Satellite remote sensing of environmental variables can predict acoustic activity of an orthopteran assemblage

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Passive acoustic monitoring (PAM) is a promising method for biodiversity assessment, which allows for longer and less intrusive sampling when compared to traditional methods (e.g., collecting specimens), by using sound recordings as the primary data source. Insects have great potential as models for the study and monitoring of acoustic assemblages due to their sensitivity to environmental changes. Nevertheless, ecoacoustic studies focused on insects are still scarce when compared to more charismatic groups. Insects' acoustic activity patterns respond to environmental factors, like temperature, moonlight, and precipitation, but community acoustic perspectives have been barely explored. Here, we provide an example of the usefulness of PAM to track temporal patterns of acoustic activity for a nocturnal assemblage of insects (Orthoptera). We integrate satellite remote sensing and astronomically measured environmental factors at a local scale in an Andean Forest of Colombia and evaluate the acoustic response of orthopterans through automated model detections of their songs for nine weeks (March and April of 2020). We describe the acoustic frequency range and diel period for the calling song of each representative species. Three species overlapped in frequency and diel acoustics but inhabit different strata: canopy, understory, and ground surface level. Based on the acoustic frequency and activity, we identified three trends: i) both sampled cricket species call at lower frequency for shorter periods of time (dusk); ii) all sampled katydid species call at higher frequency for longer time periods, including later hours at night; and iii) the diel acoustic activity span window seems to increase proportionally with dominant acoustic frequency, but further research is required. We also identified a dusk chorus in which all the species sing at the same time. To quantify the acoustic response to environmental factors, we calculated a beta regression with the singing activity as a response variable and moon

phase, surface temperature and daily precipitation as explanatory variables. The response to the moon phase was significant for the katydids but not for the crickets, possibly due to differences in diel activity periods. Crickets are active during dusk, thus the effects of moonlight on acoustic activity are negligible. The response to precipitation was significant for the two crickets and not for the katydids, possibly because of higher likelihood of rain interrupting crickets' shorter diel activity period. Our study shows how the local survey of orthopteran acoustic assemblages, with a species taxonomic resolution coupled with remote-sensing environmental measurements can reveal responses to environmental factors. In addition, we demonstrate how satellite data might prove to be a useful alternative source of environmental data for community studies with geographical, financial, or other constraints.

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Abstract

Passive acoustic monitoring (PAM) is a promising method for biodiversity assessment, which allows for longer and less intrusive sampling when compared to traditional methods (e.g., collecting specimens), by using sound recordings as the primary data source. Insects have great potential as models for the study and monitoring of acoustic assemblages due to their sensitivity to environmental changes. Nevertheless, ecoacoustic studies focused on insects are still scarce when compared to more charismatic groups. Insects' acoustic activity patterns respond to environmental factors, like temperature, moonlight, and precipitation, but community acoustic perspectives have been barely explored. Here, we provide an example of the usefulness of PAM to track temporal patterns of acoustic activity for a nocturnal assemblage of insects (Orthoptera). We integrate satellite remote sensing and astronomically measured environmental factors at a local scale in an Andean Forest of Colombia and evaluate the acoustic response of orthopterans through automated model detections of their songs for nine weeks (March and April of 2020). We describe the acoustic frequency range and diel period for the calling song of each representative species. Three species overlapped in frequency and diel acoustics but inhabit different strata: canopy, understory, and ground surface level. Based on the acoustic frequency and activity, we identified three trends: i) both sampled cricket species call at lower frequency for shorter periods of time (dusk); ii) all sampled katydid species call at higher frequency for

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53 alternative source of environmental data for community studies with geographical, financial, or
54 other constraints.
55
56 ## Introduction
57
58 Many animals use acoustic signaling as their principal form of communication (Bradbury &
59 Vehrencamp, 2011), contributing to the biotic component of a soundscape (Pijanowski et al.
60 2011). Ecological questions regarding behavior, seasonal activity, or response to external factors
61 at different ecological and temporal scales of acoustic communities can be addressed with
62 acoustic monitoring (Sugai et al., 2019; Gottesman et al., 2021; Chhaya et al., 2021); such
63 monitoring can be with in-person recording in the field (Drewry & Rand, 1983; Diwakar &
64 Balakrishnan, 2007a) or with automatic, passive recording (Deichmann et al., 2018). Favored by
65 the increasing access to new recording technologies and computational power, passive acoustic
66 monitoring (PAM) has become one of the trending methods to obtain environmental recordings
67 (Riede, 2018; Sugai et al., 2019). PAM consists of the deployment of autonomous passive
68 recorders in the field. Its advantages for biodiversity monitoring include longer term assessment
69 periods, less intrusive monitoring methods, increase of data collection, and increased potential
70 for community bioacoustics research at different scales, when compared to classical monitoring
71 approaches such as specimen collection in the field (Blumstein et al., 2011; Deichmann et al.,
72 2018; Sugai et al., 2020). Furthermore, PAM allows the classification of calling songs into
73 recognizable taxonomic units, also referred to as acoustic morphospecies or sonotypes (Riede,
74 1998; Aide et al., 2013; Ferreira et al., 2018). Despite that, there are still challenges when
75 applied to high diverse taxonomic groups with lees availability of taxonomic and acoustic
76 descriptions, as insects (Riede, 2018). To address these challenges, we acoustically monitored a
77 nocturnal orthopteran assemblage and matched the sonotypes with taxonomic species identified
78 from voucher specimens captured at the same location.
79

