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Acoustic monitoring reveals diversity and surprising dynamics in tropical freshwater soundscapes

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Abstract

1. Freshwater systems are globally threatened and in need of enhanced monitoring and assessment. We applied soundscape recording and analysis—which presents an opportunity for long-term, high-resolution animal community monitoring and assessment—to a freshwater context to better understand the acoustic diversity and dynamics of these systems.
2. We recorded the aquatic soundscape of a Neotropical freshwater swamp in Costa Rica for 23 days in January and February 2015 during the dry season. We classified biological sound types in these recordings and developed measurements of richness and occupancy based on this classification. We also calculated six complementary acoustic indices to assess soundscape diversity and daily and longer-term soundscape dynamics, and we examined correlations between these acoustic indices and sound type metrics.
3. We found rich soundscapes in which biological sounds were almost always present, and we classified 18 sound types that we attribute to aquatic insects. These sound types showed distinct daily patterns and exhibited temporal and spectral acoustic niche partitioning. Sound type richness was most correlated with the number of peaks index (correlation = .36; $p < .001$), while sound type occupancy was most correlated with the Bioacoustic Index (correlation = .92; $p < .001$). In contrast to generally high levels of acoustic activity, there were brief (approximately 1 hr), unexpected quiet periods around dawn and dusk.
4. This study represents an early attempt to comprehensively describe tropical freshwater soundscapes in a systematic and quantitative manner. We demonstrate that sound type classification and the quantification of acoustic occupancy capture aspects of soundscape diversity and dynamics that are complementary to those assessed by acoustic indices. Our analyses reveal that the soundscapes of this tropical wetland were diverse and exhibited daily dynamics that differed from those found in other ecosystems.

KEYWORDS

acoustic, aquatic insects, freshwater, monitoring, soundscape

1 | INTRODUCTION

Globally, human activities are rapidly degrading freshwater systems, threatening the biodiversity they host and the ecosystem services they provide (Daniels & Cumming, 2008; Thomsen et al., 2012). Conservation of these systems depends on enhanced understanding of their ecological dynamics, especially in ecologically important and data-deficient regions like the tropics (Revenga, Campbell, Abell, de Villiers, & Bryer, 2005). In these difficult-to-access aquatic environments where visibility can be limited, sound is often a principle means of animal communication, and this acoustic communication presents an opportunity for researchers to conduct long-term, high-resolution acoustic monitoring (Jansson, 1974; Luczkovich, Mann, & Rountree, 2008). Thus far, almost all underwater acoustic studies that aim to evaluate biological diversity or habitat condition have focused on marine habitats (Coquereau, Lossent, Grall, & Chauvaud, 2017; Freeman et al., 2014; Harris, Shears, & Radford, 2016; Miksis-Olds, 2013; Parks, Miksis-Olds, & Denes, 2014; cf. Desjonquères et al., 2015). Freshwater acoustic research has principally focused on characterising the bioacoustics of individual species, as opposed to the diversity and dynamics of habitat soundscapes.

Soundscapes are collections of all sounds occurring at a place over a given time frame and are composed of biological, geophysical and anthropic sounds (Pijanowski, Villanueva-Rivera, et al., 2011). Biological sound sources represent a subset of the biological community present. By quantifying the diversity and occurrences of biological sounds, it is possible to assess animal

activity patterns and in some cases evaluate biodiversity or habitat condition. Recent research has proven the utility of soundscape recording and analysis for monitoring biodiversity and habitat condition in terrestrial and marine systems (Fuller, Axel, Tucker, & Gage, 2015; Harris, Shears, & Radford, 2016; Pekin, Jung, Villanueva-Rivera, Pijanowski, & Ahumada, 2012). Benefits of soundscape monitoring in contrast to more traditional survey methods include (1) non-invasive sampling, (2) high temporal resolution, (3) the ability to sample in remote locations, at night and through disturbance events, (4) digital data that are preserved for long-term studies or later reanalysis, (5) relatively low cost and (6) the ability to automate approaches to provide near-real-time assessments.

Soundscape approaches could enhance existing freshwater monitoring and assessment efforts. One aquatic habitat in need of biological monitoring advances is the forested freshwater area of Central America (15,000 km²), which is located within the global biodiversity hotspot of Mesoamerica (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). These forested wetlands recharge aquifers, control floods, store nutrients and provide numerous other ecosystem services (Mitsch et al., 2008), but assessing this habitat is especially challenging due to a dearth of full species inventories (Ellison, 2004). A small portion of these 15,000 km² falls within La Selva Biological Station in northeastern Costa Rica (Figure 1). This wetland complex includes Cantarana Swamp, a small endorheic wetland that is the focus of this study in which we use underwater passive acoustic monitoring to assess the acoustic composition and dynamics of soniferous aquatic animals.

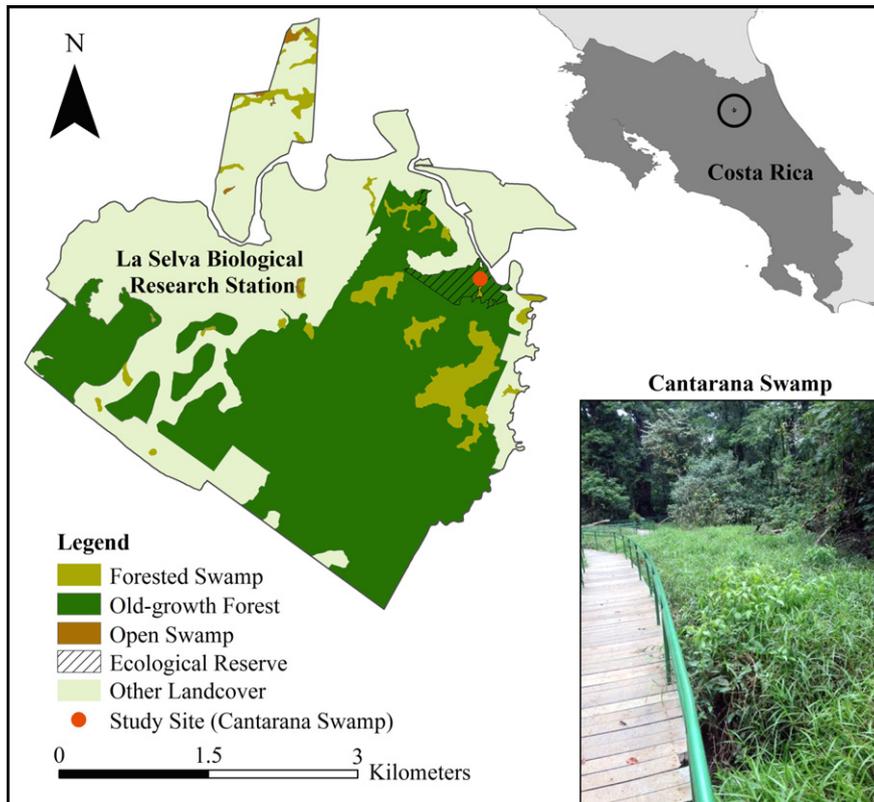


FIGURE 1 Maps of Costa Rica and La Selva Biological Research Station and a photograph of Cantarana Swamp where the acoustic recorder was deployed. On the map of Costa Rica, the encircled dot is La Selva Biological Research Station

This study represents an early attempt at comprehensively describing tropical freshwater soundscapes in a systematic and quantitative manner. Our central goal was to measure Cantarana Swamp soundscapes and to evaluate the diversity and dynamics of biological sounds based on those measurements. To describe the soundscape diversity and dynamics, we (1) manually classified sound types and statistically evaluated this classification, (2) quantitatively measured soundscapes and their diversity using acoustic indices and sound type presence/absence, richness, and occupancy and (3) visualised and described the daily and longer-term soundscape dynamics based on these acoustic metrics. To assess how well acoustic indices captured sound type richness and occupancy, we compared these measurements. We interpreted soundscape diversity and dynamics in the context of known present taxa, environmental conditions and theories of animal communication and soundscape ecology. As part of this discussion, we examined the nature and extent of temporal and spectral acoustic niche partitioning of the identified sound types.

