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Satellite remote sensing of environmental variables can explain acoustic activity of a tropical orthopteran community

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Abstract

Passive acoustic monitoring (PAM) of biodiversity is a promising method, which allows for longer and less intrusive sampling by using sound recordings as the primary data source. Insects have great potential as models for the study and monitoring of acoustic communities due to their sensitivity to environmental changes and diel activity. Nevertheless, ecoacoustic studies focused on insects are still far behind other more charismatic groups such birds, amphibians, or mammals. 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 nocturnal communities 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 pattern matching and random forest modeling 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) crickets call at lower frequency for shorter time periods (sunset); ii) katydids call at higher frequency for longer time periods, including later hours at night; and iii) the ~~calling~~ activity seems to increase proportionally with dominant acoustic frequency. We also

acoustic window

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identified a dusk chorus in which all the species sing simultaneously. 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 katydid species but not for the cricket species, possible due to shifts in activity patterns. Crickets are active while sunlight is still available (dusk), thus the effects of moonlight on acoustic activity are negligible. The response to precipitation was significant for the two cricket species and not for the katydids, possibly because of higher likelihood of rain interrupting the calling time of crickets. Our study shows how the local survey of orthopteran acoustic communities, with a species taxonomic resolution coupled with remote-sensing environmental measurements in a community approach 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.

Introduction

Many animals use acoustic sound signaling as their principal form of communication (Bradbury & Vehrencamp, 2011), contributing to the biotic acoustic component of a soundscape (Pijanowski et al. 2011). Ecological questions regarding behavior, seasonal activity, or response to external factors at different ecological and temporal scales of acoustic communities can be addressed with acoustic monitoring (Sugai et al., 2019; Gottesman et al., 2021; Chhaya et al., 2021), with direct *in situ* recording (e.g. Diwakar & Balakrishnan, 2007a; Drewry & Rand, 1983) or with automatic, passive recording (Deichmann et al., 2018). Favored by the increasing access to new recording technologies and computational power, passive acoustic monitoring (PAM) has become one of the trending methods to obtain environmental recordings (Riede, 2018; Sugai et al., 2019), it consists of the deployment of autonomous passive recorders in the field. The advantages of PAM for biodiversity monitoring include longer ~~term~~ assessment periods, less intrusive monitoring ~~arranges~~, increase d ~~of~~ data collection, and increased potential for community bioacoustics research at different scales, when compared to classical monitoring approaches (Blumstein et al., 2011; Deichmann et al., 2018; Sugai et al., 2020). Although PAM allows the classification of calling songs into recognizable taxonomic units, also referred to as acoustic morphospecies or sonotypes (Riede, 1998; Aide et al., 2013; Ferreira et al., 2018) there are challenges when applied to insects, especially in tropical environments: higher species diversity, and less availability of taxonomic and acoustic descriptions (Riede, 2018). To address these challenges, we acoustically monitored a nocturnal orthopteran community and matched the sonotypes with taxonomic species identified from voucher specimens captured *in situ*.

Insect sounds drive tropical soundscapes by contributing acoustic signaling in that varies in ~~varying~~ time, acoustic frequency, and ~~space~~ spatial scales (Aide et al., 2017). In addition, insect sounds have high potential as acoustic bioindicators, especially at local scales, due to their higher sensitivity to

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environmental change (McGeoch, 2007; Jeliazkov et al., 2016; Riede, 2018). Within insects, crickets and katydids (Orthoptera: Ensifera) are some of the most important acoustic contributors to soundscapes. They produce sound by rubbing together specialized structures in their wings, namely stridulation. Between the different types of stridulatory calls, the "calling song" is used by males to attract the opposite sex (Grimaldi & Engel, 2005; Buellesbach, Cash & Schmitt, 2018). Calling songs are actually the most common insect signals to be found in natural soundscapes, and they are often used in taxonomic and evolutionary studies (e.g. Tan et al., 2021) due to their stereotyped characteristics and high species-specificity (Grimaldi & Engel, 2005). However, few ecoacoustics studies include detailed taxonomic resolution for orthopterans or other insects (e.g. Diwakar & Balakrishnan, 2007a; Gasc et al., 2018), and many community approaches are rather focused on charismatic vertebrates such as birds (Tobias et al., 2014), anurans (Villanueva-Rivera, 2014), or mammals (Heinicke et al., 2015). When it comes to the community scale, matching acoustic species with taxonomic species will help to unveil biological communities' structure and change over time (Chhaya et al., 2021).