80   Insect sounds drive tropical soundscapes by contributing acoustic signaling that varies in time,
81   acoustic frequency, and spatial scales (Aide et al., 2017). In addition, insect sounds have high
82   potential as acoustic bioindicators, especially at local scales, due to their sensitivity to
83   environmental change (McGeoch, 2007; Jeliazkov et al., 2016; Riede, 2018). Within insects,
84   crickets and katydids (Orthoptera: Ensifera) are some of the most important acoustic contributors
85   to soundscapes. They produce sound by rubbing together specialized structures in their wings, a
86   behavior called elytral stridulation (Baker & Chesmore, 2020). Between the different types of
87   stridulatory calls, the "calling song" is used by males to attract the opposite sex (Grimaldi &
88   Engel, 2005; Buellesbach, Cash & Schmitt, 2018). Calling songs are the most common insect
89   signals to be found in natural soundscapes, and they are often used in taxonomic and
90   evolutionary studies (Tan et al., 2021) due to their stereotyped characteristics and high species-
91   specificity (Grimaldi & Engel, 2005). However, few ecoacoustics studies include detailed
92   taxonomic resolution for orthopterans or other insects (Diwakar & Balakrishnan, 2007a; Gasc et
93   al., 2018), and many community approaches are rather focused on charismatic vertebrates such
94   as birds (Tobias et al., 2014), anurans (Villanueva-Rivera, 2014), or mammals (Heinicke et al.,
95   2015). When it comes to the community scale, matching acoustic species with taxonomic species
96   will help to unveil biological communities' structure and change over space and time (Chhaya et
97   al., 2021).
98
99   At a community level, the changes in acoustic activity patterns can be explained by the influence
100   of a set of biotic and abiotic factors (Chhaya et al., 2021). On one hand, explanations of how
101   biotic factors influence acoustic patterns have been formalized by different theories (Farina,
102   2014). The acoustic niche hypothesis for example, states that animals respond to other signalers
103   by partitioning their acoustic activity (Krause, 1993) in order to avoid acoustic masking (or
104   overlap) in time, spectral frequency, and space, thus optimizing the signal transmission (Schmidt,
105   Römer & Riede, 2013). However, high time overlap is usual in tropical orthopteran assemblages,
106   especially during dusk chorus (Riede, 1996; Jain et al., 2014). The tendency of animals from
107   different species to concentrate their singing at the same time window has been previously
108   referred to as clustering (Tobias et al., 2014), and may benefit individual singers by lowering
109   predation risks (Jain et al., 2014; Farina & Ceraulo, 2017). On the other hand, abiotic
110   environmental factors such as temperature, precipitation or moonlight are known to predict
111   acoustic patterns in vertebrate animal communities (Bruni, Mennill & Foote, 2014; Pérez-
112   Granados, Schuchmann & Marques, 2022), as well as insects (Lang et al., 2006; Franklin et al.,
113   2009). Acoustic activity can be a very useful description of circadian and seasonal patterns (Aide
114   et al., 2013), and species responses to environmental variables (Pérez-Granados, Schuchmann &
115   Marques, 2022).
116
117   Most studies at community ecological scales gather environmental information locally, by
118   directly measuring the variables in the field, or by gathering it from local weather stations
119   (Ospina et al., 2013). However, field environmental information could be difficult or even

120   impossible to obtain in some circumstances, due to the sparse distribution or absence of weather
121   stations in some areas, remote location of study sites, or budget constraints. Satellite remote
122   sensing could be an alternative in such cases because it is spatially and temporally
123   comprehensive, despite lower resolution. Data gathered from satellite remote sensing has been
124   useful for ecological studies at landscape or habitat levels (Pettorelli et al., 2014; Pasetto et al.,
125   2018), but its potential for local community scale questions, such as the relationship with
126   acoustic activity remains unexplored.
127
128   Here, we characterize the acoustic activity of an orthopteran assemblage, measuring occurrence
129   of calling events per time unit and the level of inter-specific overlap in temporal and frequency
130   range. We expected to find a cluster of singing species during dusk (dusk chorus), but no species
131   overlapping in all three dimensions (time, frequency, and space). We also decided to explore the
132   implementation of satellite remote sensing data of environmental variables (surface temperature,
133   daily precipitation) along with astronomical calculated moon illuminated fraction, to describe
134   their species-specific effect on acoustic activity of an orthopteran assemblage in the tropical
135   Andes of Colombia. In addition, we recorded and collected insects (including some new species
136   for science that are being described) to identify sonotypes to species taxonomic level (when
137   possible). This work serves as an important basis for future acoustic monitoring protocols of
138   insects by identifying acoustic bioindicators and using available remote sensing data to provide
139   further insight for localized community ecology studies.
140

Materials & Methods

141

142

143   *Study site and acoustic sampling*
144   We sampled the soundscape at the Los Tucanes Natural Reserve, located in Gachantivá, Boyacá,
145   Eastern Andes of Colombia (5.789, -73.550; 2300 $\pm$ 25m asl). This private reserve includes an
146   area of 0.16 km^2 of sub-Andean Forest dominated by Andean oak (*Quercus humboldtii*) in
147   different regeneration states, with an annual temperature of 15°C. Annual precipitation is about
148   1450 mm, in two rainy seasons: from March to May and from October to November (Climate-
149   Data.org, 2019). Overall, this forest is a ~20 years old secondary forest with early successional
150   grasslands after agricultural abandonment. We used the acoustic monitoring data from an
151   Audiomoth 1.0.0 recorder deployed at a height of 1.5 m from the ground, with a sampling rate of
152   48kHz and resolution of 16 bits, set to record for 1 minute every 30 minutes during the rainy
153   season, from March to May of 2020 (Tovar Garcia & Acevedo-Charry, 2021).
154

155   The recording set (number of recordings, n=2851) was normalized to -3dB and uploaded to the
156   ARBIMON online platform by Rainforest Connection-RFCx (arbimon.rfcx.org), download
157   information available in Supplemental Data 11. From there, we manually explored a subsample
158   of recordings (Supplemental Table S1, training set size) to annotate the presence or absence of
159   the acoustic species most consistently observed throughout the days. We defined sonotypes

