

Estimation of katydid calling activity from soundscape recordings

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Academic editor: Klaus-Gerhard Heller | Received 31 August 2021 | Accepted 22 January 2022 | Published 4 October 2022

<https://zoobank.org/B0753435-8F72-4601-8B46-6B1D77224F91>

Citation: Symes LB, Madhusudhana S, Martinson SJ, Kernan CE, Hodge KB, Salisbury DP, Klinck H, ter Hofstede H (2022) Estimation of katydid calling activity from soundscape recordings. *Journal of Orthoptera Research* 31(2): 173–180. <https://doi.org/10.3897/jor.31.73373>

Abstract

Insects are an integral part of terrestrial ecosystems, but while they are ubiquitous, they can be difficult to census. Passive acoustic recording can provide detailed information on the spatial and temporal distribution of sound-producing insects. We placed recording devices in the forest canopy on Barro Colorado Island in Panamá and identified katydid calls in recordings to assess what species were present, in which seasons they were signaling, and how often they called. Soundscape recordings were collected at a height of 24 m in two replicate sites, sampled at three time-windows per night across five months, spanning both wet and dry seasons. Katydid calls were commonly detected in recordings, but the call repetition rates of many species were quite low, consistent with data from focal recordings of individual insects where calls were also repeated rarely. The soundscape recordings contained 6,789 calls with visible pulse structure. Of these calls, we identified 4,371 to species with the remainder representing calls that could not be identified to species. The identified calls corresponded to 24 species, with 15 of these species detected at both replicate sites. Katydid calls were detected throughout the night. Most species were detected at all three time points in the night, although some species called more just after dusk and just before dawn. The annotated dataset provided here serves as an archival sample of the species diversity and number of calls present in the forest canopy of Barro Colorado Island, Panama. These hand-annotated data will also be key for evaluating automated approaches to detecting and classifying insect calls. In changing forests and with declining insect populations, consistent approaches to insect sampling will be key for generating interpretable and actionable data.

Keywords

bush cricket, community ecology, passive acoustic monitoring (PAM), seasonality, Tettigoniidae

Introduction

Insects are integral to terrestrial ecosystems but are often difficult to monitor. Recent research suggests that some, perhaps most, insect species are experiencing steep population declines likely in response to human activities (Dirzo 2014, Thomas 2016,

Wagner 2020). It is possible that a quarter to half of the world's insect abundance has disappeared nearly unnoticed, with largely unquantified impacts on higher trophic levels, herbivory, nutrient cycling, and other core ecological processes (Hallmann et al. 2017, Wagner 2019). The uncertainty about these potential losses highlights how little is known about most insect species, from their natural history to their ecology, behavior, and population trends (Simmons et al. 2019, Thomas et al. 2019). To begin to grapple with questions about population changes and trends, we need to understand ecological fundamentals such as what species are present and how communities change across space and time (Montgomery et al. 2020).

In dense forests, many insects are elusive, but not all are silent. Orthopterans (e.g., crickets and katydids), Homopterans (e.g., cicadas), and many other insect species produce sounds (Cigliano et al. 2019) that can reveal their presence. Many of the loudest and most repetitive sounds are mating signals, which are often species-specific, at least within a given habitat (Greenfield 1997, Gerhardt and Huber 2002, Symes 2014). Documenting these sounds can provide a detailed window into the biology and population dynamics of insect species that are central to many food webs (Riede 1998, 2018, Hugel 2012, Penone et al. 2013).

Tropical forests are particularly species rich (Kricher 1999, Hillebrand 2004, Basset et al. 2012), and audio recordings from these environments contain many sounds that can provide clues to the presence, distribution, behavior, and abundance of insects (Riede 1993, Schmidt et al. 2013, Jain et al. 2014). Currently, natural history knowledge of tropical Orthopterans is extremely limited. For most species, little is known about where they occur in the forest, what time of year they mate, and how dramatically populations fluctuate from year to year. Long-term passive acoustic recordings can help address some of these questions. In recent decades, passive acoustic methods have been widely used for monitoring research (Sugai et al. 2019). However, the advertisement calls of many tropical Orthopterans have never been recorded or described. The lack of call descriptions has made it difficult to extract detailed information from long-term audio recordings.

In a small but growing number of locations, careful descriptions of insect acoustic signals have created a way of accessing the rich information contained within acoustic recordings (Danielsen et al. 2009, Cigliano et al. 2019, ter Hofstede et al. 2020).

For this study, we collected acoustic recordings from tropical lowland rainforest in Panamá and used recently published call descriptions (ter Hofstede et al. 2020) to manually identify katydid calls from the recordings, providing information about the spatial and temporal distribution of these katydid species. First, we assessed what species were detected acoustically in the forest canopy, how commonly these species appeared on recordings, and how many signals were detected per unit of time when the species was present. Second, we compared two different recording sites in similar habitats to assess local variations in species composition and call rate. Finally, we assessed how detections varied over short and long timescales, comparing three time-windows within a night, as well as comparing recordings during the wet and dry seasons.