At a community level, the changes in acoustic activity patterns can be explained by the influence of a set of biotic and abiotic factors (Chhaya et al., 2021). On one hand, explanations of ~~the~~ how ~~influence of~~ biotic factors ~~over~~ influence acoustic patterns ~~had~~ have been formalized by different theories (Farina, 2014). The acoustic niche hypothesis for example, states that animals respond to other signalers by partitioning their acoustic activity (Krause, 1993) in order to avoid acoustic masking (or overlap) in time, spectral frequency, and space, thus optimizing the signal transmission (Schmidt, Römer & Riede, 2013). However, high time overlap is usual in tropical orthopteran communities, especially during ~~dusk, commonly referred to as a~~ dusk chorus (Riede, 1996; Jain et al., 2014). The tendency of animals from different species to concentrate their singing at the same time window has been previously referred to as clustering (Tobias et al., 2014), and may benefit individual singers by lowering predation risks (Jain et al., 2014; Farina & Ceraulo, 2017). On the other hand, abiotic environmental factors such as temperature, precipitation or moonlight are known to predict acoustic patterns in vertebrate animal communities (e.g. Bruni et al., 2014; Pérez-Granados et al., 2021), as well as insects (e.g. Franklin et al., 2009; Lang et al., 2006). Acoustic activity can be a very useful description of community temporal patterns (Aide et al., 2013), and species response to environmental variables (Pérez-Granados, Schuchmann & Marques, 2022).

Most studies at community ecological scales gather environmental information locally, by directly measuring the variables *in situ*, or by gathering it from local weather stations (Ospina et al., 2013). However, *in situ* environmental information could be difficult or even impossible to ~~get~~ obtain in some circumstances, su~~ch as spa~~re due to the sparse distribution or absence of weather stations in some areas, remote location of study sites, or budget constraints. Satellite remote sensing could be an alternative in such cases, because of being geographically and ~~time~~ temporally comprehensive, despite lower resolution. Data gathered from satellite remote sensing has been useful for ecological studies at

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landscape or habitat levels (Pettorelli et al., 2014; Pasetto et al., 2018), but its potential for local community scale questions, such as the relationship with acoustic activity remains unexplored.

Here, we characterize the acoustic activity of an orthopteran community, measuring occurrence of calling events per time unit and the level of inter-specific overlap in temporal and frequency range. We expected to find a cluster of singing species during dusk (dusk chorus), but no species overlapping in all three dimensions (time, frequency, and space). We also decided to explore the implementation of satellite remote sensing data of environmental variables (surface temperature, daily precipitation) along with astronomical calculated moon illuminated fraction, to describe their species-specific effect on acoustic activity of an orthopteran community in the tropical Andes of Colombia. Within our framework, we went beyond by finding taxonomic units in our community (including some new species for science under ~~current description~~) and exploring potential mechanisms that could drive acoustic activity using remote sensing data. This work serves as an important basis for future acoustic monitoring protocols of insects by identifying acoustic bioindicators and using available remote sensing data to provide further insight for localized community ecology studies.

Does method allow partitioning of time + freq. overlapping signals?

that are now being described

Materials & Methods

average

high/low/median?

Study site and acoustic sampling

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

Concentrated

The recording set (n=2851) was normalized to -3dB and uploaded to the ARBIMON online platform by Rainforest Connection-RFCx (arbimon.rfcx.org), download information available in Supplemental Data 11. From there, we sampled a subsample of recordings (Supplemental Table S1, training set size) to annotate the presence or absence of the acoustic species most consistently observed throughout the days. We defined sonotypes before identifying taxonomic species (see below) which were then used during the data analysis. Other sonotypes with sporadic acoustic activity were not considered in the analyses given the difficulty of training detection models from very few annotated recordings. Then, we trained random forests (Supplemental Data S1, S2, S4, S6) and pattern matching (Supplemental Data S3, S5, S7) automatic recognition models

Where is 1-16?