160   before identifying taxonomic species (see below) which were then used during the data analysis.
161   Other sonotypes with sporadic acoustic activity were not considered in the analyses given the
162   difficulty of training detection models from very few annotated recordings. Then, we trained
163   random forests (Supplemental Data S1, S2, S4, S6) and spectrogram template matching (or
164   pattern matching) (Supplemental Data S3, S5, S7) automatic recognition models using RFCx
165   ARBIMON integrated tools for each sonotype, using the annotated recordings as the training
166   dataset (Supplemental Table 1) in order to detect the occurrences of sonotypes for every
167   recording. We determined that the detection performance of spectrogram pattern matching was
168   better for katydids, while random forests was significantly better for crickets based on
169   preliminary tests. A detailed performance comparison between available detection models
170   (including those made for other animal groups) for orthopteran species remains as an interesting
171   issue to address, the more when new promising tools have recently been launched (e.g. Lapp et
172   al., 2021; Steinfath et al., 2021). Model output was manually revised, false positives were
173   discarded, and detection precision was calculated as suggested by Aide et al. (2013): all detection
174   models include a precision above 70% (Supplemental Table S2). After post validation, the model
175   output was a presence/absence per recording matrix for the complete recording dataset. We
176   defined the acoustic activity as the presences detected per time unit: hours and days (Aide et al.,
177   2013). Using the acoustic activity per hour, we described the average daily activity per species
178   and measured the temporal partition between pairs of species by the overlap of kernel densities,
179   which is a coefficient that reflects extent of overlap between activity patterns, as a measure of
180   similarity (Ridout & Linkie, 2009). In addition, we use the activity per day to fit models of
181   satellite remote-sensed environmental variables (see below).
182
183   To assign sonotypes with better taxonomic resolution, we collected specimens in the field and
184   conducted taxonomic delimitation by actively looking for the emitters of each signal of
185   sonotypes selected (those most consistently observed in PAM dataset) during two field trips,
186   from September and October 2020. Observations of microhabitat (height) and singing behavior
187   were made during these field trips. The collected specimens were deposited at the Instituto
188   Humboldt's entomological collection (IAvH-E) in Villa de Leyva (Boyacá) following extended
189   specimens' guidelines (Acevedo-Charry et al., 2021), with a genetic voucher (foreleg) also
190   deposited at the Instituto Humboldt's tissue collection in Palmira (Valle del Cauca, Colombia).
191   Specimens were identified to the highest taxonomic resolution possible. For some species, we
192   were unable to collect specimens (i.e., canopy dwellers), thus we assigned a sonotype temporary
193   name (e.g., "Flutist") to the acoustic signal (Aide et al., 2017; Ferreira et al., 2018). In addition,
194   we made recordings from some individuals in captivity (species: Katydid1, Katydid3, Katydid4)
195   or directly in the field (Katydid5) with an Audiomoth 1.0.0 recorder at a sampling rate of 384
196   kHz and a resolution of 16 bits. Reference recordings for other species (Cricket1, Cricket2 and
197   Katydid2) were taken in the field using a Sennheiser ME67 shotgun microphone attached to a
198   first generation SoundDevice Mix Pre 3 recorder. Acoustic recordings were deposited in the

199   Instituto Humboldt's sound collection - Colección de Sonidos Ambientales *Mauricio Álvarez-*
200   *Rebolledo* (IAvH-CSA-18783 to IAvH-CSA-18805).
201
202   *Environmental variables from remote sensing data*
203   With the detection dates across our study time, we evaluate the relationship of the acoustic
204   activity per day of each species with satellite-detected local temperature, precipitation, and
205   moonlight. We extracted the time series from the pixel overlaying the sampling point from daily
206   generated raster files using the software Quantum GIS (QGIS Development Team, 2022).
207   Temperature was obtained from a 1km resolution dataset using Land Surface Temperature (LST)
208   parameter and generated using Moderate Resolution Imaging Spectroradiometer (MODIS) LST
209   products (Zhang et al., 2021, 2022); this dataset includes a measurement at 01:00 and another at
210   13:00 hours, equivalent to minimal and maximal daily temperature. On the other hand,
211   precipitation values were obtained from a 10km resolution dataset estimated using the Integrated
212   Multi-satellitE Retrievals for Global Precipitation Measurement (IMERG) (Huffman et al.,
213   2022). Environmental data used for the analysis is provided in Supplemental Data S8.
214   Preliminary analysis showed high correlation with the nearest national station at Santa Sofía,
215   Boyacá (10 km away of our study site) but IMERG data include more steady values (i.e., no gaps
216   in days as Santa Sofía had). Finally, moon illuminated fraction was retrieved through the
217   function *getMoonIllumination* from the R package *suncalc* for our sampling site coordinates
218   (Thieurmel & Elmarhraoui, 2019).
219
220   *Data analysis*
221   For temporal variables, diel acoustic activity of each species was analyzed using the package
222   *overlap* in R (Ridout & Linkie, 2009). First, we generated the von Mises kernel density
223   distribution of the diel acoustic activity for each species during the complete sampling period
224   (March to April) given that daily acoustic activity patterns correspond to a circular distribution.
225   Then, we computed the delta coefficient ($\hat{\Delta}_4$) of overlapping between every pair of species, as
226   recommended for samples sizes bigger than 75 (Ridout & Linkie, 2009) with the default
227   smoothing value. Confidence intervals were calculated by using a smoothed bootstrap with
228   10,000 samples, adjusted for bias (Ridout & Linkie, 2009).
229
230   Spectral variables, *i.e.,* dominant frequency (frequency with the most energy), frequency
231   bandwidth from minimum (-5dB below dominant frequency) to maximum frequencies (+5dB
232   over dominant frequency), were measured manually from the FFT analysis window (Hamming
233   window, 256 samples) of the software *ocenaudio* (ocenaudio Team, 2015) for the dominant
234   harmonic of 18 syllables, as defined by (Baker & Chesmore, 2020) for katydid species, and
235   eighteen 1s segments for cricket species. Segments were selected from the recordings with less
236   noise from the passive recording dataset for each species (Supplemental Data S10). Additional
237   harmonics were not measured as they were not constantly detected by the recorders due to
238   attenuation (Romer & Lewald, 1992; Hung & Prestwich, 2004). To assess frequency overlap, we

239   contrasted the measurements (minimum, maximum and dominant frequencies) for each species
240   by randomly resampling the measurements with 10,000 iterations. Each iteration per species and
241   measurement includes a mean value and confidence intervals of 95% of the data (Supplemental
242   Table S3).