Methods

Our study was conducted in 2019 on Barro Colorado Island (BCI), a protected lowland rainforest in Gatun Lake in the Panama Canal. The vegetation of BCI is predominantly old secondary growth forest with remnant primary forest, particularly in ravines and on steep hillsides (Ricklefs 1975). This forest receives approximately 2600 mm of rain per year, with a dry season that typically begins in December or January and ends in late April or early May (Leigh 1999). To represent rainfall dynamics immediately preceding and during the sampling period, we obtained monthly rainfall data from Nov 2018 to Aug 2019 (Paton 2021). This was compared against the average monthly rainfall from 1979–2019 (Fig. 1).

Recording site selection.—We selected two recording locations, both in large canopy trees [Site 1: 9.16074°N, 79.84073°W, Site 2: 9.16367°N, 79.84038°W]. For each tree, we used a basal area prism to calculate the basal area of the surrounding forest and a spherical densiometer to estimate percent open canopy (Lemmon 1956, Thompson et al. 2006). Forestry measurements were available from sampling that occurred in 2016, three years prior to recording. Measurements were collected by tree climbing during the dry season at 24, 16, and 8 m. One site was comparatively open, while the other was more densely vegetated (Table 1), providing an opportunity to capture more of the potential variation in species composition.

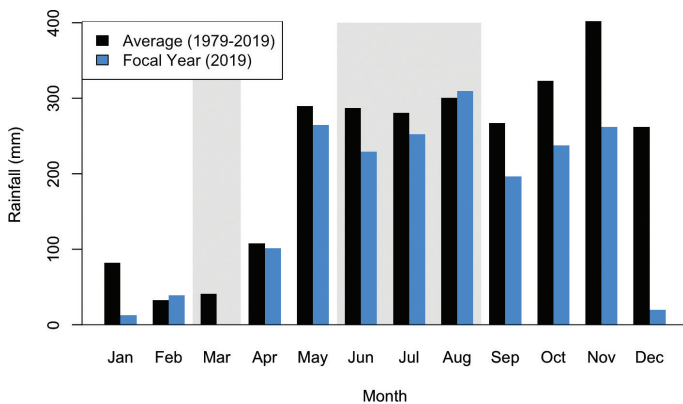


Fig. 1. Monthly rainfall totals showing a 40-year average and during the study period. Gray highlighting indicates months with analyzed acoustic recordings. Rainfall data are adapted from Paton (2021).

Table 1. Site characteristics of recording locations.

Height (m)	Percent Canopy Cover		Basal Area (ft ² /ha)	
	Site 1	Site 2	Site 1	Site 2
24	90.6	6.4	80	10
16	97.9	59.4	90	30
8	99.0	81.3	80	40

Acoustic data.—We collected acoustic recordings of the BCI soundscape using Rugged Swift autonomous recording units (K. Lisa Yang Center for Conservation Bioacoustics, Cornell University). The units were suspended at a height of 24 m (corresponding to the canopy layer) and were configured to record for ten minutes at the beginning of each hour from dusk until dawn. The Swifts recorded continuously (mono, WAV format) throughout the deployment using a sampling rate of 96 kHz (16-bit resolution). The sampling rate excluded two of the species described in the ter Hofstede 2020 paper—*Eppia truncatipennis* Stål, 1875 (peak frequency 50 kHz) and *Ischnomela gracilis* Stål, 1873 (peak frequency 74 kHz) (ter Hofstede et al. 2020). The frequency response of the Rugged Swift microphone is relatively flat from 10–25 kHz, but sensitivity decreases linearly by 17 dB between 25 and 45 kHz (Suppl. material 1: Fig. S1). However, *Agraecia festae* (peak frequency ~40 kHz) was commonly detected on the recordings, indicating that ultrasonic species were readily detectable. The microphone sensitivity of the Swift was -44 dBV/Pa (+/-3 dB) based on 0 dB = 1 V/pa at 1 kHz, and the clipping level of the analog-to-digital (ADC) converter was +/- 0.9 V. The units were set with a gain of +35 dB.

We analyzed recordings from five dates corresponding to new moon nights, the darkest time of the month and a time when katydids are known to be most active (Lang et al. 2006, Romer et al. 2010). The selected dates included a day in the extreme dry season (5th March) and four dates during the longer wet season (5th June, 2nd July, 1st and 30th August) (Fig. 1). The dry season sampling only included recordings from Site 2 due to equipment malfunction. To capture the variation in species composition and activity, we analyzed recordings from three time windows on each date: shortly after nightfall (1900 h), at midnight, and just before dawn (0500 h) local time. Times were selected throughout the night to try to capture sounds from any species with limited windows of activity. This sampling strategy resulted in a total of 270 minutes of analyzed recordings. Soundscape recordings and annotation data are publicly available in Dryad (Symes et al. 2021).