"sample period?" (likely night)

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using RFCx ARBIMON integrated tools for each sonotype, using the annotated recordings as the training dataset (Supplemental Table 1). Model output was manually revised, false positives were discarded, and detection precision was calculated: all detection models include a precision above 70% (Supplemental Table S2). After post validation, the model output was a presence/absence per recording matrix for the complete recording dataset. We defined the acoustic activity according to Aide et al., (2013), as the ~~presences~~ events detected per time unit: hours and days. Using the acoustic activity per hour, we described the average daily activity per species and measured the temporal partition(ing) between pairs of species by the overlap of kernel densities. In addition, we use the activity per day to fit models of satellite remote-sensed environmental variables (see below).

recall?

70% before discard?

To assign sonotypes with better taxonomic resolution, we collected specimens *in situ* and conducted taxonomic delimitation by actively looking for the emitters of each signal during two field trips, from September and October 2020, field study approval document available at Supplemental Article S1. Observations of microhabitat and singing behavior were made when possible. The collected specimens were deposited at the Instituto Humboldt's entomological collection in Villa de Leyva (Boyacá) following the guidelines by Acevedo-Charry et al. (2021), with a genetic voucher (foreleg) also deposited at the Instituto Humboldt's tissue collection in Palmira (Valle del Cauca, Colombia). Specimens were identified to the highest taxonomic resolution possible. For some species, we were unable to collect specimens (i.e., canopy dwellers), thus we assigned a sonotype temporal name (e.g., "Flutist") to the acoustic signal (Aide et al., 2017; Ferreira et al., 2018). In addition, we made recordings from some individuals in captivity (species: Gr8, Gr13, Gr22) or directly in the field (Gr20) with an Audiomoth 1.0.0 recorder at a sampling rate of 384 kHz and a resolution of 16 bits. Reference recordings for other species (Gr2, Gr4 and Gr12) were taken in the field using a Sennheiser ME67 shotgun microphone attached to a first generation SoundDevice Mix Pre 3 recorder. Acoustic recordings were deposited in the Instituto Humboldt's sound collection - Colección de Sonidos Ambientales *Mauricio Álvarez-Rebolledo* (IAvH-CSA-18783 to IAvH-CSA-18805).

— what [illegible]?

sampling rate?

Environmental variables from remote sensing data

With the detection dates across our study time, we evaluate the relationship of the acoustic activity per day of each species with satellite-detected local temperature, precipitation, and moonlight. We extracted the time series from the pixel overlaying the sampling point from daily generated raster files using the software Quantum GIS (QGIS Association). Temperature was obtained from a 1km resolution dataset using Land Surface Temperature (LST) parameter and generated using Moderate Resolution Imaging Spectroradiometer (MODIS) LST products (Zhang et al., 2021, 2022); this dataset includes a measurement at 01:00 and another at 13:00 hours, equivalent to minimal and maximal daily temperature. ~~On the other hand~~, Precipitation values were obtained from a 10km resolution dataset estimated using the Integrated Multi-satellitE Retrievals for Global Precipitation Measurement (IMERG) (Huffman et al., 2022).

- wouldn't min/max occur later?
(05:00 and
16:00 or 17:00?)

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Environmental data used for the analysis is provided in Supplemental Data S8. Preliminary analysis showed high correlation with the nearest national station at Santa Sofía, Boyacá (10 km away of our study site) but IMERG data include more steady values (i.e., no gaps in days as Santa Sofía had). Finally, moon illuminated fraction was retrieved through the function *getMoonIllumination* from the R package *suncalc* for our sampling site coordinates (Thieurmel & Elmarhraoui, 2019).

Data analysis

For temporal variables, diel acoustic activity of each species was analyzed using the package *overlap* in R (Ridout & Linkie, 2009). First, we generated the von Mises kernel density distribution of the diel acoustic activity for each species during the complete sampling period (March to April) given that daily acoustic activity patterns correspond to a circular distribution. Then, we computed the delta coefficient ($\hat{\Delta}_4$) of overlapping between every pair of species, as recommended for samples sizes bigger than 75 (Ridout & Linkie, 2009) with the default smoothing value. Confidence intervals were calculated by using a smoothed bootstrap with 10,000 samples, adjusted for bias (Meredith & Ridout, 2021).