2 | METHODS

2.1 | Study area and time period

Cantarana Swamp is located in La Selva Biological Research Station (10.428683°N, 84.004767°W; hereafter referred to as “La Selva”), where the high biodiversity is noteworthy even with respect to other Costa Rican or Central American rainforests (McDade, Bawa, Hespeneheide, & Hartshorn, 1994). The high richness of vertebrate species—48 amphibian species (Donnelly & Guyer, 1994), 412 bird species (McDade et al., 1994) and 120 mammal species (McDade et al., 1994)—is dwarfed by the invertebrate species richness, which has been estimated to be in the hundreds of thousands (De la Rosa, 2017b). The climate of La Selva is characteristic of Atlantic tropical wet forests. The 23-day study period (22 January–13 February 2015) occurred during La Selva’s dry season (December–April) when monthly rainfall totals typically drop to approximately 80 mm below the monthly average of 330 mm (McDade et al., 1994). Sunrise ranged from 05:56 to 05:59, and sunset ranged from 17:36 to 17:44. Mean solar radiation, which was collected by La Selva in 30-min intervals, was above zero from 05:00 to 18:30 (see Supporting Information for further meteorological details; McDade et al., 1994). A new moon occurred on 27 January 2015.

Cantarana Swamp is situated in an area of old-growth forest about 600 m from the main campus of La Selva (Figure 1). When full, the swamp can measure 70 × 90 m and at least 1-m deep (De la Rosa, 2017a). It lacks an inlet or an outlet but fills from rainfall and occasional flooding from nearby rivers, and it drains through infiltration and evaporation. It can dry out intermittently for up to several months, usually between February and April.

As Cantarana Swamp is in a zero-extraction zone at La Selva, we were unable to obtain complete species inventories of animals that inhabit or frequent the swamp. Through

communication with scientists who have worked near this swamp, however, we were able to obtain information based on personal observations and inferences based on other local studies. Generally speaking, aquatic animals that utilise the wetland include amphibians, fish, reptiles and insects. The further detail that we have on 11 frog species, a single known family of fish, and insect taxa likely to be in Cantarana Swamp is presented in the discussion and Supporting Information (De la Rosa, 2017b; Whitfield, 2017).

2.2 | Acoustic data collection and processing

BP and AG deployed a hydrophone (HTI-96-MIN, High Tech, Inc., Long Beach, MS, U.S.A.) 5 m from the edge of Cantarana Swamp on 22 January 2015. The depth of the swamp during the time of deployment was 0.5 m (B. Pijanowski and A. Gasc, personal observation), and the hydrophone was placed at the bottom of the swamp. An automated acoustic recorder (Song Meter SM2, Wildlife Acoustics, Maynard, MA, U.S.A.) was fastened to a wooden boardwalk that runs through the swamp, and the hydrophone was attached to one input port while a terrestrial microphone (SMX-II, Wildlife Acoustics, Maynard, MA, U.S.A.) was attached to the other port. Recordings were obtained in .wav file format at a 44.1 kHz sampling rate using 16 bits. The HTI hydrophone had a factory-reported sensitivity of -165 dB V/ μ Pa, and the SMX-II microphone had a factory-reported sensitivity of -36 dB V/Pa. A gain of $+36$ dB was applied to each track. The sensor was programmed to record 10 min every hour and 1 min every 15 min from 13:30 on 22 January–15:45 on 13 February 2015, producing 2,121 sound files. Each file was cropped to the first minute, and the hydrophone channel was separated from the terrestrial channel. Sound pressure levels (SPL) did not substantially decline over the course of the study period in the hydrophone channel, indicating that any hydrophone submersion in the swamp sediment was negligible in terms of acoustic dampening.

2.3 | Analysis overview and audio library definition

To find and differentiate between sound types, BG listened to numerous files while viewing their spectrograms and then determined rules that could distinguish between the 18 found sound types (see section 2.3.1 and Figure 2 for more details). Clips of individual sound types were extracted and used to quantitatively evaluate the manual classification. Full sound files were used to assess soundscape diversity and dynamics by quantifying sound type occupancy and calculating acoustic indices. To perform these analyses, three audio libraries were created. Audio Library A consisted of ten instances of each sound type ($n = 180$) that had high signal-to-noise (SNR) ratios and were unmasked by other sound types. All clips were taken from separate audio files, unless there were not enough files with unmasked clips, in which case multiple sound type clips were taken from the same audio file. Audio Library B was a stratified-random subset of 240 files. Files with

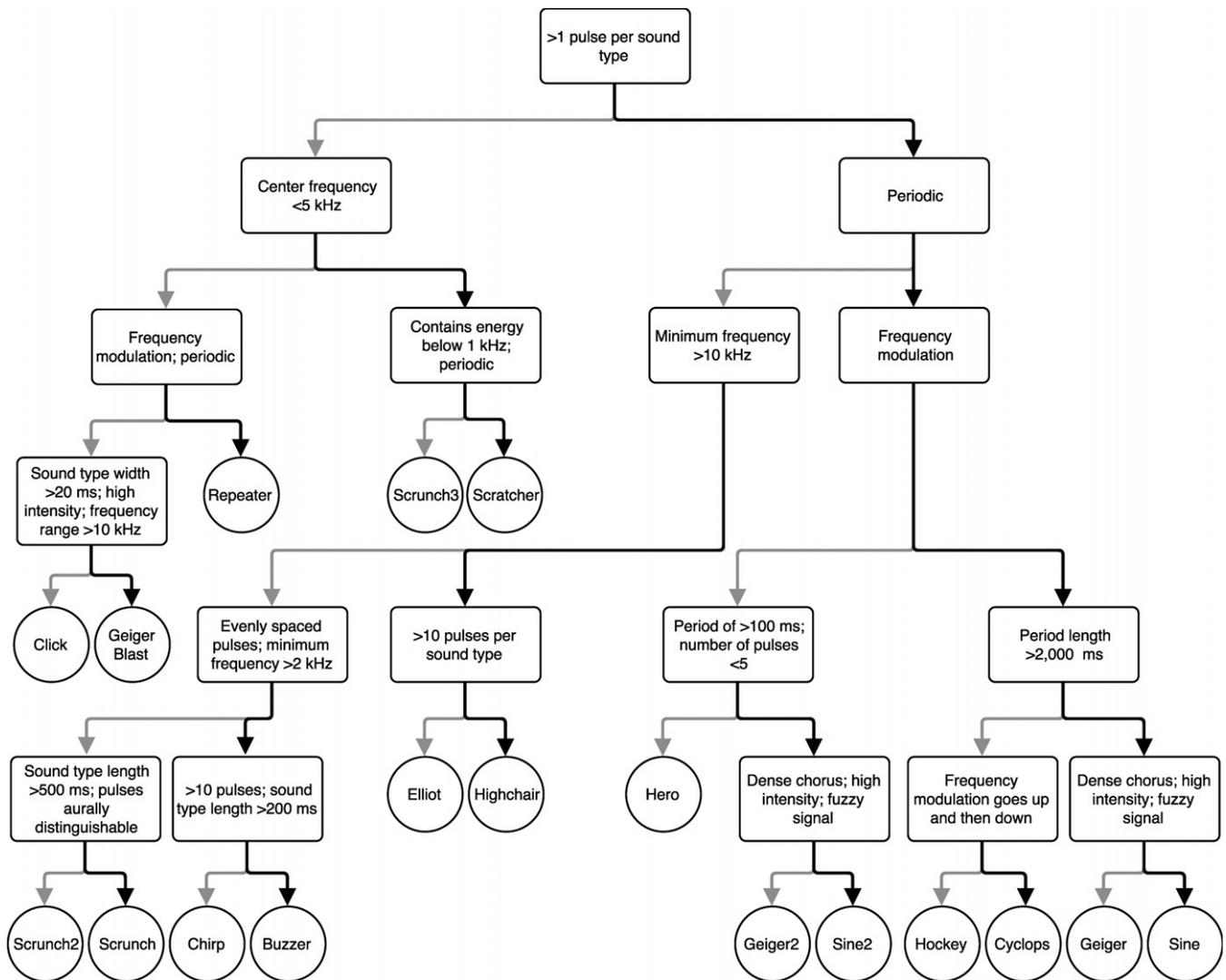


FIGURE 2 Decision tree used to classify the 18 sound types. Each node contains at least one binary classification rule. Sound types that satisfy a binary rule follow the black arrow, while sound types that do not satisfy a binary rule follow the grey arrow

rain were excluded, and ten files were selected for each hour of the day (five from January and five from February). For each file, a clip of each sound type present in the file was selected to calculate additional acoustic measurements (as defined in 2.4.2). Audio Library C (1,699 files) was the full set of audio files excluding those containing rain. Prior to all analyses on libraries B and C, sound files were reordered using a random number generator to ensure that temporal variation in sound type presence and occupancy was not influenced by listening order.