243

244   We explored the relationship of the proportion of detections of each species in each day with the
245   four continuous remote-sensed variables through a beta regression, using the package *betareg* in
246   R (Cribari-Neto & Zeileis, 2010). We assumed a beta distribution because the values were
247   continuous and bounded between 0 and 1 (Bolker, 2007), scaling the occurrence detections with
248   the formula $Detections_{(b)} = [Detections_{(a)} * (N - 1) + 0.5]/N$, where N is the sample size and
249   $Detections_{(b)}$ is our response variable for the beta regression (Smithson & Verkuilen, 2006). To
250   select the variable that better fits the response variable (proportion of detections) for each
251   species, we scaled the predictor variables (min and max temperature, precipitation, and moon
252   fraction) by centering around the mean and dividing by two standard deviations (Schielzeth,
253   2010). For each species, we compared 16 additive models with different combinations of
254   predictor variables, including a null model. We identified the most frequency top-ranked model
255   (π_i) based on the delta Akaike Information Criteria (ΔAIC) and Akaike weight (w_i) after
256   resampling 10,000 times. To estimate better the top ranked model, in each resampling we
257   randomly select only 50 of the 61 days of recordings and estimate the percentage of times each
258   top-ranked model was selected (π_i) (Supplemental Data S9). We conducted our analyses in R,
259   and our code and data are available (https://github.com/diegryllid).

260

261   **Results**
262   We focused on seven identified orthopteran species for our analysis of the acoustic assemblage.
263   Two species of crickets (superfamily Grylloidea): "Flutist" (Cricket1) and Podoscirtinae
264   (Cricket2) and five katydids (family Tettigoniidae): *Copiphora colombiae* (Katydid1),
265   *Neoconocephalus brachypterus* (Katydid3)*,* Cocconotini (gen. nov.) (Katydid4), "Sprinkler"
266   (Katydid2), and "Rattler" (Katydid5). Although not all the species in the acoustic assemblage
267   were covered, these seven species were the most representative ones in terms of acoustic activity
268   (the ones detected most of the days) along the sampling period, as defined after the manual
269   annotation of recordings.

270

271   *Male singing behavior, microhabitat partitioning and songs of the assemblage*

272

273   We detected species dwelling in different microhabitats by sonotype *in situ*. In the upper side of
274   the forest, we detected the canopy dwellers (Cricket1, Katydid2, Katydid5). In the middle strata,
275   among shrubs and low tree branches (<4m), we detected Podoscirtinae (Cricket2). Similarly, we
276   detected Cocconotini gen. nov. (Katydid4) mostly at heights of ~4m at most. Finally, we
277   detected Katydid1 and Katydid3 in more open areas and early successional shrubs. *Cophiphora*
278   *colombiae* (Katydid1) sings from underneath the leaves or on top of the stems of understory

279   shrubs around 2 m above the ground, while *N. brachypterus* (Katydid) always sings from clumps
280   of grass, very close to the ground (0.5-1m). The heights here referred are visual estimates, hence
281   we recommend direct measurement of heights of individuals for a detailed description of spatial
282   distribution in forest strata. We detected two main singing behaviors as well. The first one was a
283   cryptic singing behavior consisting of singing undercover, observed in two species (Cricket2 and
284   Katydid4). The cricket species Podoscitinae (Cricket2) always sing from inside rolled oak leaves,
285   while the katydid species Cocconotini gen. nov. (Katydid4) sings from its own carved burrow in
286   live tree trunks (Cadena-Castañeda, Gómez-Morales, Acevedo-Charry, Benavides-López,
287   *Unpublished manuscript*). The second behavior was singing exposed, consisting of calling from
288   the top of leaves and branches, observed in two katydid species: *C. colombiae* (Katydid1) and *N.*
289   *brachypterus* (Katydid3). We could not observe singing behavior for the canopy dwellers
290   (Cricket1, Katydid2, Katydid5).
291
292   *Diel acoustic activity*
293   Diel acoustic activity varied across the night, reflecting two strategies. All katydids have a
294   completely nocturnal singing behavior (Katydid1, Katydid2, Katydid3, Katydid4, Katydid5),
295   although "Rattler" (Katydid5) showed a few, sparse detections during the day (Supplemental
296   data S7). These five species start singing at dusk (~17:30 hrs); then, three species show a higher
297   density of detections in specific times of the night (Katydid1: ~20:30, Katydid2: ~01:30,
298   Katydid3: ~20:00) shown as the peak acoustic activity density (Fig. 1). It is important to point
299   out that these three species are still active throughout the whole night, and their activity peaks are
300   subtle (less than 0.1 difference in acoustic activity density when compared to the mean of the rest
301   of the hours of activity). The remaining two katydids (Katydid4, Katydid5) showed relatively
302   constant acoustic activity throughout the night and a faster decrease in activity from 04:00 until
303   sunrise (~06:00). On the other hand, both crickets have a crepuscular schedule, singing mainly
304   during dusk. Podoscirtinae (Cricket2) showed a much more restricted singing schedule, from
305   18:00 to 19:00 with a very abrupt decrease in activity afterwards. Flutist (Cricket1) showed a
306   slower decrease in activity, maintaining a considerable number of detections after ~21:00.
307   Overall, we identified a chorus time when all the members of the assemblage sing at the same
308   time, from 18:00 to 20:00 (Fig. 1).
309
310   *Diel and spectral overlap*
311   Species density distribution pairwise analysis showed two overlap trends (Table 1). Crickets
312   have less probability of overlapping with the katydids' singing schedules (low coefficient values
313   <0.6). Of these two, Podoscirtinae (Cricket2) was the most specialized, having a very short
314   singing schedule (Fig. 1). Conversely, katydids overlap in their singing periods (high coefficient
315   values >0.6).
316
317   The mean dominant frequency was considerably lower for crickets, and higher for katydids.
318   While cricket bandwidth was narrow, katydid frequency bandwidth varied across species,