For the spectral variables, *i.e.*, frequency bandwidth from minimum to maximum frequencies and dominant frequencies were measured with FFT analysis feature (Hamming window, 1024 bins) of the software *ocenaudio* (ocenaudio Team) for five syllables, as defined by Baker & Chesmore (2020) for katydid species, and five 1s segments for cricket species at -10dB. Segments were selected from either reference recordings taken from captive individuals, or directional field recordings for the species with or without physical specimen and were normalized to -10dB before measurement (Supplemental Data S10). To assess frequency overlap, we contrasted the measurements (minimum, maximum and dominant frequencies) for each species by randomly resampling the measurements with 10,000 iterations. Each iteration per species and measurement includes a mean value and confidence intervals of 95% of the data (Supplemental Table S3).

bins or samples?

We explore the relationship of the proportion of detections of each species in each day with the four continuous remote-sensed variables through a beta regression, using the package *betareg* in R (Cribari-Neto & Zeileis, 2010). We assumed a beta distribution because the values were continuous and bounded between 0 and 1 (Bolker, 2007), scaling the detections with the formula $Detections_{(b)} = [Detections_{(a)} * (N - 1) + 0.5]/N$, where N is the sample size and $Detections_{(b)}$ is our response variable for the beta regression (Smithson & Verkuilen, 2006). To select the variable that better fits the response variable (proportion of detections) for each species, we scaled the predictor variables (min and max temperature, precipitation, and moon fraction) by centering around the mean and dividing by two standard deviations (Schielzeth, 2010). For each species, we compared 16 additive models with different combinations of predictor variables, including a null model. We identified the most frequency top-ranked model (π_i) based on the delta Akaike Information Criteria (ΔAIC) and Akaike weight (w_i) after resampling 10,000 times.

Check

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To estimate better the top ranked model, in each resampling we randomly select only 50 of the 61 days of recordings and estimate the percentage of times each top-ranked model was selected (π_i) (Supplemental Data S9). We conducted our analyses in R, and our code and data are available (https://github.com/diegryllid).

Results

We identified seven orthopteran species for the acoustic community. Two species of crickets (superfamily Grylloidea): "Flutist" Gr2 and Podoscirtinae (Gr4) and four katydids (family Tettigoniidae): *Copiphora colombiae* (Gr8), *Neoconocephalus brachypterus* (Gr13), Cocconotini (gen. nov.) (Gr22), "Sprinkler" (Gr12), and "Rattler" (Gr20). Although not all of the species in the acoustic community were covered, these seven species were the most representative ones in terms of acoustic activity (the ones detected most of the days) along the sampling period, as defined after the manual annotation of recordings.

Estimate % of community

Male singing behavior, microhabitat partitioning and songs of the community

canopy? Height?

We detected species dwelling in different microhabitats by sonotype *in situ*. In the upper ~~side~~ of the forest, we detected the canopy dwellers (Gr2, Gr12, Gr20). In the middle strata, among shrubs and low tree branches (<4m), we detected Podoscirtinae (Gr4). Similarly, we detected Cocconotini gen. nov. (Gr22) at heights of ~4m at most. Finally, we detected Gr8 and Gr13 in more open areas and early successional shrubs. *Cophiphora colombiae* (Gr8) sing from underneath the leaves or on top of the stems of shrubs around 2 m above the ground, while *N. brachypterus* (Gr13) always sings from clumps of grass, very close to the ground (0.5-1m). We detected two main singing behaviors as well. The first one was a cryptic singing behavior consisting of singing undercover, observed in two species (Gr4 and Gr22). The cricket species Podoscitinae (Gr4) always sing from inside rolled oak leaves, while the katydid species Cocconotini gen. nov. (Gr22) sings from its own carved burrow in live tree trunks (Cadena-Castañeda, Gómez-Morales, Acevedo-Charry, Benavides-López, *Unpublished manuscript*). The second behavior was singing exposed, consisting of calling from the top of leaves and branches, observed in two katydid species: *C. colombiae* (Gr8) and *N. brachypterus* (Gr13). We could not observe singing behavior for the canopy dwellers.

layer or strata

How high is this layer?

