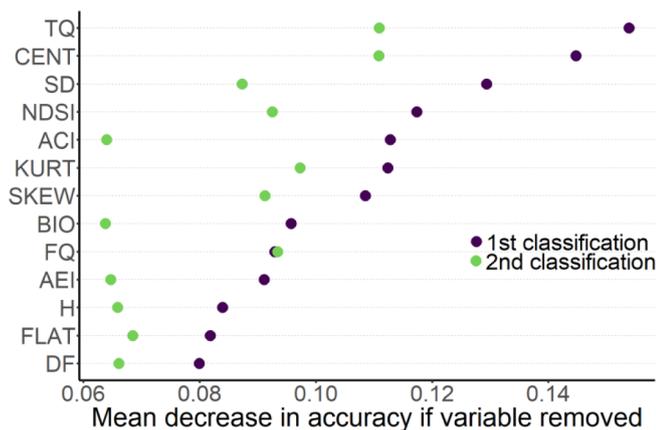


Fig. 2. Importance of acoustic indices at classifying eight habitat types (1st classification) and three broader habitat types (2nd classification) grouping the eight habitats. Graph shows the mean decline in accuracy of the models if a variable is removed. Accuracy of the first classification was 74% while in the second classification increased to 87%.

internal error, 13%, than the first classifier and accuracy of the model to predict habitat types within the testing dataset increased to 87% (Table 3). TQ and CENT were again the most important acoustic indices, reflecting a proportional drop of 0.11 in the classification accuracy if either was removed. The least important indices were ACI and BIO (Fig. 2).

The PERMANOVA revealed that diurnal and nocturnal soundscapes were different across all habitats ($F_{1,3447} = 2493.7, p < 0.001$; Table S3) and supported the RF classification because it showed a significant effect of habitat type on acoustic indices ($F_{7,3447} = 421.6, p < 0.001$). FLAT, H, SD, and TQ values were lower during the day and higher at night for open habitats, while forested habitats had the opposite pattern. BIO, DF, FQ, and NDSI were the only indices with consistent diel patterns across habitats; they were lower during the day and higher at night. Diel patterns of ACI, AEI, CENT, KURT, and SKEW were more marked for open than forested habitats; values in open habitats were higher during day than night, except for CENT that had the opposite pattern (Fig. 1).

3.2. Relationships between vegetation structure and soundscapes

Across the top performing models (Table S4), 11 of 13 acoustic indices were significantly associated with percent canopy cover (Fig. 3). We found a positive relationship between canopy cover and BIO, CENT, DF, FQ, H, NDSI, and TQ, and a negative relationship between canopy cover and ACI, AEI, KURT, and SKEW (Fig. 3). Other vegetation variables appeared in some top performing models, but their effect was not significant (Fig. 3). The only exception was the significant negative association of ACI with the number of large trees, but this effect was smaller than canopy cover (Fig. 3). A null model appeared between the two top performing models for the index FLAT, therefore we did not consider this index to be significantly related with vegetation structure (Table S4). Conditional R^2 of models with significant vegetation effects ranged from 19% to 81% while marginal R^2 of canopy cover ranged from 5% to 81% (Table S5).

4. Discussion

Determining the ability of soundscapes to discriminate habitat types and the response of acoustic indices to changes in vegetation structure is critical for improving ecological monitoring using ecoacoustic methods. In the present study, we found that eight habitat types in the Amazon biome have unique and predictable soundscapes. We found that, in general, acoustic indices that rely on statistical features of recordings (Bormpoudakis et al., 2013; Mitrović et al., 2010) were better at identifying habitat-specific soundscapes than acoustic indices based on signal complexity (Sueur et al., 2014). We also found that canopy cover was the primary vegetation variable explaining variance in acoustic indices. These results expand our knowledge regarding which acoustic indices best link changes in habitats to changes in soundscapes. These findings are particularly important for diverse ecosystems, like the Amazon, which are known to have complex soundscapes with sound producing animals that are difficult to detect with traditional survey methods (e.g., visual transects).