2.3.1 | Manual sound type classification

BG listened to a random collection of sound files to become acquainted with the data and to identify the various sound types present in these recordings. Since there was no existing sound library for aquatic animals from Costa Rica, or even for Central America, we could not classify sounds to any taxonomic level. Instead, we developed a classification system based on sound types,

in a similar fashion to Desjonquères et al. (2015) and Anderson, Rountree, and Juanes (2008).

Sound types were classified based on audible differences and visual inspection of spectrograms. While there was a large degree of plasticity in most of the sound types identified, BG was able to develop rules from which classifications could be made. If no rule could distinguish between sets of sounds, they were grouped into one type (see Figure 2 and Supporting Information S2.0 for a hierarchical outline of classification rules and additional information on sound type classification). By comparing terrestrial recordings with the hydrophone recordings, it was possible to ascertain whether any sounds in the hydrophone channel originated from above water, and those sounds were not analysed as sound types. All sound type classification was performed in Raven Pro (*Raven Pro: Interactive Sound Analysis Software*, 2016). BG listened to each file at least once while viewing the spectrogram (1,024-sample window length, 50% frame overlap and Hanning window type; following Warrington, McDonald, Rollins, & Griffith, 2014).

2.3.2 | Quantitative analysis of sound types

Quantitative acoustic measurements were calculated for each sound type clip in libraries A and B to (1) validate the manual sound type classification, (2) test the utility of automated classification and (3) develop sound type-based measures of acoustic occupancy. We calculated the following 11 acoustic measurements (additional sound type measurements are provided in Table S1):

1. “Center frequency,” the frequency at which the sound can be divided into two frequency intervals of equal energy;
2. “Peak frequency,” the frequency with the highest average power;
3. “Bandwidth 90%,” the difference between the 5% frequency (above which 95% of the energy is contained) and the 95% frequency (below which 95% of the energy is contained);
4. “High frequency,” the highest frequency of the selection;
5. “Low frequency,” the lowest frequency of the selection;
6. “Delta frequency,” the difference between high frequency (4) and low frequency (5);
7. “Delta time,” the length of the selection;
8. “Aggregate entropy,” the proportion of energy in each frequency bin times its log (base 2), summed over all frequency bins;
9. “Average entropy,” the aggregate entropy (8) divided by the number of discrete Fourier transform frames in the clip;
10. “Average power,” the sum of the power spectral density of each spectrogram pixel divided by the number of pixels in the selection.
11. “Periodicity,” the regular repetition of sounds—“true” if a sound type repeated at least five times in a recording with consistently spaced intervals.

We then performed a linear discriminant analysis (LDA) with leave-one-out cross-validation to determine whether these 11 features would differentiate between sound types in accordance with the manual classifications (Venables & Ripley, 2002). Due to misclassifications between two sound types, Geiger and Sine (Figure S1), we also quantified the period length, pulse width and interpulse distance for randomly selected Geiger and Sine clips from Library B. We determined whether these additional features would differentiate between these two sound types using a *k*-means test (Hartigan & Wong, 1979) and a logistic regression (McLeod & Xu, 2017). Please refer to Supporting Information for detailed protocol and source code for the LDA and the period and pulse quantification.

2.4 | Sound type composition and dynamics

We evaluated the presence/absence of each sound type within each recording in Library C. We did not evaluate the abundance of each sound type within these files. We calculated the total number of occurrences of each sound type (maximum possible: one occurrence per file = 1,699 occurrences) and the total number of occurrences

per hour of each sound type (maximum possible: 23 days of recording \times 4 recordings made each hour = 92 occurrences). For each recording, we also calculated sound type richness—the number of sound types present in a file—within each hour and over the 23-day recording period. When calculating mean daily sound type richness, only full recording days ($n = 21$) were considered.

In addition to the above analyses, we employed a new acoustic measurement, “temporal occupancy,” along with frequency and amplitude measurements, to quantify the occupancy of sound types within the acoustic space of each file in Audio Library B. Temporal occupancy refers to the proportion of time within a file that the amplitude of a sound type occurrence was non-negligible—spaces between pulses and between separate sound type instances were excluded from temporal occupancy. It was estimated for each sound type through visual examination of the spectrogram for each file. We consider the acoustic space at any location to have two dimensions: time and frequency. The occupancy of acoustic space is a scalar field in which amplitude is the scalar value at each time–frequency point in acoustic space.

We developed three occupancy measures to quantify the use of acoustic space within each file in Library B. Occupancy 1 only considers the dimension of time. It is equal to the sum of sound types’ temporal occupancies. Occupancy 2 considers the dimensions of time and frequency and is equal to the sum of the products of sound types’ temporal occupancies and their delta frequencies. Occupancy 3 similarly considers the dimensions of time and frequency, but also accounts for amplitude. It is equal to the sum of the product of sound types’ temporal occupancies, their delta frequencies and their average powers. Delta frequency and average power were calculated on at least one representative instance of each sound type present within a file. In cases when delta frequency and average power measures were calculated on multiple instances of a sound type within a file, these measures were averaged to attain one delta frequency and average power value per sound type per file.

2.5 | Soundscape diversity and dynamics

Acoustic indices are measurements of a soundscape that yield ecologically meaningful information about biodiversity and biological activity patterns. They have been employed in many habitat types, including freshwater habitats (Desjonquères et al., 2015; Harris et al., 2016; Pieretti, Farina, & Morri, 2011). We computed 20 acoustic indices for each 1-min recording in Audio Library C. All acoustic indices (other than acoustic occupancy, SPL and the standard deviation of SPL) were from Towsey, Wimmer, Williamson, and Roe (2014) and Sueur, Farina, Gasc, Pieretti, and Pavoine (2014), and all other than SPL and the Standard Deviation of SPL were calculated in the R statistical computing environment using version 3.2.4 (R Core Team, Vienna, Austria). Most of these indices are available in the R packages “seewave” (Sueur, Aubin, & Simonis, 2008) and “soundecology” (Villanueva-Rivera & Pijanowski, 2016), and others were coded by the authors (code available through GitHub; see

Supporting Information for details). SPL and its standard deviation were calculated in MATLAB (The MathWorks, Inc., Natick, MA, U.S.A.) using PAMGuide (Merchant et al., 2015) with a frequency range of 1–22,050 Hz, a window length of 512 samples, a 50% overlap and a “Hann” window. For each file, there were 10,334 SPL values. We calculated the mean and standard deviation of these values for each recording. A table of all indices used in this analysis, their original references, the chosen settings, and correlation coefficients and *p*-values for tests described below is included in Supporting Information (Table S2).

We performed correlation tests to determine which acoustic indices were correlated with sound type richness and sound type occupancy. Since the sound type richness data and values for one acoustic index were not continuous, we employed Spearman’s formula (Daniel, 1978). For each acoustic index, we performed one correlation test for Audio Library C comparing acoustic index values against sound type richness, and four correlation tests for Audio Library B comparing acoustic index values against sound type richness, Occupancy 1, Occupancy 2 and Occupancy 3. All *p*-values were adjusted using a Bonferroni family-wise alpha correction (Holm, 1979). Prior to calculating the correlation tests for Library C, we employed first differencing on the acoustic index and sound type richness time-series in order to reduce autocorrelation in these series (Dickey & Pantula, 1987). We determined whether autocorrelation was adequately reduced by viewing the autocorrelation function plot for each time-series using a maximum lag of 530 (25% of the 2,212 files). We verified that time-series had fewer than 5% of the lag times outside of the 95% confidence interval bounds. Since the four correlation tests for Library B were performed on a stratified-random subset, we did not transform these data before performing these correlation tests. Six indices of the 20 calculated are included in the results and discussion based on their high correlation coefficients and the fact that they measure different aspects of a soundscape. These indices are the Bioacoustic Index (BI), background noise (BN), number of peaks (NP), SPL, the standard deviation of SPL (SDSPL) and the root mean square (RMS) amplitude. BI represents the energy between a mean spectrum curve and the minimum value of that curve (Boelman, Asner, Hart, & Martin, 2007). BN is the mode of windowed average amplitude values between a minimum dB threshold and 10 dB above that threshold (Towsey et al., 2014). NP is the number of peaks in a mean spectrum (Gasc, Sueur, Pavoine, Pellens, & Grandcolas, 2013). RMS is the square root of the mean of squared recorded pressure values (Sueur et al., 2008). SPL is the mean RMS calculated for separate windows within a recording, and SDSPL is the standard deviation of those RMS values (Merchant et al., 2015).