Diel acoustic activity

Diel acoustic activity varied across the night, reflecting two strategies. All katydids have a completely nocturnal singing behavior (Gr8, Gr12, Gr13, Gr22, Gr20), still "Rattler" (Gr20) showed a few, sparse detections during the day (Supplemental data S7). These five species start singing at sunset (~17:30 hrs); then, three species show a higher density of detections in specific times of the night (Gr8: 20:00-20:30, Gr12: 00:00-02:00, Gr13: 18:30-20:30). The remaining two katydids (Gr22, Gr20) showed relatively constant acoustic activity throughout the night and a faster decrease in activity from 04:00 until sunrise (~06:00). On the other hand, both crickets

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24 hr.
Spectro

(Gr2, Gr4) have a crepuscular schedule: they sing mainly during dusk. Podoscirtinae (Gr4) showed a much more restricted singing schedule, from 18:00 to 19:00 with a very abrupt decrease in activity afterwards. Flutist (Gr2) showed a slower decrease in activity, maintaining a considerable number of detections after ~21:00. Overall, we identified a chorus time when all the members of the community sing at the same time, from 18:00 to 20:00 (Fig. 1).

Diel and spectral overlap

Species density distribution pairwise analysis (Table 1) showed two overlap trends. Crickets Gr4 and Gr2 have less probability of overlapping with the katydids' singing schedules (low coefficient values <0.6). Of these two, Gr4 is the most specialized, having a very short singing schedule (Fig. 1). Conversely, katydids overlap in their singing periods (high coefficient values >0.6).

The mean dominant frequency was considerably lower for crickets, and higher for katydids. While cricket bandwidth was narrow, katydid frequency bandwidth varied across species, reflecting spectral overlap in four species (Fig. 2). The species used a higher frequency also include a higher bandwidth (Gr20, Gr22, Gr13), overlapping among them. The species with higher bandwidth, *N. brachypterus* (Gr13), overlapped additionally with a canopy dweller species, Gr12, which included a lower frequency bandwidth. Although most of the species had harmonic components in their calling song (all excepting Gr2) with ultrasonic harmonics for all the katydids except Gr12, those were not considered given their high amplitude and shorter traveling distance due to attenuation (Romer & Lewald, 1992; Hung & Prestwich, 2004). Although we did not test the relationship between frequency and duration of the calling activity, our preliminary data suggests that species with lower dominant frequencies tend to call for shorter periods (Fig. 3).

Acoustic activity response to environmental variables

The ~~response of the~~ acoustic activity ~~varied by~~ of the species ~~and~~ varied with environmental variables obtained from satellite remote sensing sources (Fig. 4, Table 2). Acoustic activity of ~~other~~ katydid species included a negative relationship with moon fraction for Gr8 ($\beta = -0.28$, $p = 0.003$), Gr12 ($\beta = -0.34$, $p < 0.001$), Gr13 ($\beta = -0.36$, $p < 0.001$), Gr22 ($\beta = -0.13$, $p < 0.001$), and Gr20 ($\beta = -0.07$, $p = 0.02$). Both cricket species showed a negative relationship only with the precipitation (Gr2: $\beta = -0.31$, $p = 0.006$; Gr4: $\beta = -0.32$, $p = 0.002$) while in katydids the response was more complex. In addition to the cricket species, precipitation was also a strong detrimental variable for acoustic activity of Gr8 ($\beta = -0.25$, $p = 0.02$), but less for Gr20 ($\beta = -0.06$, $p = 0.05$). Minimum temperature showed a positive trend for both Gr8 ($\beta = 0.26$, $p = 0.007$) and Gr12 ($\beta = 0.21$, $p = 0.04$), and maximum temperature was significantly detrimental for Gr20 only ($\beta = -0.07$, $p = 0.03$). In general terms, daily precipitation is better explanatory for the acoustic activity of crickets, while moon fraction for acoustic activity of katydids.

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Discussion

Despite insect~~s~~ acoustic activity driving ~~drives~~ the soundscapes of tropical ecosystems (Aide et al., 2017), they are rarely identified with accurate taxonomic resolution in ecoacoustic studies. We used the acoustic signaling footprint of different species from passive acoustic sampling to characterize a tropical Andean community. With the daily acoustic activity pattern for each sonotypes, we were able to sample the prioritized species and match four out of seven species. Despite recent improvement in taxonomic work in the group for Colombia (Cadena-Castañeda et al., 2020, 2021), and impressive research on sound production and reception (e.g. Baker et al., 2019; Celiker et al., 2020), we found taxonomic novelties from this community (Cadena-Castañeda, Gómez-Morales, Acevedo-Charry, Benavides-López, *Unpublished manuscript*). In addition, we explored the relationship of acoustic activity of each species with environmental variables extracted from satellite remote sensing data. We experienced difficulties in collecting canopy dwellers, for which we recommend the use of specialized methods such as fogging (Montealegre-Z et al., 2014) or specialized manual tracking (Diwakar & Balakrishnan, 2007b) for future studies. As studies on environmental effects on insect acoustic communities are still rare, our study is an important precedent, and serves as a good example on how satellite remote sensing data can be used along with acoustic monitoring schemes in areas with low ~~accessibility~~ access to ground-based methods of environmental measurement, such as weather stations.