4.1. Habitat-specific soundscape patterns

We evaluated the ability of 13 acoustic indices to distinguish soundscapes of eight habitat types in the Amazon. In our study, TQ and CENT were the best indices at distinguishing habitat-specific soundscapes (Fig. 2), similar to results reported from Greece (Bormpoudakis et al., 2013). In both our first classification of eight habitat types and second classification of three habitat groups, the top indices for variable importance were statistical in nature and the majority of the indices based on signal complexity were in the bottom half of variables. Acoustic indices that rely on statistical features, like the TQ and CENT,

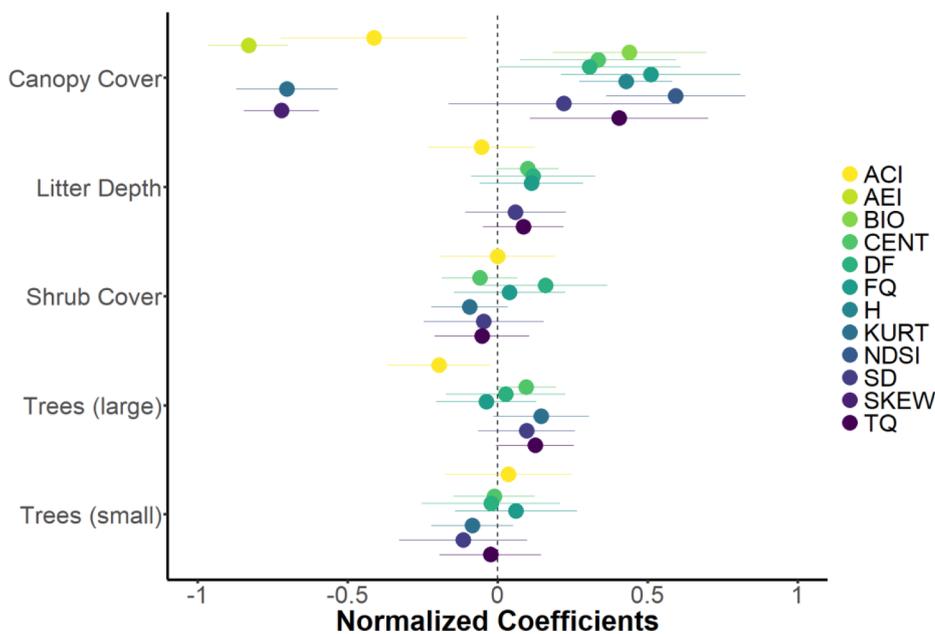


Fig. 3. Results of linear mixed models for 12 acoustic indices showing the effects of five vegetation variables on the indices. Dots are the normalized coefficients' values and lines represent the 95% confidence intervals. Coefficients were normalized by subtracting raw values by the mean and dividing by the standard deviation. Index FLAT is not shown because top performing model included a null model.

indicate at which frequency the majority of species are producing sounds, while signal complexity indices, like the AEI and H, measure overall acoustic diversity over a pre-defined range (e.g., 0 – 1). While one type of index performed better than the other, they all contributed to the predictive power of the RF classifications, and because they reflect different aspects of soundscapes (Table 2), they can facilitate the interpretation of patterns when analyzed together (Bradfer-Lawrence et al., 2019, 2020).

One of the main soundscape features that separated habitat types was the diel patterns of the indices (Fig. 1). Based on our field observations and listening to the original recordings, open habitats have insect activity at nighttime but during the day were mostly devoid of animal sounds. In contrast, the soundscapes of forested habitats have a lot of animal sounds over 24-h periods, leading to the subtler differences between day and night. In addition, each of the habitats is known to have a unique composition of bird species which can further help explain the differences in soundscapes observed among the habitats (Laranjeiras et al., 2014). To the best of our knowledge, indices based on statistical features of recordings (DF, FQ, KURT, FLAT, SD, SKEW, and TQ) have not had their diel patterns described (with the exception of CENT; Eldridge et al., 2018), but they all showed differences between nocturnal and diurnal soundscapes in our study. This feature likely increased the ability of these indices to identify habitat-specific soundscapes, and could make these indices useful in distinguishing habitats in other regions. For the signal complexity indices that have had their diel patterns previously described (ACI, AEI, BIO, H, and NDSI), it seems that differences between the day and night are dependent on the region, habitat type, and components of soundscapes due to inconsistent reports in the literature (Bradfer-Lawrence et al., 2019; Fuller et al., 2015; Gage et al., 2017; Ng et al., 2018; Pieretti et al., 2015).

4.2. Vegetation structure and acoustic indices

In general, we found that the amount of tree cover, represented by percent canopy cover and large trees, were the most important variables explaining soundscapes. For some acoustic indices, such as AEI and SKEW, canopy cover substantially explained their variances (81% and 52%, respectively), but for other indices, such as DF, even though there was a significant relationship with canopy cover, only a small percent of the variance was explained (5%). Besides canopy cover, the other vegetation variables we measured did not appear important in

explaining acoustic indices despite their appearance in some top performing models (Fig. 3).