3 | RESULTS

3.1 | Sound type descriptions

The 18 sound types that were classified and named are presented in Figures 3 and 4 (example sound type recordings are provided in Supporting Information). The frequencies of the sound types spanned the full spectrum of recordings (0–22.05 kHz). On the low

end, Scratcher’s broadband *raps*, which sounded like scratches against a substrate, contained energy reaching below 40 Hz. On the high end, Elliott was cut off at the top portion of the frequency spectrum. In this rich sonic environment, the acoustic space was dominated by four sound types: Geiger, Geiger2, Sine and Sine2. Sine and Sine2 occurred at night, while Geiger and Geiger2 were the most frequently occurring sound types during the day-time, although they were less intense than their night-time counterparts. Because the frequency ranges of ten sound types, including Geiger, Geiger2, Click, Geiger Blast, Sine, Sine2, Cyclops, Hockey, Hero and Buzzer, partially overlapped in the range of 7–15 kHz, this acoustic space was densely occupied. Repeater, Hockey and Cyclops were frequently masked by Geiger and Sine, while Buzzer, though short in duration, was prominent even amongst the dominant sound types.

All sounds were composed of single impulses or pulses. We define impulses as the smallest discernible temporal units of a sound type and pulses as groups of impulses. While several of the sound types were relatively simple, merely consisting of evenly spaced pulses or impulses that became closer together over the course of each pulse (as in the case of Scrunch and Scrunch2), some sound types had complex frequency and amplitude modulations. Geiger, Sine, Cyclops, Repeater and Hockey all exhibited dramatic frequency modulations with differences up to 9 kHz between the centre frequencies of low- and high-frequency portions. Sometimes, the high-frequency portions of these sound types had a different pulse rate, pulse width, interpulse distance or amplitude than the low-frequency portions.

Some sound types may have originated from the same source. Geiger, Geiger2 and Geiger Blast frequently co-occurred in recordings and often immediately followed each other at similar amplitudes, suggesting that one animal may have produced these different sound types (see Figure 3 for spectrograms and oscillograms). Sine and Sine2 most likely come from the same producer because Sine was a frequency-modulated version of Sine2 and the two almost always co-occurred. Scrunch and Scrunch2 also occurred in the same frequency range, and both sound types were single pulses in which the interval between impulses decreased over the course of the sound type. Scrunch, however, was much longer (1–2 s) and exhibited greater interimpulse intervals than Scrunch2 (0.2 s), for which impulses were “scrunched” together and could not be aurally differentiated.

3.2 | Sound type validation

The LDA correctly classified 87% of the observations in our feature set model (first and second axes accounting for 76% and 13% of variance) as opposed to our null model that correctly classified only 10% of observations. Excluding Geiger (20% accuracy), Click (60% accuracy) and Sine (60% accuracy), the other 15 sound types were classified with 95% accuracy. Click’s four misclassifications were distributed across three groups; 75% of Geiger’s eight misclassifications were attributed to Sine, and 100% of Sine’s misclassifications were

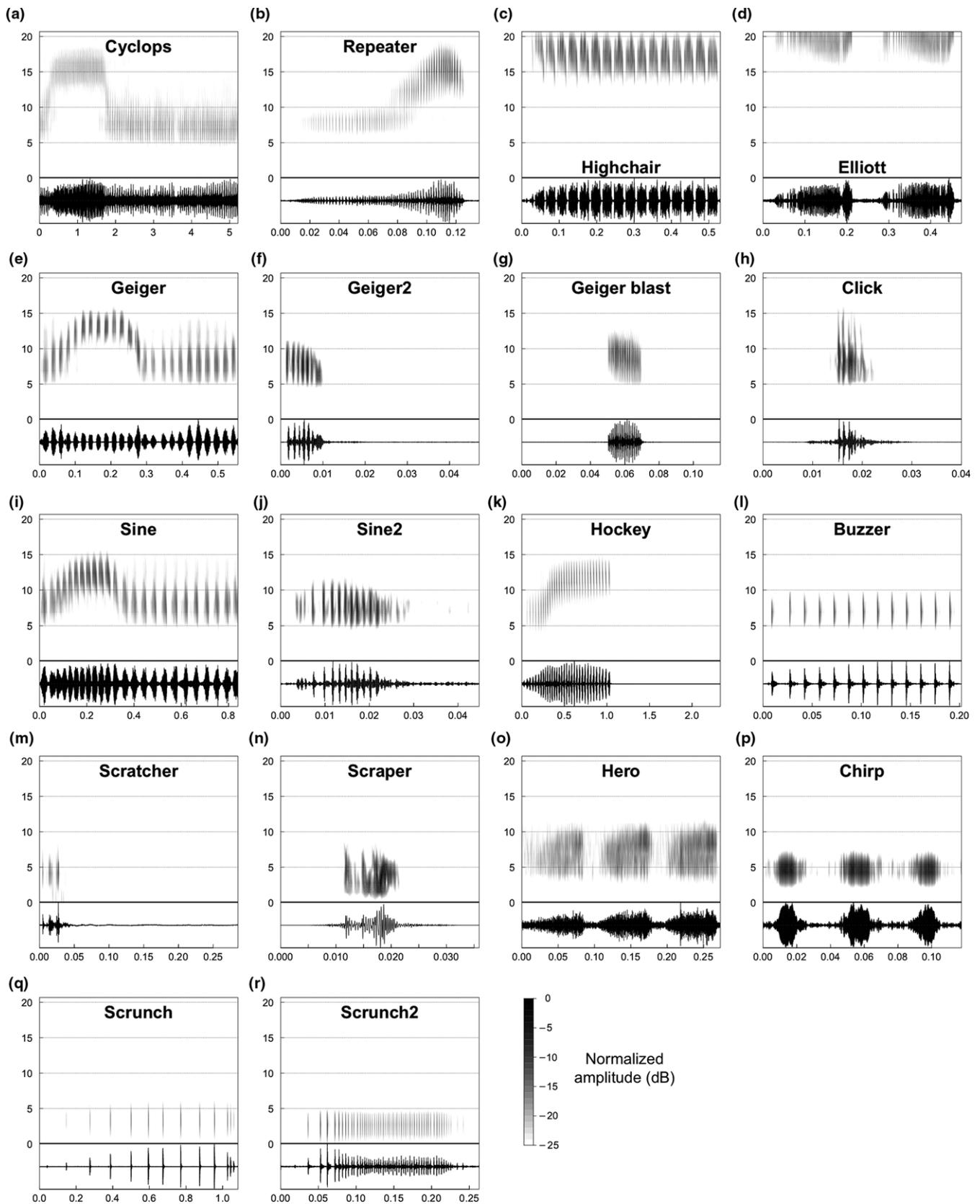


FIGURE 3 Spectrograms and oscillograms (below the spectrograms) of each sound type. Time (seconds) is presented on the x-axis. Frequency (kHz) is presented on the y-axis of spectrograms. Spectrogram normalised amplitude (dB) is indicated by the gradient at the far right of the figure