Representative species

Our focused species were representative of nocturnal orthopteran insects in our sampling site, diurnal species had relatively low detectability within our data set (Grasshoppers mostly) and were barely detected, which confirms previous observations for the group (Diwakar & Balakrishnan, 2007a). For studies with the aim of extensively describing an acoustic community, or analyzing interactions between species, we recommend using more extensive sampling in both space (more recording units) and time (longer monitoring periods) along with more intensive annotation of recordings. The use of multiple recording units can also enhance the detectability of low amplitude song species, which may have been under-detected in our study. Despite that, given their high activity and detectability, combined with our ability to match taxonomic resolution of most of the species, we consider the representative species here taken into consideration are adequate and sufficient for analyzing single species relations with environmental factors. Therefore, we recommend this approach of species prioritization of crickets and katydids over grasshoppers for environmental studies with time or methodological constraints.

Why not grasshoppers?

Time and spectral overlap

We observed that the higher the dominant frequency of their calling song (Fig. 2), the broader the diel acoustic activity range tended to be (Fig. 1; Fig. 3). While ~~cricket's~~ the low frequency cricket calling, narrowly clusters during dusk (Fig. 1, dotted line), katydids cluster their calling widely

But exposure as possible mechanism?

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throughout the night: medium frequency calling katydids (Fig. 1, dashed line) show clear activity peak times, and the high frequency ones (Fig. 1, dashed line) maintain constant activity levels throughout the night. Previous studies found a negative relationship between calling signal duration and daily signaling rate in neotropical katydids as result of acoustic trade-offs (Symes et al., 2021), our data suggests that there might be a positive relationship between the dominant frequency and the daily acoustic activity as well. Although we did not measure body size for the species in our community, crickets were smaller than katydid species, thus our observation is contrary to the predictions of the morphological adaptation hypothesis (Farina, 2014), ~~proved~~ in birds (Wallschläger, 1980), mammals (Fletcher, 2004), and frogs (Boeckle, Preininger & Hödl, 2009). On the other hand, previous studies have shown that nocturnal predators, like bats, eavesdrop and select their prey based on certain signal properties including peak frequency, and vary among species present in a community (Falk et al., 2015); then in this case, lower peak frequency species in this community could be under stronger predation pressures, and respond by concentrating their singing in shorter time periods to lowering that risk (Farina & Ceraulo, 2017). Further research on these topics for insects remains needed through experimentation.

– supported

In addition to the aggregation in time, there is a clear preference for sunset times by crickets, that can be explained by the fact that it is the time of the day when diurnal predators are already becoming inactive plus nocturnal predators being still not at their peak (Jain et al., 2014). Also, this is the time where all the katydid species start to become active as well, so the simultaneous interspecific singing can lower individual risk by "confusing" the predator who now has many choices (Farina & Ceraulo, 2017). We previously referred to this period as the "sunset chorus", and many other factors may be influencing this phenomenon. Moreover, the relatively high katydid temporal overlapping (Table 1; Fig. 1) suggests that katydids are also aggregating their acoustic activity in time, ~~only that in a different fashion;~~ by concentrating on their activity later and extending it during the whole night. Maintaining a continuous sing-along but extending their signaling for several hours also comes with its downsides, which require further adaptations in response to visual predators, as we will discuss later. Previous works have described how katydid aggregation in space can lower the effectiveness of bat captures (Prakash et al., 2021), but none in our knowledge have ever established a relationship with species diel schedules. Further research including more taxa and sampling locations, along with the measurement of acoustic interactions with bats and other predators in this community are necessary to confirm the "frequency-acoustic activity relation", the predatory preference for call properties in this community, the relationship of diel activity aggregation with predation pressures, and the mechanisms explaining the sunset chorus.