Species identification protocol.—We visually reviewed spectrograms using Raven Pro 1.6 (Bioacoustics 2019) with an FFT size of 409 samples (4.26 ms duration with 3 dB filter bandwidth of 338 Hz), 50% frame overlap, and default settings for brightness and contrast. We advanced through the ten-minute recording in increments of approximately three seconds, with frequency presets that displayed 9.5–48 kHz. After locating a call, the window parameters were adjusted as needed to optimize visualization for a specific call. The katydid species with the lowest documented frequency on BCI had a peak frequency of 9.7 kHz (ter Hofstede et al. 2020). Therefore, we annotated calls with a visible pulse structure above 9.5 kHz. We used the dominant frequency of the call to identify potential species matches, and then the duration, interpulse interval, and other unique call characteristics described in ter Hofstede et al. (2020) to verify the species identification. Recordings were initially annotated by a single observer (KBH or DPS) and were subsequently reviewed by two additional observers (LBS and SM).

Nearly all katydid species recorded on BCI have acoustically unique calls. One pair of species, *Anaulacomera* sp. "wallace" and *Hetaira* sp., had exceptionally similar calls, with overlapping ranges of all acoustic parameters (ter Hofstede et al. 2020). These species are differentiated morphologically and genetically (T Robillard, personal communication), and the call similarity is almost certainly convergent. Within the forest, these species may be differentiated by microhabitat preference or diel patterns, but from acoustics alone, it is not possible to differentiate the species. Consequently, calls that fit the acoustic parameters of these species were annotated as [*Anaulacomera* sp. "wallace"/*Hetaira* sp.] to reflect the dual possibilities.

For soundscape recordings, we assessed the total number of calls detected per recording and the number of species present. For each species, we report the median number of calls present in a 10-minute recording that contained the species, as well as the maximum number of calls that we ever detected in a 10-minute soundscape recording.

We compared the soundscape call rate data against call rate data for individual captive insects to begin to assess how many individuals of a given katydid species are detected on a recording. To measure the calling activity of focal insects, we followed the methods of Symes et al. (2020). In brief, individual males were placed singly in mesh cages in a greenhouse and recorded for 24 hours with a Tascam DR-40 recorder at a sampling rate of 96 kHz. Calls were extracted using a custom script and R software (R Core Team 2018), and detections were validated by hand. For the species *Agraeia festae*, sounds were extracted using the template detector in the Raven Pro 2.0 software, with manual review to ensure detection. *A. festae* produces calls that consist of highly variable numbers of pulses, and to capture the variation in the calling activity of this species, we counted the individual two-pulse units that comprise the repetitive component of the call rather than the variable duration calls (for details of call structure, see ter Hofstede et al. (2020)).

In canopy recordings, animals are only known to be present when they are calling, whereas in our captive recordings, we knew that a single focal animal was present at all times. To generate comparable metrics between canopy and captive recordings, we divided 24-hour captive recordings into 10-minute recordings and determined how many of the 10-minute recordings contained calls. Using captive recordings that contained calls, we calculated the median number of calls per recording and the maximum number of calls in any recording for each individual. For each species, we then found the average number of captive recordings containing calls and the average number of calls in captive recordings that contained calls. Finally, we calculated the maximum number of calls observed in any 10-minute recording for any individual.

In addition to identifying calls, we also marked calls that could not be identified to species, referred to here as unmatched calls. The unmatched call class encompasses calls with measurable pulse structure that did not align with any of the katydid calls described in ter Hofstede et al. (2020). Bat echolocation calls could be identified by spectral and temporal patterns, particularly the increasing and then decreasing amplitudes as the bat flew past the microphone, and these calls were excluded from analyses. Although it is possible that some of these unmatched calls were produced by animals other than katydids, it is more likely that they are katydid signals because few other animals are known to produce pulsed signals like these at high frequencies. Including the unmatched class of signals allowed us to evaluate the total number of calls detected by time, date, and location.

By aggregating the data from the individual recordings, we were able to calculate the number of calls and the proportion of recordings that contained each species by site, date, and time of night.

Results

We detected 6,789 total calls, with calls present in all ten-minute recordings. Of these calls, 4,371 were identified to species (Table 2, see supplemental materials for recordings and annotation tables). The remaining 2,418 were unmatched signals that had clear acoustic structures and differed from the described calls of 50 katydid species in ter Hofstede et al. (2020) (Fig. 2). In total, the identified calls represented 23 species, plus a combined class for the acoustically indistinguishable calls of *Anaulacomera* sp. "wallace" and *Hetaira* sp. The number of species detected per recording ranged from one to seven. Some species were detected more often than others, with four of the species being detected only in a single recording. *Anaulacomera spatulata* and *Anaulacomera furcata* were both present in more than 40% of the recordings. These species produced a two-pulse call with stereotyped frequency and interpulse interval, leading to high confidence in these call identifications. These species are the most abundant and second-most abundant species, respectively, among species captured at lights, giving a high congruence between acoustic and light trap sampling (unpublished data).