319   reflecting spectral overlap in four species (Fig. 2). The species which used a higher frequency
320   also include a higher bandwidth (Katydid5, Katydid4, Katydid3), overlapping among them. The
321   species with higher bandwidth, *N. brachypterus* (Katydid3), overlapped additionally with a
322   canopy dweller species, Katydid2, which included a lower frequency bandwidth. Although most
323   of the species had harmonic components in their calling song (all excepting Cricket1) as
324   observed in the directional recordings (Fig. 2a) with ultrasonic harmonics for all the katydids
325   except Katydid2. (Romer & Lewald, 1992; Hung & Prestwich, 2004). Ultrasonic harmonics were
326   not recorded or analyzed because of the sampling rate used in our PAM setting; audible
327   harmonics other than the dominant one (the harmonic with the highest amplitude) where not
328   analyzed either, as their lower amplitude made them undetectable in the automated field
329   recordings.
330

331   *Acoustic activity response to environmental variables*
332   The response of the acoustic activity varied by species and environmental variables obtained
333   from satellite remote sensing sources (Fig. 3, Table 2). Acoustic activity of katydid species
334   included a negative relationship with moon fraction for Katydid1 ($\beta = -0.28$, $p = 0.003$),
335   Katydid2 ($\beta = -0.34$, $p < 0.001$), Katydid3 ($\beta = -0.36$, $p < 0.001$), Katydid4 ($\beta = -0.13$, $p <$
336   0.001), and Katydid5 ($\beta = -0.07$, $p = 0.02$). Both cricket species showed a negative relationship
337   only with the precipitation (Cricket1: $\beta = -0.31$, $p = 0.006$; Cricket2: $\beta = -0.32$, $p = 0.002$) while
338   in katydids the response was more complex. In addition to the cricket species, precipitation was
339   also strongly negatively related to acoustic activity of Katydid1 ($\beta = -0.25$, $p = 0.02$), but less for
340   Katydid5 ($\beta = -0.06$, $p = 0.05$). Minimum temperature showed a positive trend for both Katydid1
341   ($\beta = 0.26$, $p = 0.007$) and Katydid2 ($\beta = 0.21$, $p = 0.04$), and maximum temperature was
342   significantly negatively related for Katydid5 only ($\beta = -0.07$, $p = 0.03$). In general terms, daily
343   precipitation is a better explanatory for the acoustic activity of crickets, while moon fraction for
344   acoustic activity of katydids.
345

346   **Discussion**
347

348   Despite insects' acoustic activity is driving the soundscapes of tropical ecosystems (Aide et al.,
349   2017), they are rarely identified with accurate taxonomic resolution in ecoacoustic studies. We
350   used the acoustic signaling footprint of different species from passive acoustic sampling to
351   characterize an orthopteran assemblage. With the daily acoustic activity pattern for each
352   sonotype, we were able to sample the prioritized species and match four out of seven species.
353   Despite recent improvement in taxonomic work in the group for Colombia (Cadena-Castañeda
354   et al., 2020, 2021), and impressive research on sound production and reception (Baker et al.,
355   2019; Celiker, Jonsson & Montealegre-Z, 2020), we found taxonomic novelties from this
356   community (Cadena-Castañeda, Gómez-Morales, Acevedo-Charry, Benavides-López,
357   *Unpublished manuscript*). In addition, we explored the relationship of acoustic activity of each
358   species with environmental variables extracted from satellite remote sensing data. We

359 experienced difficulties in collecting canopy dwellers, for which we recommend the use of
360 specialized methods such as fogging (Montealegre-Z et al., 2014), light trapping (e.g., Symes et
361 al., 2021), or specialized manual tracking (Diwakar & Balakrishnan, 2007b) for future studies. As
362 studies on environmental effects on insect acoustic communities are still rare, our study is an
363 important precedent, and serves as a good example on how satellite remote sensing data can be
364 used along with acoustic monitoring schemes in areas with low accessibility to ground-based
365 methods of environmental measurement, such as weather stations.
366
367 *Audible representative species*
368 Our focused species represent the most common nocturnal audible orthopteran insects in our
369 sampling site. Our approach, focusing in low frequency (audible spectrum) conspicuous species
370 has benefits and challenges. By focusing on from the most common species: On one hand, we
371 were able to describe the assemblage sonotopes identity as well as the overall trend of singing
372 behaviors that dominate the community. On the other hand, it left aside other species which are
373 rare or undetectable by our methods. Diurnal species, for instance, had relatively low
374 detectability within our data set (Grasshoppers mostly) and were barely detected, which confirms
375 previous observations for the group in tropical forests (Diwakar & Balakrishnan, 2007a). For
376 studies with the aim of extensively describing an acoustic community, or analyzing detailed
377 interactions between species, we recommend using more extensive sampling in both space (more
378 recording units) and time (longer monitoring periods) along with more intensive annotation of
379 recordings. For example, by using ultrasonic sampling for propper detection of some Neotropical
380 katydid species. The use of multiple recording units can also enhance the detectability of low
381 amplitude song species, which may have been under detected in our study. Despite that, given
382 their high activity and detectability, combined with our ability to match taxonomic resolution of
383 most of the species, we consider the representative species here taken into consideration are
384 adequate and sufficient for analyzing single species relations with environmental factors for
385 ecoacoustic monitoring purposes. Therefore, we recommend this approach of species
386 prioritization for environmental studies with time or methodological constraints.
387
388 *Time and spectral overlap*
389 We observed that the higher the dominant frequency of their calling song (Fig. 2), the broader
390 the diel acoustic activity range seemed to be (Fig. 1; Supplemental Figure 1). But such pattern
391 must be studied in detail in further research, focusing on the underlying mechanism regarding
392 interspecific competition, morphological constraints, and/or predator-prey relationships. While
393 cricket species had low frequency calling, narrowly clusters during dusk (Fig. 1, dotted line),
394 katydids dispersed their calling widely throughout the night. Furthermore, medium frequency
395 calling katydids (Fig. 1, dashed lines; Katydid1, Katydid2, Katydid3) show clear activity peak
396 times, and the high frequency ones (Fig. 1, solid lines; Katydid4, Katydid5) maintain constant
397 activity levels throughout the night. Previous studies found a negative relationship between
398 calling signal duration and daily signaling rate in neotropical katydids as result of acoustic trade-