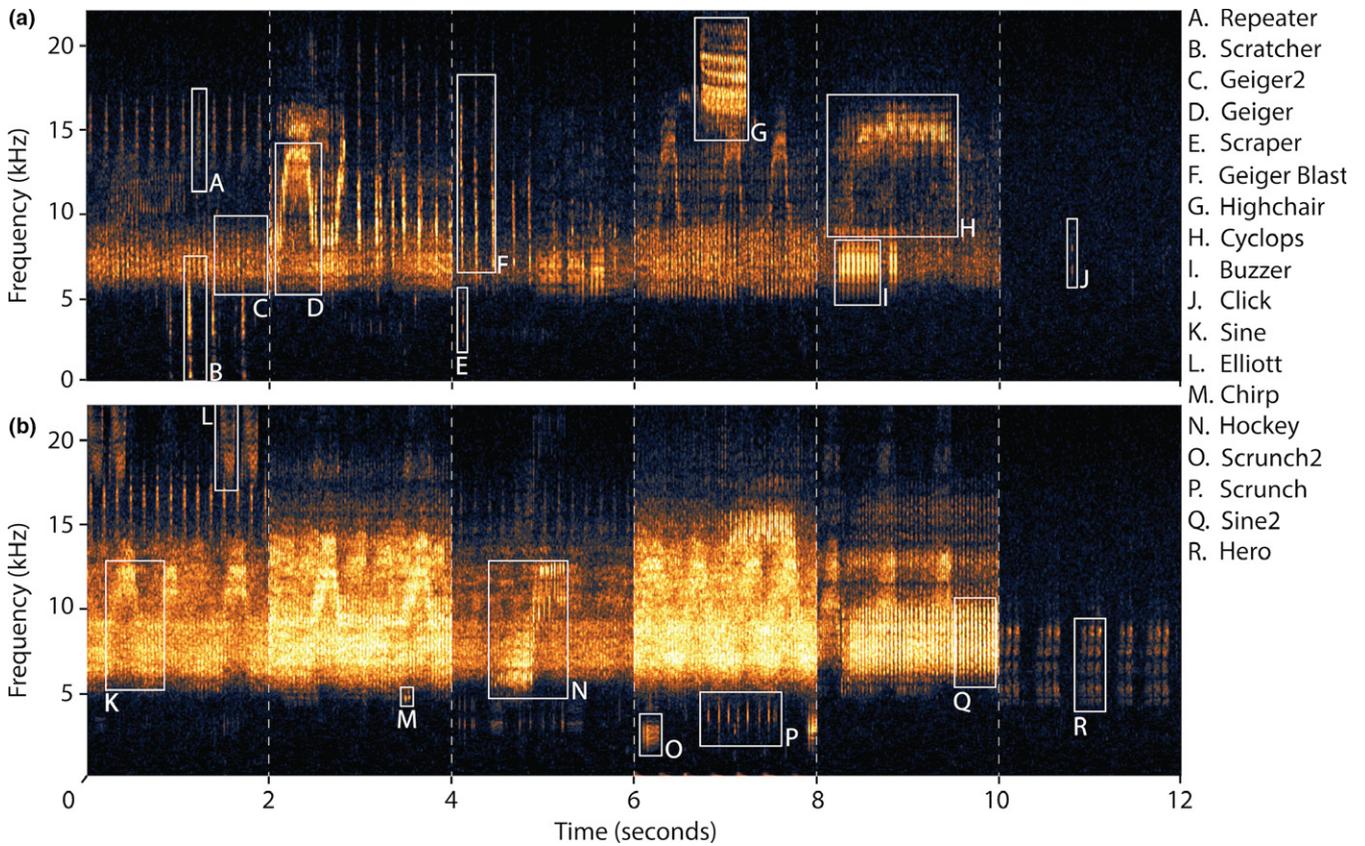


FIGURE 4 Spectrograms of 12 2-s clips that include all 18 sound types, each of which is outlined by a white rectangle. The top row of spectrograms contains recordings from during the daytime (from left to right: 08:00, 08:00, 11:15, 14:30, 16:30 and 18:00). The bottom row contains recordings taken from night-time (from left to right: 22:00, 22:00, 22:00, 03:30, 01:00 and 04:30). Spectrograms were produced using iZotope RX (iZotope RX, 2014) with a Hanning window of 1,024 samples

attributed to Geiger. Despite this apparent similarity, the period and pulse features differentiated between Geiger and Sine (see Figure 3 for spectrograms and oscillograms of these sound types). A *k*-means test differentiated between Geiger and Sine with 89% accuracy based on these features. A logistic regression revealed that “pulse interval of high-frequency portion” and “pulse width of low-frequency portion” differed significantly between Geiger and Sine (pulse interval of high-frequency portion: $Z = -2.07, p = .039$; pulse width of low-frequency portion: $Z = -3.12, p = .002$). Due to these results, Geiger and Sine were considered as two different sound types.

3.3 | Sound type occurrences

The most common sound type was Scrunch, which occurred in approximately 50% of the recordings (Figure 5). The least common was Hero, which was found in 0.3% of the recordings. Some sound types exhibited consistent diurnal patterns, while other sound types displayed no clear daily variation (example soundscape recordings from various times of day are provided in Supporting Information). Acoustic activity of Geiger, Geiger2, Geiger Blast, Hockey, Elliott, Buzzer and Scraper was highest between the hours of 06:00 and 17:00. Sine and Sine2 were present mainly between 19:00 and 04:00. Scrunch and Scrunch2 occurred considerably more at night,

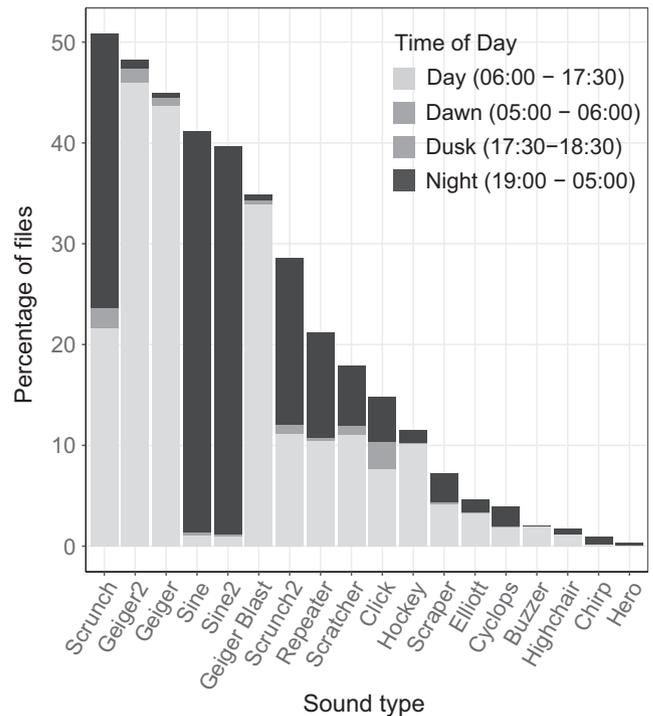


FIGURE 5 Percentage of files within which a sound type occurred. Shading denotes time of day

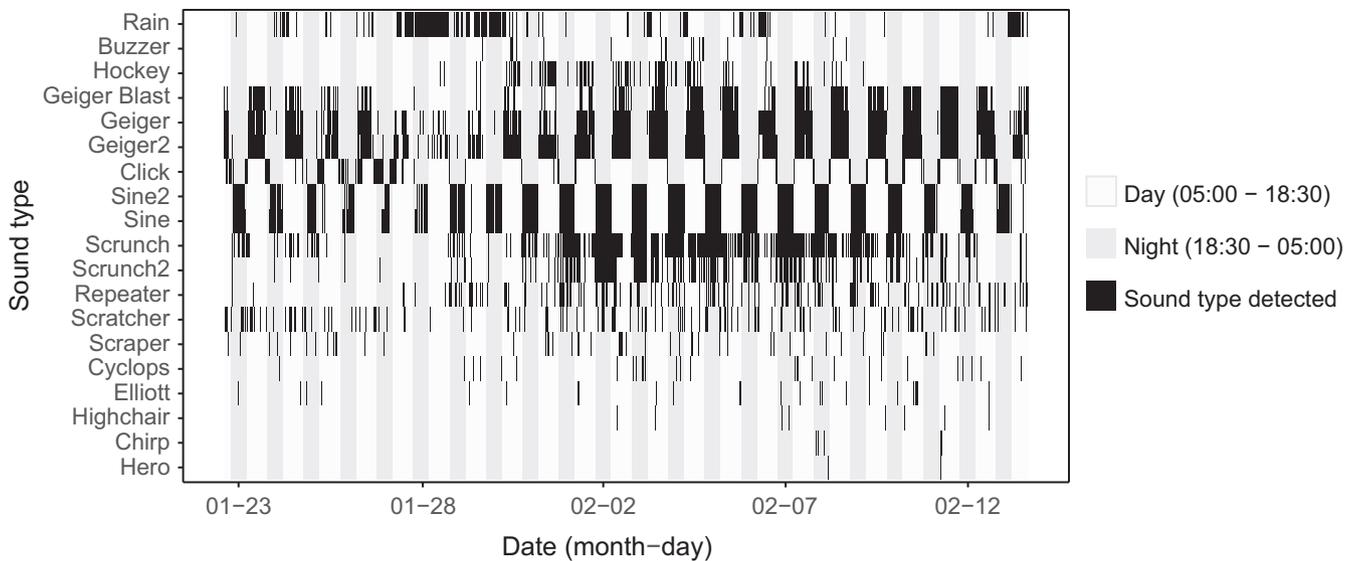


FIGURE 6 Detections of sound types and rain over the 23-day deployment. Light grey shading denotes daytime (05:00–19:00) and dark grey shading denotes night-time (19:00–05:00). The presence of rain is included because it could bias detection and influence the presence/absence of some sound types

and Chirp was detected almost exclusively during the night. Click occurred most at dawn (05:00–06:00) and dusk (17:30–18:30). Hero and Repeater had the highest activity just after dawn and dusk, while Scratcher intensified during morning hours (04:00–11:00). Cyclops and Highchair were active during the day and night.