The calls of *Philophyllia ingens* and *Anaulacomera* sp. "goat" were described in ter Hofstede et al. (2020) and were not identified in these recordings because the calls could not be distinguished reliably from the sounds produced by female phaneropterine katydids during the mating duet. Male *Philophyllia ingens* produce a single short pulse at 10.8 kHz, and *Anaulacomera* sp. "goat" males produce a single short pulse at 27 kHz. In the phaneropterine subfamily, many species engage in mating duets, with females producing a single tick or short series of pulses at a species-specific interval after the male call. Although the signals of female phaneropterine katydids at this site are not described, the soundscape recordings include a variety of short pulses across a range of frequencies that are consistent with the signals of female phaneropterines (Spooner 1995, Heller et al. 2015). We were not confident in our ability to differentiate the calls of

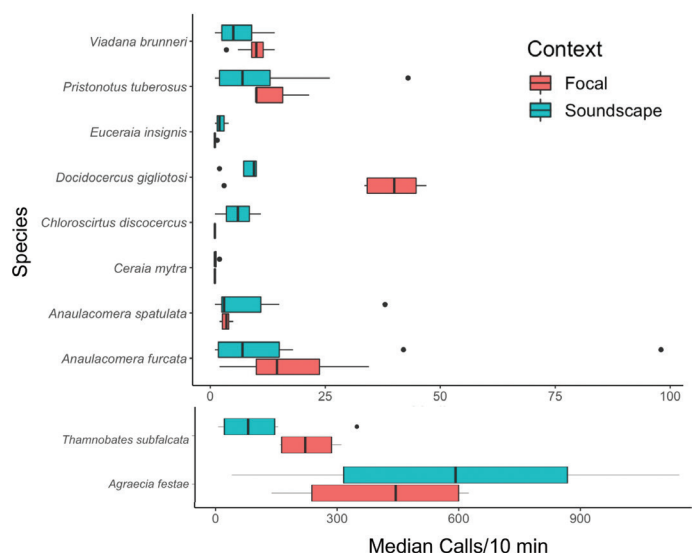


Fig. 2. Comparison of signaling rates between focal and soundscape recordings.

Table 2. A comparison of the number of calls detected in soundscape recordings and in recordings of captive focal individuals. For the soundscape data, total calls represents the number of calls detected across all recordings. Focal data for *Anaulacomera furcata*, *Anaulacomera spatulata*, *Ceraia mytra*, and *Euceraia insignis* are from Symes et al. (2021). Data for *Chloroscirtus discocercus* and *Viadana brunneri* are from Symes et al. (2020). Median recordings with calls represents the median number of 10-minute recordings in 24 hours that contained calls.

Species	Soundscape				N ind	Focal		
	Total Calls	Prop. files present	Calls/10 min when present			Median recordings with calls	Calls/10 min when present	
			Median	Max			Median	Max
Unmatched signals	2418	0.96	53.5	376				
<i>Acantheremus major</i> (Naskrecki, 1997)	10	0.04	10.0	10				
<i>Acanthodis curvidens</i> (Stål, 1875)	1	0.04	1.0	1				
<i>Agraecia festae</i> (Griffini, 1896)	1155	0.07	577.5	1118	5	61.0	433.0	1853
<i>Anapolisia colossea</i> (Brunner von Wattenwyl, 1878)	3	0.07	1.5	2				
<i>Anaulacomera furcata</i> (Brunner von Wattenwyl, 1878)	207	0.44	7.0	98	7	60.0	14.5	318
<i>Anaulacomera</i> sp. "ricotta"	1	0.04	1.0	1				
<i>Anaulacomera spatulata</i> (Hebard, 1927)	93	0.41	3.0	38	5	46.0	3.5	20
<i>Anaulacomera</i> sp. "wallace"/ <i>Hetaira</i> sp.	52	0.22	3.0	36				
<i>Ceraia mytra</i> (Grant, 1964)	5	0.15	6.0	2	6	11.0	1.0	2
<i>Chloroscirtus discocercus</i> (Rehn, 1918)	12	0.07	1.0	11	8	22.0	1.0	4
<i>Docidocercus gigliotosi</i> (Griffini, 1896))	31	0.15	9.5	10	6	44.5	40.0	59
<i>Dolichocercus latipennis</i> (Brunner von Wattenwyl, 1891)	9	0.15	2.5	3				
<i>Ectemna dumicola</i> (Saussure & Pictet, 1897)	47	0.19	3.0	27				
<i>Euceraia atryx</i> (Grant, 1964)	5	0.11	1.0	3				
<i>Euceraia insignis</i> (Hebard, 1927)	7	0.11	2.0	4	5	8.0	1.0	7
<i>Erioloides longinoi</i> (Naskrecki & Cohn, 2000)	34	0.26	3.0	11				
<i>Hyperphrona irregularis</i> (Brunner von Wattenwyl, 1891)	19	0.15	4.0	10				
<i>Ischnomela pulchripennis</i> (Rehn, 1906)	1622	0.11	711.0	910				
<i>Microcentrum championi</i> (Saussure & Pictet, 1898)	3	0.04	3.0	3				
<i>Montezumina bradleyi</i> (Hebard, 1927)	157	0.15	41.5	73				
<i>Phylloptera quinquemaculata</i> (Bruner, 1915)	2	0.04	2.0	2				
<i>Pristonotus tuberosus</i> (Stål, 1875)	182	0.63	7.0	43	3	64.0	10.0	35
<i>Thamnobates subfalcata</i> (Saussure & Pictet, 1898)	677	0.26	37.0	350	4	33.0	214.5	481
<i>Viadana brunneri</i> (Cadena-Castañeda, 2015)	37	0.22	5.0	14	9	21.0	10.0	129