399 offs (Symes et al., 2021), our data suggests that there might be a positive relationship between
400 the dominant frequency and the daily acoustic activity as well. In addition, although we did not
401 measure body size or specific size and properties of the producing sound structures for the
402 species in our assemblage, crickets were overall smaller than katydid species, thus our
403 observation might be contrary to the predictions of the morphological adaptation hypothesis
404 (Farina, 2014), previously proved in birds (Wallschläger, 1980), mammals (Fletcher, 2004), and
405 frogs (Boeckle, Preininger & Hödl, 2009). Such hypothesis may not even apply to orthopterans,
406 given that their way of producing sound (elytral stridulation) is completely different. For
407 example, Godthi et al. (2022) found a relationship of the size and properties of the stridulatory
408 apparatus with acoustic frequency, independent to body size. Further examination of our
409 vouchered specimens at IAvH-E might be useful for testing morphological hypotheses. Finally,
410 previous studies have shown that nocturnal predators, like bats, eavesdrop and select their prey
411 based on certain signal properties including peak frequency, and vary among species present in a
412 community (Falk et al., 2015); then in this case, lower peak frequency species in this assemblage
413 could be under stronger predation pressures, and respond by concentrating their singing in
414 shorter time periods to lower that risk (Farina & Ceraulo, 2017). Further research on these topics
415 for insects remains needed through experimentation.
416
417 In addition to the aggregation in time, there is a clear preference for dusk times by crickets, that
418 can be explained by the fact that it is the time of the day when diurnal predators are already
419 becoming inactive plus nocturnal predators being still not at their peak (Jain et al., 2014). Also,
420 this is the time where all the katydid species start to become active as well, so the simultaneous
421 interspecific singing can lower individual risk by "confusing" the predator who now has many
422 choices (Farina & Ceraulo, 2017). We previously referred to this period as the "dusk chorus",
423 and many other factors may be influencing this phenomenon. Moreover, the relatively high
424 katydid temporal overlapping (Table 1; Fig. 1) suggests that katydids are also aggregating their
425 acoustic activity in time, only in a different fashion; by concentrating on their activity later and
426 extending it during the whole night. Maintaining a continuous sing-along but extending their
427 signaling for several hours also comes with its downsides, which require further adaptations in
428 response to visual predators, as we will discuss later. Previous works have described how katydid
429 aggregation in space can lower the effectiveness of bat captures (Prakash et al., 2021). Although
430 we did not test the relationship between acoustic frequency and duration of the diel calling
431 activity, our preliminary analysis seems to suggest that species with lower dominant frequencies
432 tend to call for shorter periods (e.g. Cricket1 vs Katydid5; Supplemental Figure 1). Further
433 research including more taxa and sampling locations and taking into account the mechanisms
434 behind the dusk chorus along with the acoustic interactions with predators are necessary to
435 confirm the "frequency-acoustic activity relationship". In addition, we did not account for
436 phylogenetic or evolutionary constraints by contrasting these two groups of insects with very
437 different limitations on the frequency of their songs, leaving open such research topic to better
438 understand the orthopteran acoustic assemblage.

439
440   Even though four species show spectral overlap (Fig. 2), those might have different microhabitat
441   preferences: Katydid2 seems to dwell in the canopy, while Katydid3 was always found at ground
442   level grass chunks. Although we noted microhabitat observations based on opportunistic
443   sampling, our results provide an approach to try to understand spectral and temporal overlap for
444   some species. The species Katydid4 and Katydid5, which overlap in both time and frequency,
445   inhabit the understory and canopy, respectively, and may be avoiding masking because of
446   differential attenuation at different heights (Ellinger & Hödl, 2003). However, other studies have
447   found conflicting evidence (Jain & Balakrishnan, 2012). Further research is required to test this
448   hypothesis, as the effect of forest stratification over signal interference in insects remains unclear
449   (Schmidt & Balakrishnan, 2015). In addition, measurement of smaller scale time features could
450   help to confirm temporal masking avoidance at smaller scales (Symes et al., 2021), as Katydid4
451   and Katydid5 pulse rates and syllable duration seem to differ greatly.
452
453   *Environmental factors effects and Remote sensing data*
454   Katydid species decrease acoustic activity 0.70 to 0.93 times with a unit increase in moon
455   fraction light (from new moon at 0.0 to full moon at 1.0). The negative relationship found
456   between moon fraction and katydid species acoustic activity (Table 1, Fig. 3) corroborates the
457   findings of previous studies. For example, response to more moonlight led to avoidance of visual
458   predators, either by lowering their overall activity (Lang et al., 2006), or increasing the use of
459   alternate communication channels, such as tremulation (Römer, Lang & Hartbauer, 2010), as part
460   of katydids' repertoire of adaptations for predation by bats (ter Hofstede et al., 2017). Response
461   to moonlight is probably the consequence of the above-mentioned continuous time aggregation
462   as opposed to crickets', which in fact, did not show any relationship to moonlight (Table 2),
463   perhaps because during the dusk there is still plenty of sunlight, so moonlight would not make
464   any difference.
465
466   Regarding precipitation, cricket and two katydid species decrease acoustic activity 0.73 to 0.94
467   times with a unit increase in rainfall (mm per day). Such negative effect mainly over the acoustic
468   activity of the two cricket species (Cricket1 and Cricket2; Fig. 3) confirms previous observations
469   (Alexander & Meral, 1967) and our own during the field: whenever it rained during the chorus
470   time, the crickets barely sang. Although rain noise may have affected detectability on rainy days,
471   our manual revision of recordings and observations in the field give us confidence in the model
472   detections reflecting acoustic activity even during rainy days. Still, we recommend using
473   acoustic detection models accounted for rain detection itself as a way of measuring rain impacts
474   over detection of orthopterans in future studies. The katydids did not show that unique
475   relationship with daily precipitation, except for Katydid1 and Katydid5 which included other
476   covariates. However, something to consider is that given the shorter time span of crickets calling
477   time, they had a greater chance of being interrupted by rain, as has been observed in other
478   species (Alexander & Meral, 1967; Franklin et al., 2009), while broader katydid calling spans

479   may have improved their detectability even after short rainy periods during the night. Our
480   opinion is that rain may affect orthopterans singing at a finer time scale in addition to the
481   accumulated daily effects, as opposed to moonlight, given that daily precipitation can be either
482   sparsely or densely distributed during the day. In addition, other external factors such as wind
483   (Velilla et al., 2020), or ultrasonic background noise (Römer & Holderied, 2020) can affect
484   signaling behavior of katydid species as well. A comparison of both locally measured
485   precipitation and satellite remote sensing data with community acoustic activity may be useful to
486   confirm this relationship.