Over the 23-day recording period, some sound types exhibited wide variation in daily detection rates, while others were detected evenly (Figure 6). We calculated the standard deviation of the number of daily occurrences on all full recording days except for January 27–29, when heavy rains made it difficult to detect certain sound types. Of the 12 sound types with over 100 detections (Scrunch, Geiger2, Geiger, Sine, Sine2, Geiger Blast, Scrunch2, Repeater, Scratcher, Click, Hockey and Scraper), Sine2, Geiger, Geiger2, Scraper and Scratcher had the lowest standard deviation of daily abundance values ($SD = 2.8\text{--}8.4$), meaning that they had the most consistent acoustic activity throughout the 23-day study period. Repeater, Hockey, Geiger Blast and Click were more variable in their abundances ($SD = 9.5\text{--}11.5$), and Scrunch and Scrunch2 had the highest variation in daily abundances ($SD = 18.3\text{--}27.6$). Following a 209-mm precipitation event from January 27–29, the occurrences of Scrunch, Scrunch2, Hockey and Repeater increased considerably. Similarly, for the sound types with fewer than 100 detections (Chirp, Highchair, Buzzer, Hero, Elliott and Cyclops), 89% of the detections occurred over a 15-day window after January 29.

3.4 | Sound type richness

Hourly sound type richness was highest from 06:00 to 10:00 with an average of 4.79 ± 1.50 (\pm notation denotes “mean \pm standard deviation” throughout this article) sound types detected per recording. Fifty-four per cent of recordings with sound type richness greater than six occurred during this time period (as opposed to

17%, if such recordings had been uniformly distributed throughout the day). 05:00 and 18:00 had the fewest sound types present, with average sound type richness of 2.55 ± 1.41 and 2.57 ± 1.38 sound types, respectively (Figure 7).

The average daily sound type richness was 3.64 ± 1.22 . However, daily sound type richness varied considerably over the 23-day study period. From February 1–8, sound type richness peaked with a mean of 4.68 ± 0.26 . Mean daily richness of the remaining days was 3.09 ± 0.52 (Figure 8).

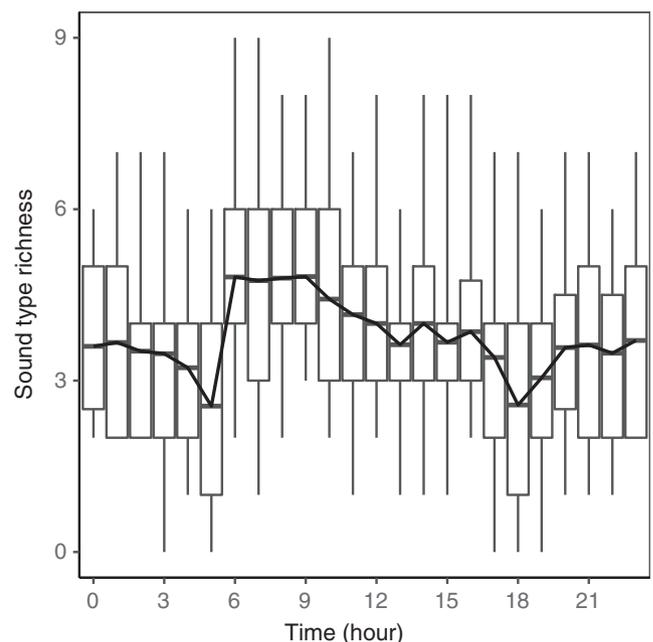


FIGURE 7 Mean sound type richness calculated for each hour. The lower bound of each box is the 25% quantile and the upper bound is the 75% quantile; whiskers extend to the minimum and maximum values for each hour

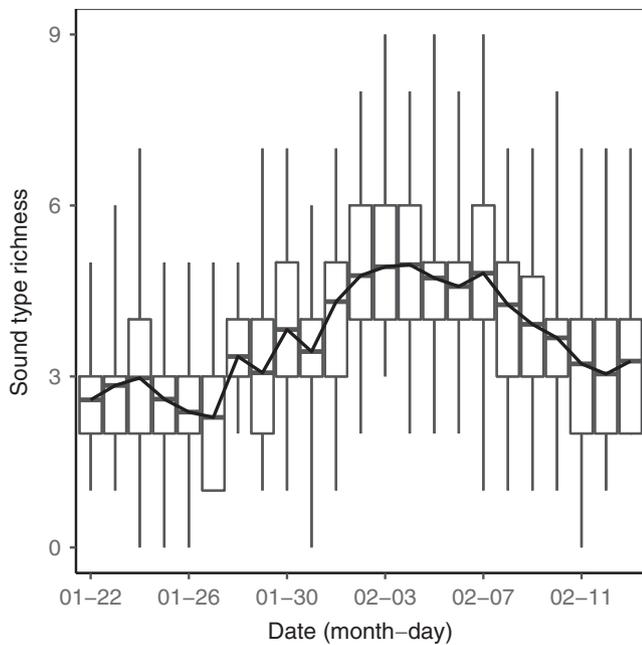


FIGURE 8 Mean sound type richness calculated for each day over the 23-day study period. The lower bound of each box is the 25% quantile, and the upper bound is the 75% quantile; whiskers extend to the minimum and maximum values for each day

3.5 | Sound type occupancy

The three occupancy measurements displayed similar trends to each other, with the night-time acoustic space more occupied than that of the daytime (see Supporting Information and Figure S3 for more details). The acoustic space at dawn and dusk was almost unoccupied, with vacant temporal and frequency niches that were occupied during other times of day. Of daytime values for Occupancies 1 and 2 (which do not factor in the amplitude of the sound types), highest occupancy was generally between 06:00 and 10:00, which coincided with the period of highest sound type

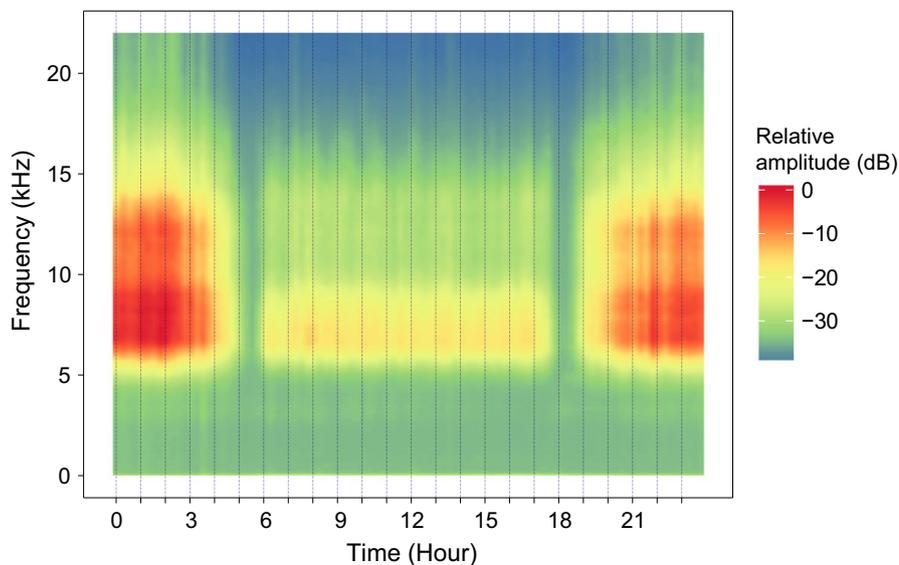


FIGURE 9 Average spectrogram depicting the daily soundscape pattern. In this spectrogram, the intense night choruses, the sparser daytime soundscape and the silences at dawn and dusk, are all evident. The faint yellow band from 3 to 4 kHz represents the activity of sound types Scrouch and Scrouch2

richness. Occupancy 3 had a larger difference between daytime and night-time occupancies because the intensity of the night-time soundscapes was higher than that of the daytime by approximately 12 dB. These daily occupancy trends were reflected by the average daily spectrogram (Figure 9).

3.6 | Comparing sound type and soundscape diversity

Sound type richness was significantly correlated with the majority of the acoustic indices we tested. NP was most highly correlated with sound type richness in both Library B and Library C, with correlations of 0.35 ($p < .001$) and 0.15 ($p < .001$), respectively. The acoustic indices were much more related to sound type occupancy. The acoustic index mostly highly correlated with Occupancy 1 was BN, with a correlation of 0.79 ($p < .001$). For Occupancies 2 and 3, BI displayed the strongest relationship, with correlations of 0.85 ($p < .001$) and 0.92 ($p < .001$), respectively.