Philophyllia ingens and *Anaulacomera* sp. "goat" males from the calls of females of the many phaneropterine species that occur in these forests and excluded these species. Among the approximately 80 katydid species we captured at lights, *Philophyllia ingens* ranked 25th and *Anaulacomera* sp. "goat" ranked 22nd in abundance (unpublished data). By excluding these two species, these species are not represented in the total number of calls detected or the number of species per recording, meaning that the overall call count and species diversity may be slightly underrepresented.

Calling rate in cages and soundscapes.—The number of calls produced by a focal individual in a cage fell within the range of the number of calls produced per 10 minutes when a species was present (Table 2, Fig. 2).

Approximately 32% of the clearly visible calls did not correspond to any of the 50 species described in ter Hofstede et al. (2020). We did not attempt to separate these events into sonotypes but present exemplars of some of these sounds (Fig. 3).

Spatial variation.—At Site 1, we detected 17 species, including two species that were detected only at this site (Table 3). At Site 2, we detected 22 species, including seven species that were detected only at this site. Fifteen species were detected in both locations. The proportion of the recordings in which a species was detected was relatively consistent across both sampling locations (Table 3).

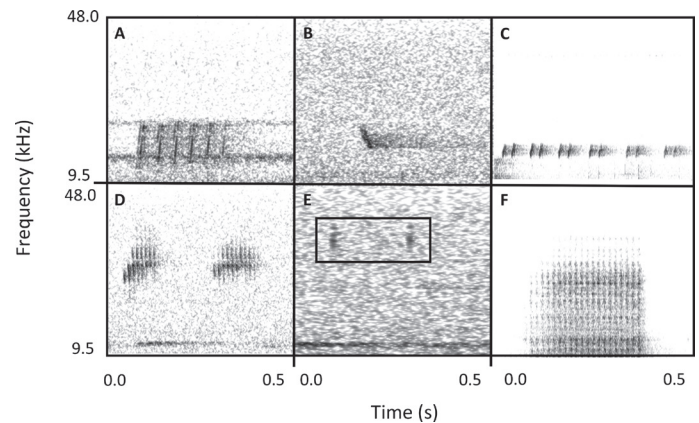


Fig. 3. Examples of calls with visible pulse structures that did not match the acoustic characteristics of the katydid calls described in ter Hofstede et al. (2020). A. Clip_009 1:00; B. Clip_022 6:19; C. Clip_009 7:39; D. Clip_013 4:33; E. Clip_014 4:33; F. Clip_025 0:54.

Time of night.—For species that were detected in the recordings, 63% of species were detected at least once at 1900 h, 63% of species were detected at least once at midnight, and 71% of species were detected at least once at 0500 h (Table 4).

Table 3. The proportion of the recordings in which a species was detected for both sampling sites and the difference in proportion between sites.

Species	Site 1	Site 2	Difference
Unmatched signals	0.92	1.00	-0.08
<i>Acantheremus major</i>	0.08	0.00	0.08
<i>Acanthodis curvidens</i>	0.00	0.07	-0.07
<i>Agraecia festae</i>	0.08	0.07	0.02
<i>Anapolisia colosseae</i>	0.00	0.13	-0.13
<i>Anaulacomera furcata</i>	0.42	0.47	-0.05
<i>Anaulacomera</i> sp. "ricotta"	0.08	0.00	0.08
<i>Anaulacomera spatulata</i>	0.33	0.47	-0.13
<i>Anaulacomera</i> sp. "wallace"/ <i>Hetaira</i> sp.	0.25	0.20	0.05
<i>Ceraia mytra</i>	0.08	0.20	-0.12
<i>Chloroscirtus discocercus</i>	0.00	0.13	-0.13
<i>Docidocercus gigliotosi</i>	0.17	0.13	0.03
<i>Dolichocercus latipennis</i>	0.08	0.20	-0.12
<i>Ectemna dumicola</i>	0.33	0.07	0.27
<i>Euceraia atryx</i>	0.00	0.20	-0.20
<i>Euceraia insignis</i>	0.08	0.13	-0.05
<i>Erioloides longinói</i>	0.00	0.47	-0.47
<i>Hyperphrona irregularis</i>	0.25	0.07	0.18
<i>Ischnomela pulchripennis</i>	0.17	0.07	0.10
<i>Microcentrum championi</i>	0.00	0.07	-0.07
<i>Montezumina bradleyi</i>	0.08	0.20	-0.12
<i>Phylloptera quinquemaculata</i>	0.00	0.07	-0.07
<i>Pristonotus tuberosus</i>	0.50	0.73	-0.23
<i>Thamnobates subfalcata</i>	0.17	0.33	-0.17
<i>Viadana brunneri</i>	0.17	0.27	-0.10

Seasonal variation.—Katydid calling occurred during both wet and dry months (Table 5). The number of species detected per 10-minute recording was slightly lower at the end of the dry season in March than in the other recordings.