488   Temperature analysis suggests a negative relation (decrease 0.93 times with a unit increase) with
489   daily maximum temperature only for Katydid5, and positive relation with minimum temperature
490   for Katydid1 (increasing 1.30 times with a unit increase) and Katydid2 (increasing 1.23 times
491   with a unit increase in min temperature). The underlying reasons for this response are yet to be
492   discovered, but the increase in signaling by Katydid1 and Katydid2 species are concordant with
493   previous studies in other species (Franklin et al., 2009) which found increased signaling during
494   warmer nights. As the microhabitat's preference can play a fundamental role on temperature
495   regulation, we rather recommend the use of local scale measurements to further explore calling
496   activity relationship with this variable.

498   Although previous studies have evaluated the accuracy of the satellite remote sensing products
499   here used or similar with environmental applications (e.g., Palomino-Ángel, Anaya-Acevedo &
500   Botero, 2019), or overviewed its potential for ecosystem modelling (Pasetto et al., 2018), and
501   even coupled with passive acoustic monitoring (Elise et al., 2022), none to our knowledge has
502   yet evaluated the applicability of these datasets for answering local community ecology
503   monitoring questions. We recommend further comparison of local weather station data with
504   satellite remote sensing data, in the context of local biological monitoring programs for
505   evaluating the extent of applicability of this approach.

Conclusions

508   Astronomical moonlight and satellite remote sensing precipitation data can explain the acoustic
509   activity of katydids and crickets respectively in an orthopteran assemblage, and its use may be
510   beneficial for studies with geographical, financial, or other constraints. Still, we consider that
511   further analysis including multiple sampling points is necessary before generalizing the patterns
512   observed here, given the small time and space scale of the present study. The effects of small
513   changes in environmental factors on species acoustic activity observed in our study suggest
514   orthopterans could be a successful key indicator of environmental change. How those changes
515   could be extrapolated to annual seasonality and other trophic levels is a potential endeavor to
516   better understand acoustic communities worldwide. Finally, acoustic monitoring of orthopterans
517   has a high potential for environmental assessments, in addition to answering ecological questions
518   and enriching taxonomic descriptions of under-studied biotas.

519

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533

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757

Kernel density delta coefficient for pairs of species.

Bootstrap 95% confidence intervals in parenthesis. The values go from 0 to 1, being 1 complete overlap.

	Podoscirtinae (Cricket2)	*C. colombiae* (Katydid1)	"sprinkler" (Katydid2)	*N. brachypterus* (Katydid3)	Cocconotini (gen. nov); (Katydid4)	"Rattler" (Katydid5)
"Flutist" (Cricket1)	0.49 (0.41-0.58)	0.42 (0.36-0.47)	0.34 (0.30-0.38)	0.51 (0.44-0.57)	0.36 (0.32-0.40)	0.32 (0.28-0.36)
Podoscirtinae (Cricket2)		0.16 (0.12-0.20)	0.14 (0.11-0.18)	0.21 (0.16-0.25)	0.17 (0.14-0.20)	0.12 (0.09-0.15)
C. colombiae (Katydid1)			0.86 (0.81-0.90)	0.89 (0.83-0.94)	0.81 (0.76-0.85)	0.78 (0.74-0.82)
"sprinkler" (Katydid2)				0.77 (0.71-0.81)	0.91 (0.88-0.94)	0.90 (0.87-0.93)
N. brachypterus (Katydid3)					0.74 (0.70-0.78)	0.72 (0.67-0.76)

Results of beta regressions for the seven species

Response variable is the proportion of detections per day. Explanatory variable models include minimal (MinTemp) and maximal temperature (MaxTemp), daily precipitation, and moon fraction (Moon), in parenthesis is shown the estimated slope for the log odds ratio of each variable (β). π_i shows the percentage of times a model i was top-ranked after 10,000 iterations. k is the number of estimated parameters. w_i is the Akaike weight. Φ, SE (Standard Error), LL (Log-Likelihood), z-value, and Pr(>|z|) shows the result of the beta regression for the top-ranked model (see beta regression results in Supplementary Data S8).

Species	Model (β)	π_i	k	w_i	LL	Φ	z-value	Pr(>|z|)
Cricket1 – "flutist"	Precipitation (-0.31)	76.2	3	0.28	125.80	22.89	5.09	<0.001
Cricket2 – Podoscirtini	Precipitation (-0.32)	94.8	3	0.35	142.70	41.49	5.22	<0.001
Katydid1 – *C. colombiae*	MinTemp (0.26) + Precipitation (-0.25) + Moon (-0.28)	82.4	5	0.42	73.64	13.37	5.43	<0.001
Katydid2 – "sprinkler"	MinTemp (0.21) + Moon (-0.34)	30.2	4	0.25	38.30	7.00	5.69	<0.001
Katydid3 – *N. brachypterus*	Moon (-0.36)	56.8	3	0.28	73.63	16.2	5.49	<0.001
Katydid4 – Cocconotini (gen. nov.)	Moon (-0.13)	61.7	3	0.26	77.04	51.01	5.58	<0.001
Katydid5 – "rattler"	MaxTemp (-0.07) + Precipitation (-0.06) + Moon (-0.07)	62.3	5	0.27	89.25	77.43	5.56	<0.001