3.7 | Soundscape diversity and dynamics

Over the course of an average day, NP crested with approximately 12–15 peaks between 06:00 and 08:00 (Figure 10), which coincided with the highest period of sound type richness. It declined gradually over the course of the day. NP was lowest at 05:15 (dawn) and 18:00 (dusk) with approximately 6 and 4 peaks, respectively. At night, NP values were consistently between 8 and 10 peaks. The BI, which was the most highly correlated index with Occupancies 2 and 3, was also the second most correlated index with Occupancy 1. Maximum values for BI occurred between 21:45 and 02:15, and were lowest between 04:45 and 06:00 and 17:45 and 18:45. After dusk, values rose steadily between 18:45 and 21:30, peaked and then declined rapidly from 02:15 to 05:30. Broadband SPL and RMS were highest at night. The wetland had median SPL of -20.1 ± 5.3 dB during the day, -8.6 ± 6.4 dB at night and

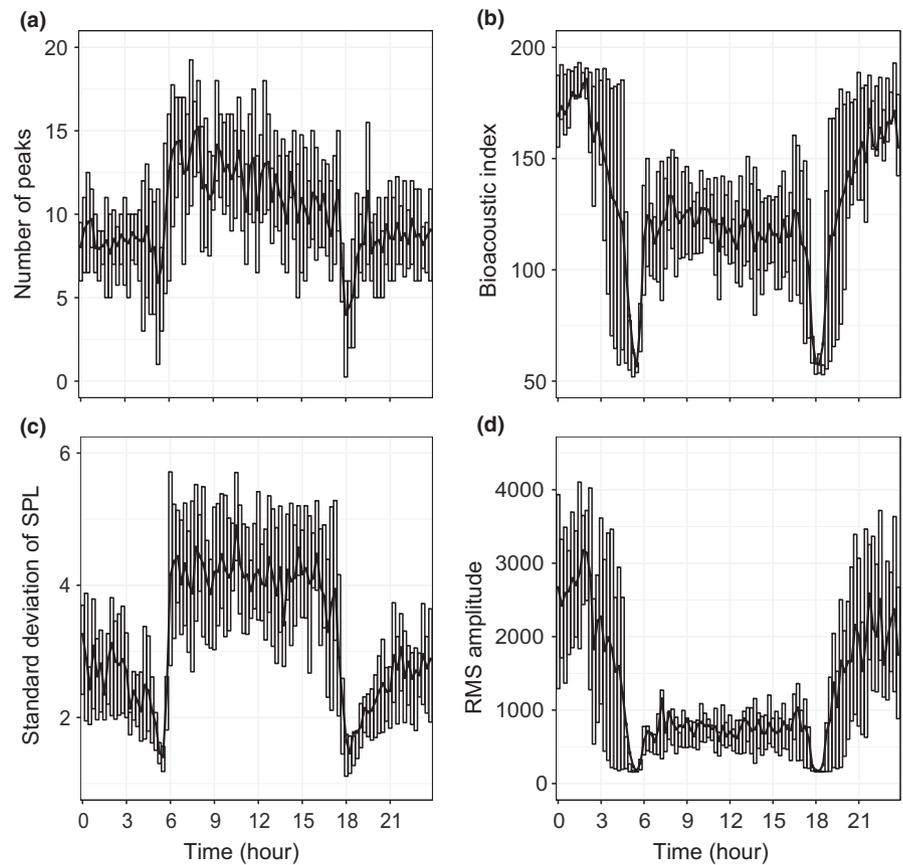


FIGURE 10 Quarter hourly mean acoustic index values including (a) number of peaks, (b) Bioacoustic Index, (c) standard deviation of the 10,334 sound pressure level (SPL) values for each 60-s file and (d) root mean square (RMS) amplitude across the full bandwidth (0–22,050 Hz). In each figure, the lower bound of each box is the 25% quantile and the upper bound is the 75% quantile

–22.5 ± 7.2 dB at dawn and dusk. At 05:30 and 18:15, when BI levels were lowest, the SPL was –23.8 ± 6.4 dB and –21.6 ± 6.7 dB, respectively. This site exhibited a large amplitude range with an average 29.1 ± 4.2 dB difference between the daily minimum and maximum SPL values (based on per-file SPL averages). Since RMS is more visually illustrative of dawn and dusk differences in intensity, it is presented instead of mean SPL in Figure 10. SDSPL values, which illustrate the variability in intensity within a given file, were higher during the day when soundscapes were sparser than at night when there was near-constant sound composed primarily of Sine and Sine2.

4 | DISCUSSION

In Cantarana Swamp, we discovered a rich soundscape composed almost entirely of biological sounds, which supports our argument that passive acoustic recording and principles from soundscape ecology can contribute to the assessment of tropical freshwater systems. These aquatic soundscapes exhibited two characteristics that enable or facilitate acoustic monitoring: a high SNR of biological sounds and a high occupancy of biological sound types. Our study demonstrates that soundscape analysis in a tropical freshwater habitat can reveal soundscape dimensions including sound type diversity and patterns of daily dynamics. By applying principles from soundscape ecology, we can relate these dimensions to biodiversity or habitat condition to enhance understanding and conservation of freshwater

ecosystems. In the context of these principles, we discuss (1) likely sources of the Cantarana sound types, (2) soundscape composition and acoustic niche partitioning between sound types, (3) patterns of temporal soundscape dynamics and potential proximate causes, (4) the efficacy of soundscape measurements used in this study and (5) directions for future freshwater soundscape monitoring research.

4.1 | Sound type attribution

We attribute all 18 sound types to aquatic insects. The sound types were all composed of multiple pulses, single pulses or impulses, suggesting that they may have been produced through some form of stridulation, which is the most common method of sound production in aquatic insects (Aiken, 1985b; Gerhardt & Huber, 2002). It is well known that many aquatic insect taxa from at least four orders utilise acoustic communication in freshwater habitats (Aiken, 1985b). Aquatic insects communicate to defend against predators, proclaim their territories, identify and discriminate between individuals and species and attract mates (Otte, 1974). In La Selva’s lentic habitats, 12 aquatic insect families have been identified, including Aeshnidae, Lestidae, Libellulidae, Belostomatidae, Hebridae, Mesoveliidae, Naucoridae, Veliidae, Dytiscidae, Gyrinidae, Hydrophilidae and Noteridae (Springer, 2017). Six of these families (Belostomatidae, Naucoridae, Veliidae, Dytiscidae, Gyrinidae and Hydrophilidae) have been shown to produce sound for communication (Aiken, 1985b). Additionally, Schlagbauer (1995) documented the presence of 33 families of aquatic insects in a similar wetland within 1 km of Cantarana Swamp;

more detailed information of the findings of that study is included in Supporting Information. Neither the single documented fish family (Synbranchidae) nor any present frog species have been shown to produce sound underwater, and we determined that no sound types in our classification originated above water.

4.2 | Sound type composition and acoustic niche partitioning

The composition of soundscapes varied greatly over the course of the day, with some sound types detected almost exclusively during the day, and others only during the night. This trend has been documented across a wide range of ecosystems (Gasc et al., 2013; Ruppé et al., 2015). Certain times of day are advantageous for sound production for a number of reasons: increasing the likelihood of conspecific reception, optimising propagation, reducing energy and time consumption, reducing predation risk and finding available acoustic niche space. For example, the night-time soundscapes composed of Sine and Sine2 consisted of multiple individuals overlapping and interlocking their sounds in an intense chorus. It appears that these signals were for courting females; Aiken (1982) explained that the density of the chorus is a characteristic of aquatic insect courtship sounds dictated by female preference. Diel periodicity—which Corbet (1966) defined as the “recurrent temporal pattern of an activity with a 24-hr period”—has been demonstrated in several aquatic insect species (Aiken, 1985a). Jansson (1973) found that within the genus *Cenocorixa* (Corixidae), different species had distinct peak sound production periods, including daytime, night-time, dusk and morning. He concluded that light intensity was regulating these temporal patterns. Sound types within Cantarana Swamp exhibited acoustic activity peaks at all of these times.