Discussion

The acoustic environment of Barro Colorado Island is diverse and rich with the sounds of many species of katydids. Every recording contained katydid calls, but even the most ubiquitous species (*Pristonotus tuberosus*) was detected in only 63% of recordings, with most species occurring much less often. Based on the katydids that are captured at lights, the katydid community of BCI is diverse and relatively even (unpublished data), a trend that is reflected in acoustic sampling as well.

For acoustic monitoring, a critical question is how many sites in a forest have to be sampled in order to thoroughly census acoustic insects. In homogeneous tropical forests, at least some insect communities have high alpha diversity and low beta diversity (Novotny et al. 2007). Using multisite sampling and species area models, Basset et al. (2012) predicted that sampling one ha of rainforest would yield approximately 60% of the insect species found by sampling 6000 ha. In this study, we analyzed two sites within the same forest separated by approximately half a kilometer. Sixteen katydid species were detected at both sites, with most species occurring at a similar frequency in both sites. Nine species were detected at only one of the sites. These nine species were generally detected in a small number of recordings, suggesting that these species might be rare overall rather than preferentially associated with one site. Despite differences in canopy cover and

Table 4. The proportion of ten-minute recordings that contained a given species, and the number of calls detected per ten-minute recording when a species was detected as a function of sampling time.

	Prop. of Recordings with Species			Calls/10 Minutes when Present		
	1900	0000	0500	1900	0000	0500
Unmatched signals	1.00	0.89	1.00	73.0	44.0	31.0
<i>Acantheremus major</i>	0.11	0.00	0.00	10.0		
<i>Acanthodis curvidens</i>	0.11	0.00	0.00	1.0		
<i>Agraecia festae</i>	0.00	0.11	0.11		37.0	1118.0
<i>Anapolisia colosseae</i>	0.00	0.00	0.22			1.5
<i>Anaulacomera furcata</i>	0.67	0.44	0.22	15.5	2.0	1.5
<i>Anaulacomera</i> "ricotta"	0.00	0.00	0.11			1.0
<i>Anaulacomera spatulata</i>	0.33	0.11	0.78	14.0	3.0	3.0
<i>Anaulacomera</i> sp. "wallace"/ <i>Hetaira</i> sp.	0.22	0.00	0.44	3.0		4.5
<i>Chloroscirtus discocercus</i>	0.11	0.11	0.00	11.0	1.0	
<i>Ceraia mytra</i>	0.00	0.33	0.11		1.0	1.0
<i>Docidocercus gigliotosi</i>	0.22	0.22	0.00	9.5	6.0	
<i>Dolichocercus latipennis</i>	0.33	0.00	0.11	3.0		1.0
<i>Ectemna dumicola</i>	0.22	0.22	0.11	21.0	1.0	3.0
<i>Euceraia atryx</i>	0.00	0.22	0.11		2.0	1.0
<i>Euceraia insignis</i>	0.00	0.00	0.33			2.0
<i>Erioloides longinói</i>	0.33	0.22	0.22	1.0	7.0	4.5
<i>Hyperphrona irregularis</i>	0.22	0.00	0.22	8.5		1.0
<i>Ischnomela pulchripennis</i>	0.11	0.22	0.00	1.0	810.5	
<i>Microcentrum championi</i>	0.00	0.11	0.00		3.0	
<i>Montezumina bradleyi</i>	0.22	0.11	0.11	44.0	1.0	68.0
<i>Phylloptera quinquemaculata</i>	0.00	0.00	0.11			2.0
<i>Pristonotus tuberosus</i>	0.44	0.89	0.56	6.0	12.0	2.0
<i>Thamnobates subfalcata</i>	0.22	0.56	0.00	78.5	37.0	
<i>Viadana brunneri</i>	0.33	0.22	0.11	10.0	4.0	4.0

forest density between the two sites, our data provide preliminary evidence that acoustic sampling of a relatively small number of locations may provide a reasonably thorough list of species found in that microenvironment, although additional research is required to understand the spatial scale at which communities vary. It is important to note that both recorders used in this study were placed 24 m from the ground. While recordings made at 24 meters might resemble other recordings made at 24 m, this does not mean that these recordings capture the presence of understory katydid species, and for censusing diversity, sampling at multiple heights may well be more important than sampling at many locations.

Katydid calls were commonly detected throughout the night and across seasons. While some species were more commonly detected early or late in the evening, nearly all of the commonly detected species produced calls that were detected at multiple times of night, mirroring the temporal calling patterns observed in recordings of captive focal katydids (Symes et al. 2020). Seasonally, katydids were well represented in all recordings, including during the wet season and at the end of an unusually dry season (Fig. 1). Katydids are caught at lights and in the forest throughout the year, with higher abundance Feb-April (Ricklefs 1975). These species may mate throughout the year, but since many species live for many months and potentially years, they may be present at times when they are not mating. However, the presence of katydid calls in all recordings suggests that at least some katydid species are mating throughout the year.