Nice connection

Even though four species show spectral overlap (Fig. 2), those have different microhabitat preferences: Gr12 dwells in the canopy, while Gr13 is always found at ground level grass chunks. The species Gr22 and Gr20, which overlap in both time and frequency, inhabit the understory and canopy respectively, and may be avoiding masking because of differential

Wolves + Sheep timing

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attenuation at different heights (Ellinger & Hödl, 2003). However, other studies have found conflicting evidence (Jain & Balakrishnan, 2012). Further research is required to test this hypothesis, as the effect of forest stratification over signal interference in insects remains unclear (Schmidt & Balakrishnan, 2015). In addition, measurement of smaller scale time features could help to confirm temporal masking avoidance at smaller scales (Symes et al., 2021), as Gr22 and Gr20 pulse rates and syllable duration seem to differ greatly.

Environmental factors effects and Remote sensing data

Katydid species decrease acoustic activity 0.70 to 0.93 times with a unit increase in moon fraction light. The negative relationship found between moon fraction and katydid species acoustic activity (Table 1, Fig. 4) corroborates the findings of previous studies. For example, response to more moonlight led to ~~avoidance of~~ behaviors to avoid visual predators, ~~either by~~ such as lowering their overall activity (Lang et al., 2006), or switching to alternate communication channels (Römer, Lang & Hartbauer, 2010), as part of katydids' repertory of adaptations for predation by bats (ter Hofstede et al., 2017). ~~Response to moonlight~~ is probably the consequence of the above-mentioned ~~continuous time aggregation as~~ opposed to crickets, which ~~in fact~~ did not show any relationship to moonlight (Table 2), perhaps because during the sunset there is still plenty of sunlight, so moonlight make not any difference.

good hypothesis

The fact that katydids responded to moonlight probably arises from the fact that they call much of the night, as

Inga-diet

proportion w/weather

Regarding precipitation, both crickets and two katydid species decrease acoustic activity 0.73 to 0.94 times with a unit increase in rainfall. Such detrimental effect mainly over the acoustic activity of the two cricket species (Gr2 and Gr4; Fig. 1) confirms previous observations of other authors (Alexander & Meral, 1967) and our own during the field work: whenever it rained during the chorus time, the crickets barely sang. The katydids did not show that unique relationship with daily precipitation, except for Gr8 and Gr20 which included other covariates. However, something to consider is that given the shorter time span of crickets calling time, they had a greater chance of being interrupted by rain, as has been observed in other species (Alexander & Meral, 1967; Franklin et al., 2009), while broader katydid calling spans may have improved their detectability even after short rainy periods during the night. Our opinion is that rain may affect orthopterans singing at a finer time scale in addition to the accumulated daily effects, as opposed to moonlight, given that daily precipitation can be either sparsely or densely distributed during the day. In addition, other external factors such as wind (Velilla et al., 2020), or ultrasonic background noise (Römer & Holderied, 2020) can affect signaling behavior of katydid species as well. A comparison of both locally measured precipitation and satellite remote sensing data with community acoustic activity may be useful to confirm this relationship.

Temperature analysis suggests a negative relation (decrease 0.93 times with a unit increase) with daily maximum temperature only for Gr20, and positive relation with minimum temperature for Gr8 (increasing 1.30 times with a unit increase) and Gr12 (increasing 1.23 times with a unit increase in min temperature). The underlying reasons for this response are yet to be discovered,

unit = °C?

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but the increase in signaling by Gr8 and Gr12 katydids are concordant with previous studies in other species (Franklin et al., 2009) which found increased signaling during warmer nights. As the microhabitats preference can play a fundamental role on temperature regulation, we rather recommend the use of local scale measurements to further explore calling activity relationship with this variable.

Although previous studies have evaluated the accuracy of the satellite remote sensing products here used or similar with environmental applications (e.g., Palomino-Ángel et al., 2019), or overviewed its potential for ecosystem modelling (Pasetto et al., 2018), none to our knowledge has yet evaluated the applicability of these datasets for answering local community ecology monitoring questions. We recommend further comparison of local weather station data with satellite remote sensing data, in the context of local biological monitoring programs for evaluating the extent of applicability of this approach.

Conclusions

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

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