Acoustic niche partitioning refers to the minimisation of temporal and spectral overlap between various sounds in acoustic space; the acoustic niche hypothesis (ANH) states that species in a species-rich community will evolutionarily or behaviourally modify their acoustic signals to produce sound in a manner that minimises temporal and spectral overlap with other regularly present sounds in the environment (Krause, 1993; Ruppé et al., 2015; Villanueva-Rivera, 2014). The two pairs of dominant sound types (Sine/Sine2 and Geiger/Geiger2) offer evidence supporting the ANH. The Sine and Geiger pairs had very similar frequency ranges, yet they almost never co-occurred (see Figure 4). Sine and Sine2 occurred during the night, and Geiger and Geiger2 occurred during the day. Either Sine, Sine2, Geiger and Geiger2 originated from the same species, or there were two species with similar frequency ranges that produced sound in complete temporal isolation from each other. The non-overlapping acoustic activity patterns of these sound types offer some support for the temporal dimension of the ANH, although their daily activity patterns could also be attributed to non-communicative reasons. In a related study, Jansson (1971) found that temporal isolation could help reduce masking between sympatric aquatic insect species with overlapping frequency ranges for *Cenocorixa bifida* and *C. expleta* in both laboratory and field conditions.

The extent to which the frequency dimension of the ANH plays a role here is less clear. Fundamental frequency correlates strongly with body length in aquatic insects (Theiß, 1982) and would therefore be difficult to change in order to occupy an open niche. Moreover, frequency modulation—changing the fundamental frequency over the course of a sound—is thought to be an ineffective communicatory strategy in shallow freshwater habitats because modulations within a range of several kHz would likely be distorted by environmental interference, which is pervasive in shallow freshwater systems (Aiken, 1985b). In contrast to studies that downplay the potential use of this strategy by aquatic insects, there was significant frequency modulation in five of the sound types in this wetland, namely Geiger, Sine, Hockey, Cyclops and Repeater, although these modulations generally exceeded several kHz. The different frequency modulations of these sound types aided our distinction between them, as their low-frequency portions often overlapped (except for Geiger and Sine, which were temporally isolated from each other and exhibited similar frequency modulations). Development of these distinct modulation patterns may aid differentiation between conspecifics and heterospecifics as well, and these differences represent a case of spectral acoustic niche partitioning.

4.3 | Daily soundscape dynamics

As in many ecosystems, the soundscapes of Cantarana Swamp exhibited daily dynamics, but one pattern distinguished them from soundscapes in other ecosystems. The most unexpected aspect of the Cantarana Swamp soundscape was silence as opposed to sound. Unlike the rest of the day when there was constant acoustic activity, dawn and dusk were nearly silent. The fact that such a wide-open acoustic space was not more fully occupied is surprising, especially when compared to many other habitat types that have peaks of acoustic activity at dawn and dusk (Bertucci, Parmentier, Berten, Brooker, & Lecchini, 2015; Depraetere et al., 2012; Pijanowski, Farina, Gage, Dumyahn, & Krause, 2011; Radford, Jeffs, Tindle, & Montgomery, 2008). In our study, the only sound type with abundance peaks at dawn and dusk was Click. Increased detection of this 0.013-s sound may only have occurred because dominant sound types masked it at other times of day. Alternatively, the sound type could have some communicative function germane to these time periods.

A proximate cause for these quiet times around dawn and dusk could be intermediate light levels that do not trigger communication amongst animals that otherwise produce sound at higher or lower light levels. However, this hypothesis is challenged by the fact that night-time sounds began to decline around 02:00, far before any uptick in solar radiation occurs. Similarly, daytime sounds began declining at around 17:15, which precedes the sunset by approximately 45 min. Air temperature during the pre-dawn period (00:00–06:00) was nearly constant, with an average range of less than 1°C. Pre-dusk (15:00–18:00) temperature was more variable, with an average range of approximately 3°C. To date, acoustic activity in aquatic insects has been demonstrated in laboratory settings to be

purely controlled by exogenous factors, with light intensity as the main factor and temperature as a contributing factor (Aiken, 1985a; Jansson, 1968). However, in this wetland, acoustic activity changed before there was any major change in these factors, implying that there was an additional exogenous component, endogenous biological clock or extreme sensitivity to temperature changes that regulated acoustic activity.

Another potential explanation for these quiet periods around dawn and dusk is that these insects decrease their sound production in an attempt to reduce the risk of predator detection. Though many animals utilise this strategy (McGregor, 2005), so far there is no evidence that predators can use aquatic insect sounds to locate prey, primarily because aquatic insect sounds have been thought to have a limited range of detection that is less than 1 m (Aiken, 1982; Jansson, 1973). However, in this system, there is reason to suspect this range of detection might be larger. The dense night-time choruses of Sine and Sine2, by far the loudest sound types, were captured on the terrestrial microphone 50 cm above the wetland, suggesting that the detection range of these sounds could be larger than 1 m, especially since these detected sounds penetrated the highly reflective water–air boundary (Aiken, 1985b). A more in-depth investigation of this system that considers insect life histories is necessary to ascertain why these periods were so quiet.

4.4 | Longer-term soundscape dynamics

The longer-term dynamics illustrate that soundscape diversity in this wetland varied over multiday periods. Since freshwater acoustic communities can change over daily and longer-term timescales, we caution that taking an acoustic snapshot (less than 1 day) of a freshwater community could underrepresent the acoustic diversity of a given site. In our study, Chirp and Hero did not occur until after 15 full days of sampling. Longer-term changes could be triggered by environmental events like precipitation. Some sound types, including nearly all of the rarer sound types, occurred more often immediately after the heavy precipitation event between January 27 and January 29. While our sampling window was relatively small, precipitation has been shown to cause changes in communication for many taxa (Ospina, Villanueva-Rivera, Corrada-Bravo, & Aide, 2013), so this correlation may not be anomalous. This observation offers evidence that precipitation might be an important cue regulating the acoustic communication of freshwater insects.

4.5 | Acoustic index- and sound type-based soundscape measurements

Acoustic index values were significantly, but only moderately correlated with sound type richness at this site. This moderate correlation suggests that single acoustic indices and sound type richness highlight different aspects of acoustic diversity. This result is unsurprising, as some sound types barely occupied any acoustic space, while others were dominant with respect to frequency and time. It would be unrealistic to assume that an acoustic index could be equally

sensitive to sound types that vary dramatically in spectral or temporal occupancy (Gasc, Pavoine, Lellouch, Grandcolas, & Sueur, 2015). In the case of this acoustic community, acoustic indices offered a much better window into overall sound type occupancy, which has recently been linked to sound type richness in terrestrial tropical habitats (Aide, Hernández-Serna, Campos-Cerqueira, Acevedo-Charry, & Deichmann, 2017). In a similar study on the soundscapes of temperate ponds, Desjonquères et al. (2015) found that only the acoustic index Acoustic Richness was marginally correlated with sound type richness (correlation of 0.2) and abundance (correlation of 0.19), once controlling for the SNR of the sound types. The lack of a strong relationship in that study was probably because the soundscapes of these ponds were composed of only sparse and faint biological sounds. In stark contrast, the biological sounds at Cantarana Swamp dominated the soundscapes on every rainless day and night.

Sound type classification offered information on acoustic diversity and dynamics that was not captured by the acoustic indices—and therefore represents an important component of the analysis of aquatic soundscapes. However, due to a lack of classification standards, this method produces results that are not currently comparable between studies or across different habitats. For example, Desjonquères et al. (2015) classified 48 sound types from three temperate ponds in France but that study found lower average sound type richness per minute (0.6, 1.0 and 2.2 in the different ponds) than we did in Cantarana Swamp (3.7). Overall sound type richness may be influenced by the classification choices of the human inspector. Sound type classification is still a subjective exercise, and in some studies, similar sounds can be lumped together, while in others, every unique temporal-spectral signal can be given its own sound type label. Devising best practices for defining sound types and developing automated sound type classification programs are important steps in addressing shortcomings in this approach. In Supporting Information S2, we have provided recommendations for conducting manual classification of sound types.

4.6 | Future directions for freshwater soundscape monitoring research

Both the findings and limitations of our study highlight the ample opportunity to expand and refine freshwater acoustic monitoring and assessment techniques. Important foci for future research include (1) ground-truthing soundscape data with in situ field sampling of biota and environmental conditions, (2) matching sound types with species, (3) using sound types to assess other freshwater habitats, (4) assessing annual and interannual dynamics and (5) considering the role of soundscapes in revealing ecological disturbance gradients. In order for soundscape methods to be effective in freshwater environments, soundscape measurements must have a sufficiently strong positive correlation with at least one ecologically meaningful facet of biodiversity, be it the presence of an indicator species or species richness, abundance, evenness or composition. Given the rich diversity and dynamics identified in our study, we would encourage such future work because soundscape recording

and analysis could be an effective tool for monitoring and assessing the biodiversity of tropical freshwater systems.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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