Table 5. Proportion of ten-minute recordings that contain each species and the number of calls detected per ten minutes when a species is present. Note that the earliest date (Mar 05) is only represented by Site 2.

	Proportion of Recordings with Species					Calls/10 Minutes when Present				
	5-Mar-19	5-Jun-19	2-Jul-19	1-Aug-19	30-Aug-19	5-Mar-19	5-Jun-19	2-Jul-19	1-Aug-19	30-Aug-19
Unmatched signals	1.00	1.00	0.83	1.00	1.00	92.0	40.0	73.0	32.0	42.5
<i>Acantheremus major</i>	0.00	0.00	0.00	0.00	0.17					10.0
<i>Acanthodis curvidens</i>	0.00	0.00	0.00	0.17	0.00				1.0	
<i>Agraecia festae</i>	0.00	0.17	0.00	0.00	0.17		37.0			1118.0
<i>Anapolisia colossea</i>	0.33	0.17	0.00	0.00	0.00	2.0	1.0			
<i>Anaulacomera furcata</i>	0.33	0.67	0.17	0.50	0.50	1.0	13.5	18.0	7.0	1.0
<i>Anaulacomera</i> sp. "ricotta"	0.00	0.00	0.00	0.17	0.00				1.0	
<i>Anaulacomera spatulata</i>	0.33	0.67	0.33	0.33	0.33	3.0	3.5	20.0	1.5	14.5
<i>Anaulacomera</i> sp. "wallace"/ <i>Hetaira</i> sp.	0.00	0.33	0.33	0.17	0.17		2.5	19.5	1.0	7.0
<i>Chloroscirtus discocercus</i>	0.00	0.00	0.17	0.00	0.17			11.0		1.0
<i>Ceraia mytra</i>	0.00	0.17	0.00	0.17	0.33		1.0		1.0	1.5
<i>Docidocercus gigliotosi</i>	0.00	0.17	0.00	0.17	0.33		10.0		2.0	9.5
<i>Dolichocercus latipennis</i>	0.00	0.17	0.00	0.33	0.17		3.0		2.0	2.0
<i>Ectemna dumicola</i>	0.00	0.17	0.00	0.33	0.33		1.0		14.0	9.0
<i>Euceraia atryx</i>	0.00	0.17	0.00	0.33	0.00		1.0		2.0	
<i>Euceraia insignis</i>	0.00	0.17	0.17	0.17	0.00		2.0	4.0	1.0	
<i>Erioloides longinoi</i>	0.33	0.50	0.17	0.33	0.00	1.0	9.0	3.0	1.0	
<i>Hyperphrona irregularis</i>	0.00	0.17	0.17	0.33	0.00		1.0	7.0	5.5	
<i>Ischnomela pulchripennis</i>	0.33	0.00	0.17	0.00	0.17	711.0		910.0		1.0
<i>Microcentrum championi</i>	0.00	0.00	0.00	0.00	0.17					3.0
<i>Montezumina bradleyi</i>	0.00	0.50	0.00	0.17	0.00		68.0		15.0	
<i>Phylloptera quinquemaculata</i>	0.00	0.00	0.17	0.00	0.00			2.0		
<i>Pristonotus tuberosus</i>	0.33	0.67	0.67	1.00	0.33	1.0	12.0	15.5	4.5	8.0
<i>Thamnobates subfalcata</i>	0.33	0.00	0.33	0.17	0.50	350.0		93.0	4.0	13.0
<i>Viadana brunneri</i>	0.00	0.33	0.33	0.17	0.17		1.5	8.0	14.0	4.0
Number of species detected	8	17	13	18	16					
Average species/10 min	3.3	6.2	4.0	6.0	5.0					

There were a surprising number of high-quality calls that did not match any species in the ter Hofstede et al. (2020) paper, which presents the calls of 50 katydid species from BCI and includes most of the species that are commonly caught at light traps. The katydids of Barro Colorado Island are comparatively well studied and recorded. The authors have caught nearly 8,000 katydids at this site and have documented ~80 species, with 1–2 additional species observed each year. The canopy soundscape recordings contained >10 repeatably recognizable calls between 15 and 40 kHz that did not match commonly recorded katydid species. It is possible that these sounds are produced by some of the 30+ katydid species that are not included in the ter Hofstede et al. (2020) paper. The species that were not included in this publication were rarely observed in light catches or did not produce sound in focal recordings (e.g., *Caulopsis* spp.). Some of these calls could also represent non-katydid insects. However, in recording 55 cricket species from Barro Colorado Island, Heiner Römer and colleagues recorded only two species with calls above 10 kHz (12.1 and 13.8 kHz) (H. Römer and A. Schmidt, personal communication). In a separate study, the cricket species *Ponca hebardii* was recorded at 17.6 kHz, suggesting that high frequency crickets are uncommon but not absent in the BCI soundscape (Benavides-Lopez 2020).