Figure 1

Acoustic activity density per species

The distribution was calculated from the number of detections every half an hour during the two-month sampling period. The acoustic activity density value corresponds to the proportion of positive detections at a given time. The shaded area demarks the probability of a dusk chorus when all species sing at the same time. The sun icons represent the sunset time and sunrise times. The type of line denotes the dominant frequency range: solid for high frequency, dashed for medium, and dotted for low.
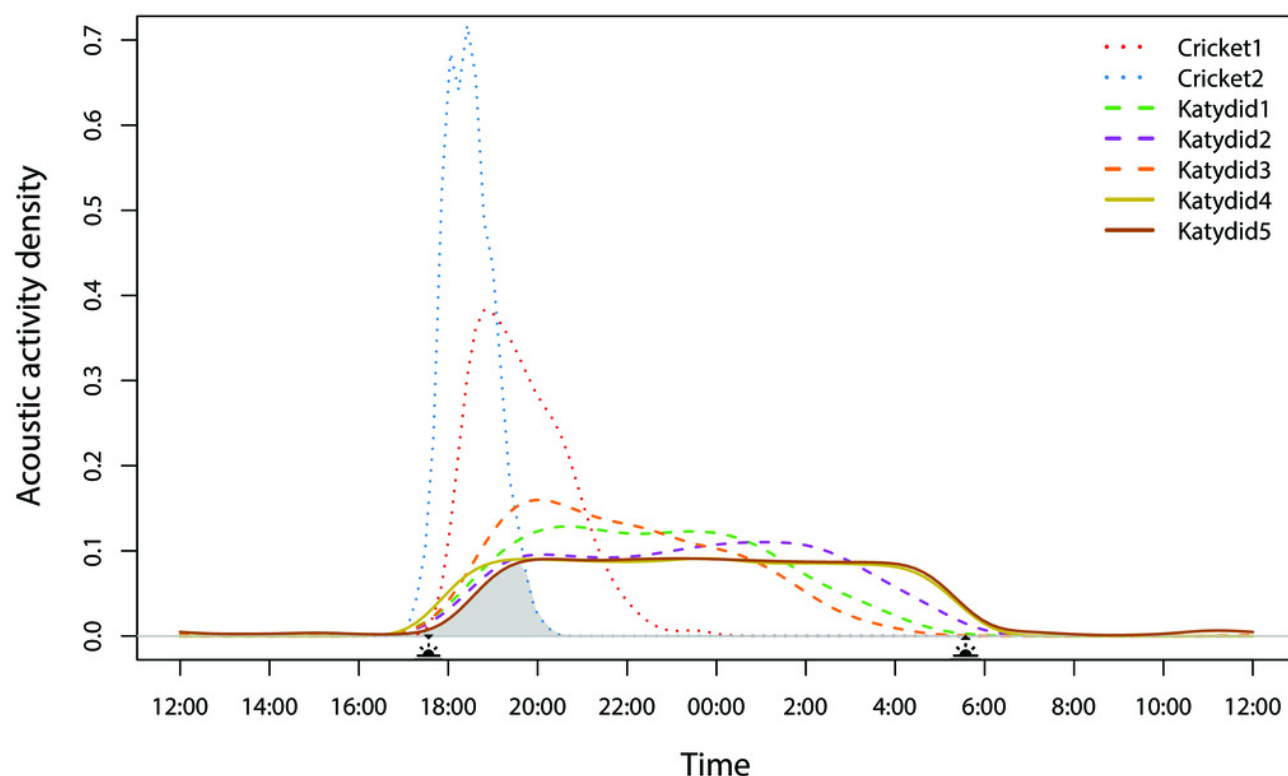
Figure 2

Frequency range per species

a) Spectrogram sections for the study species at 48kHz, same species order as in b) Average values for minimun, maximum, and dominant frequency calculated after a Bootstrap sampling of 10000 iterations.
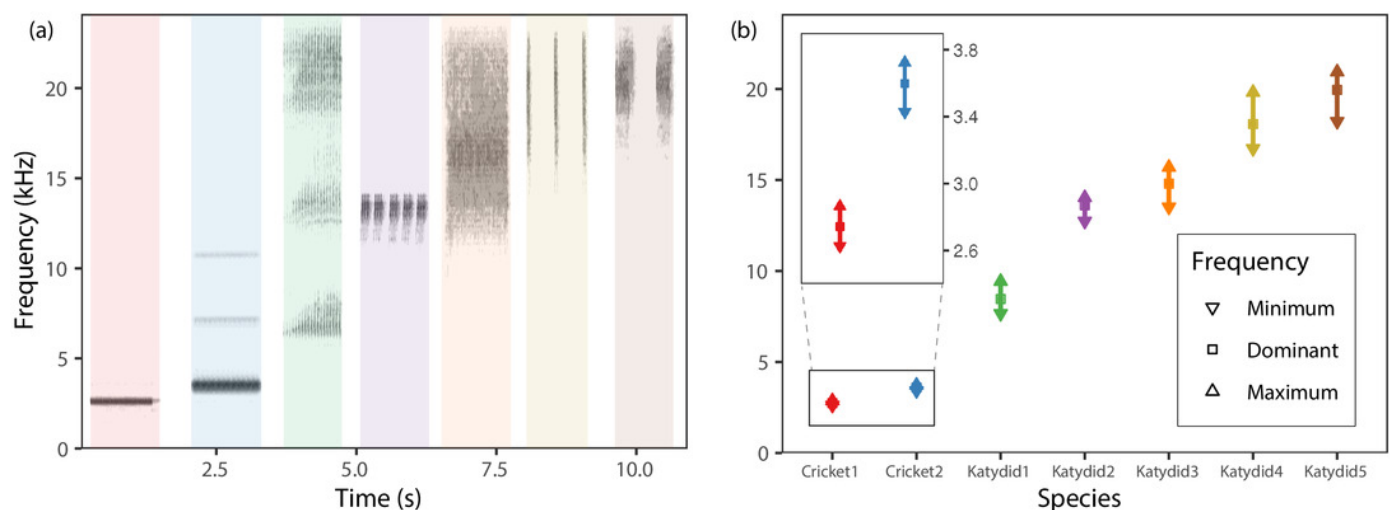
Figure 3

Relationship of acoustic detections with environmental factors

For each of the 7 focal species listed on the right axis, the inset figures show the proportion of acoustic detections as a function of 4 environmental variables measured via remote sensing: MoonFraction, Precipitation, Minimum Temperature, and Maximum Temperature. The points represent the proportion of positive detections per day during the two-month sampling period. Trend lines are shown for the significant relationships as determined by the beta regression analysis.