Soundscapes rich in frequencies were linked to high canopy cover, while soundscapes poor in frequencies were linked to low canopy cover. This is similar to the effects of canopy cover on species richness across different animal taxa (reviewed in Stein et al., 2014). In our study sites, habitats with greater layer complexity (forested habitats) have greater avian and insect richness than less complex habitats (open habitats) (Table S1). These differences in species richness can help explain the soundscape patterns observed, especially if we consider that insects are a major driver of acoustic diversity in the tropical region (Aide et al., 2017). The direction of the relationship between canopy cover and acoustic indices was positive for seven indices and negative for four indices (Fig. 3). Two indices, FLAT and SD, were not significant related to any vegetative structure variable (Table S5). The four indices with negative relationships reflect the way the indices are calculated and not lower acoustic diversity in forested sites. For example, AEI is expected to have lower values in sites with rich soundscapes (i.e., forested) because sound intensity does not vary greatly between frequency bands in such sites (Bradfer-Lawrence et al., 2019).

Our findings partially agree with past research on this topic (Table 1). For example, two independent studies in Australia found that AEI, H, and NDSI were associated with vegetation structure (Fuller et al., 2015; Ng et al., 2018), but unlike our study, they found no relationship with ACI or BIO. But, in Madagascar, it was found that the BIO was associated with vegetation structure (Rankin and Axel 2017). Also, vegetation structure seems to be an important predictor of ACI in Greece, Italy, and Panama, similar to our study (Bradfer-Lawrence et al., 2020; Farina and Pieretti, 2014; Myers et al., 2019). Our results expand the number of acoustic indices linking vegetation to soundscapes and ultimately contribute to the body of research suggesting that relationships between vegetation and soundscapes may be a widespread phenomenon across regions and ecosystems. These results further indicate that vegetation structural characteristics (especially canopy cover) may be used with acoustic indices to predict changes in habitats across large spatial scales (see Pekin et al., 2012, for a first spatial forecast attempt).

4.3. Limitations

One limitation of this study was that we could not sample all habitats simultaneously due to logistical constraints. However, we do not

think this significantly biased our data because we collected data within a short period of time (~2 months) (Table S2), in similar weather conditions (dry season), and with many replications in each habitat type that showed minimal variability. In addition, by performing the RF classification that grouped the eight habitats into broader classes, this temporal constraint was addressed because habitats were sampled randomly (Table S2). Similarly, by using habitat type as a random effect in the LMMs this issue is partially addressed. Another limitation is that we did not identify individual species in the recordings, which limits our interpretation of specific soundscape components. However, this was beyond the scope of this research.

5. Implications for biodiversity assessments

Acoustic indices have been proposed as proxies to monitor biodiversity and environmental change (Buxton et al., 2018; Krause and Farina, 2016; Sueur et al., 2014). Our findings suggest that scientists and practitioners can differentiate and predict soundscapes of different habitats by using acoustic indices. In particular, our study highlights that acoustic indices (especially TQ and CENT) are able to classify habitats, even among those that are structurally similar or share similar fauna (Table S2). For example, soundscapes of grasslands burned nine months prior to data collection were different than those of intact grasslands (campina), suggesting that acoustic indices can be used to track the impacts of wildfire, an increasing threat to tropical ecosystems (Staver et al., 2020). Similarly, soundscapes of várzea forests were different than islands forests, and because islands have species in jeopardy due plans of dam construction (Naka et al., 2020), acoustic indices could serve as a cost-effective way to monitor such species.

A second important implication of our findings for biodiversity assessments is the ability to build predictive models linking fine-scale changes in vegetation structure to acoustic diversity. While TQ and CENT indices worked best to differentiate habitats, the acoustic indices that were best linked to changes in vegetation structure (canopy cover) were AEI and SKEW. The reason that some indices might be better at some tasks than others should be explored in future studies. AEI and SKEW could be used together with vegetation remote sensing tools, such as LiDAR, to predict how habitat degradation (e.g., canopy loss due to deforestation) affects animal diversity. This synergetic approach between two scalable remote sensing methods, ecoacoustic and airborne surveys, may offer an alternative for multi-taxa animal surveys at policy-relevant extents (Bush et al., 2017; Pekin et al., 2012; Rappaport et al., 2020).

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CRediT authorship contribution statement

Leandro A. Do Nascimento: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Writing - original draft. **Marconi Campos-Cerqueira:** Writing - review & editing. **Karen H. Beard:** Funding acquisition, Methodology, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.106679>.

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