A likely possibility is that these unmatched sounds represent canopy specialist katydid species, some or many of which may not be documented, described, or captured in light catches. In a study of Peruvian katydid species (Nickle 2006), extensive terrestrial surveys generated a thorough list of local katydid species. However, canopy fogging resulted in the novel discovery of additional

species of katydids that had never been observed on the ground. Acoustic recording provides evidence to suggest that there may be katydid species on BCI that have never been captured in exhaustive light trap surveys. The prevalence of unmatched calls in these recordings suggests that the number of katydid species in this habitat could be substantially higher than the currently estimated 80 species. Unmatched calls represent a particular challenge for data archiving, particularly because some of these calls may match to species that have been described in other well-studied locations or will be in the future. The acoustic monitoring of habitats will be advanced by developing approaches for comparing unknown sounds against existing sound archives.

Numerous species were documented in ter Hofstede et al. (2020) that did not appear in the recordings made at 24 m height in the forest, even though they are common in light catch data. The absence of many species from canopy recordings may reflect habitat partitioning, with some of these species not occurring or calling in the canopy. In particular, species in the *Arota* and *Phylloptera* genera are conspicuously rare/absent in recordings, despite being common in light catch data and active callers in focal recordings.

The mean number of calls detected per ten-minute recording was generally quite similar between soundscape and focal individual recordings, providing two lines of evidence both supporting low call rates in Neotropical forest katydids. In addition, there was often remarkably good alignment between the call rates in caged focal recordings and the call rates in soundscape recordings. An exception to this is *Anaulacomera spatulata*, where the mean num-

ber of calls detected on the soundscape recording was approximately twice as high as the number detected in a focal recording of a single individual. The abundance of calls on the soundscape recording is consistent with the presence of multiple individuals within range of the microphone and is supported by the fact that *Anaulacomera spatulata* is the most common species in light catches. Another notable exception is *Docidocercus gigliotisi*, where forest recordings contained a mean of 8 calls per recording where it was detected, and focal recordings had a mean of 48 calls in ten minutes. In previous work, *D. gigliotisi* performed documented vertical migrations, calling actively at the ground level and then entering the canopy, where calling rates may be reduced during foraging (Lang and Römer 2008).

Annotation of insect calls can provide detailed insight into the spatial and temporal dynamics of calling insect communities (Riede 2018). While annotation can be time consuming, the annotation of some species is much more challenging than others. In general, distinctive multi-pulse calls with fixed pulse spacing were comparatively easy to identify to species, compared to single pulse calls, which were especially difficult to identify with confidence. In single pulse calls, the lack of repetition made it challenging to confirm species identity and to separate single pulse calls from other sounds in the rainforest, particularly the short replies used by duetting females. Ultimately, we excluded two species that produced single pulse calls (*Philophyllia ingens* and *Anaulacomera* sp. "goat") because we had low confidence in the identification of these single pulse calls. Future projects relying on manual or automated identification may consider the trade-offs between the missing information from excluding these species and the benefit of faster and more confident species identifications.

Detailed understanding of insect communities provides valuable information for conservation and management (Fischer et al. 1997, Thomas 2005). The active debate around the nature and magnitude of insect population declines highlights how little we know about insects, including information about what times of year a given species is present and whether it is active in the canopy and understory (Forister et al. 2019, Janzen and Hallwachs 2019). The absence of basic natural history information obscures trends such as declines in understory insects, or in species that breed in response to specific rainfall regimes. Although call identification is currently a time-consuming process, advances in automated processing, particularly machine learning approaches, are poised to make identification much faster and more accessible. When acoustic sampling occurs across years and sites in a standardized manner, recordings can provide metrics of relative abundance over time and between species and, when combined with information on insect call amplitude and sound attenuation, can be used to calculate absolute density. Detailed information on species composition and relative and absolute abundance will provide greater insight into a central layer of the food web, providing valuable information on the population dynamics of insects, facilitating habitat management and data-driven decision making for conservation.

Acknowledgements

We gratefully acknowledge funding from Microsoft and the National Geographic Society "Artificial Intelligence for Earth Innovation" grant NGS-57246T-18 to LBS, HMtH, SJM, and SM and from Dartmouth College to LBS and HMtH. Support for SM was provided in part by the Arthur Vining Davis Foundations Grant 1805-18683. Support for publication was provided by the Orthop-

terists' Society. Facilities and logistical assistance were provided by the Smithsonian Tropical Research Institute. We also thank Riley Fortier for assistance with the maintenance of acoustic equipment.

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Supplementary material 1

Author: Hannah ter Hofstede

Data type: image

Explanation note: Figure S1: Relative microphone sensitivity at frequencies recorded by the Rugged Swift with a sampling rate of 96 samples/s. Points are average values for 5 relative amplitude measurements (one direct recording and four recordings with the speaker 45° off-axis from the microphone with the recorder pointing left, right, up, and down). Grey shading shows \pm SD. Grey line is the smoothed moving average of 3 data points.

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Link: <https://doi.org/10.3897/jor.31.73373.suppl1>