Acta Chiropterologica, 24(1): 151–165, 2022
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS
doi: 10.3161/15081109ACC2022.24.1.012

Bat assemblages along an elevational gradient in Costa Rica

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Spatio-temporal patterns of species richness, Hill numbers, captures per species, feeding guilds, sex ratio, and biomass were studied in a Neotropical bat assemblage during 17 continuous months in four bands (low: 50–150, mid-low: 375–500, mid-high: 975–1,050, and high: 1,950–2,050 m a.s.l.) in an elevational gradient in Costa Rica. We found an effect of elevation on species richness. As expected, species richness was high in the low elevations; unexpectedly, however, we noted that species richness was highest in the mid-high band, a diversity pattern that has not been previously recorded in bats. We also found an effect of precipitation periods on species richness; in particular, at mid-high elevations, when precipitation was intermediate and highest, we observed a larger number of species. When analyzing data separately by feeding ensemble, we found an effect of elevation on species richness for three ensembles: animalivorous bats were more diverse at the mid-low band, nectarivorous bats were more diverse in the mid-high and high bands, and frugivorous bats were more diverse in the mid-low and low bands. Species richness of frugivorous bats was also affected by precipitation; when rainfall was intermediate and highest, we noted a higher species richness of this ensemble. There was no effect of elevation on species richness for the insectivorous, omnivorous or hematophagous ensemble, nor on the species capture, sex ratio or biomass. Our results not only provide further evidence of the importance of lowland forests as reservoirs of high species diversity, but also highlight the importance of tropical premontane rainforests for the conservation of bat communities given their high species richness, particularly for the nectarivorous and frugivorous ensembles. This is particularly relevant not only because this ecosystem has been heavily affected by land use changes in the Neotropical region, but also because the predicted future decrease of precipitation at this elevation could potentially affect overall species richness and particularly for certain feeding ensembles. Thus, conservation efforts in this life zone are of critical importance for maintaining functional and ecological diversity of bat communities in elevational gradients.

Key words: bats, Costa Rica, elevational gradients, spatio-temporal patterns

INTRODUCTION

Understanding the temporal and spatial dynamics of species assemblages is a main challenge in ecology (Santillán *et al*., 2018). At the temporal scale, species richness can show either seasonal fluctuations or sudden changes, and although it is well known that all ecological communities experience temporal turnover, there is still limited information on how biodiversity changes through time (Magurran and Henderson, 2010). At the spatial scale, diversity is known to vary both in latitude and elevation. For example, there is a strong trend for a decrease in species diversity with an increase in latitude for most, but not all, taxa (Stevens, 1989; Mannion *et al*., 2014; Willig and Presley, 2017). Surprisingly, the general relationship between elevation and species richness is still not well established (Smith *et al*., 2007), since different patterns have been observed in different taxa; for example, decreasing richness with increasing elevation, a plateau in richness across low elevations then decreasing with or without a mid-elevation peak, and a unimodal pattern with a mid-elevational peak (Grytnes and McCain, 2007; McCain and Grytnes, 2010). Elevational gradients offer many characteristics that make them more suitable for uncovering the underlying cause(s) of spatial variation in diversity (Sanders and Rahbek, 2012), and they experience substantial changes in temperature, rainfall, cloud interception, soil and wind exposure, with environmental conditions at the extremes that strongly challenge species tolerances in both evolutionary and physiological contexts (Willig and Presley, 2016).

Mountains are biodiversity hotspots, centers of endemism, and provide spatially compressed versions of regional and continental gradients in diversity (Munyai and Foord, 2011). Mountains comprise approximately 22% of the area of all terrestrial ecosystems and are inhabited by 13% of the world's human population, 90% of them living in developing countries (Romeo *et al*., 2015). Likewise, tropical mountains harbor some of the most anthropogenically threatened environments in the world that are changing in all continents at an unprecedented rate (Willig and Presley, 2016; Schickhoff *et al*., 2022) because of land conversion to agriculture, farming, and climate change; therefore, it is critical to identify the underlying causes of species richness patterns in tropical regions (Smith *et al*., 2007) that may thus allow focus the establishment of conservation strategies. However, biogeographic surveys in montane ecosystems are still rare, particularly in regions where these environments are difficult to access, especially when considering taxonomic groups like bats that require challenging sampling methodologies, demanding fieldwork, show elusive behavior, and produce lower sampling efficiency (Chaverri *et al*., 2016).

Neotropical bat assemblages are characterized by high diversity of species, feeding ensembles, and foraging behaviors (Kalko *et al*., 1996). However spatio-temporal patterns of Neotropical bat assemblages in elevational gradients in tropical mountains are still relatively unknown despite recent studies in Brazil (Martins *et al*., 2015; Mello *et al*., 2016; Capaverde *et al*., 2018; Coelho *et al*., 2018). The understanding of spatio-temporal patterns is of particular interest for bat conservation strategies because the spatial dimension provides the knowledge about priority areas, habitats, and resources used, whereas the temporal scale documents key bat phenomena such as movements, reproduction and ecological functioning (e.g., pollination). This information is essential for conservation policy-makers given that bats are particularly susceptible to anthropogenic changes because of their low reproductive rate, longevity, and high metabolic rates (Voigt and Kingston, 2016), and are also well known to perform important ecological services such as pollination, seed dispersal, and pest control (Kunz *et al*., 2011). Further, the understanding of current spatio-temporal patterns of bat assemblages in tropical elevational gradients is needed in order to estimate the impact of climate change on species and assemblages, and to provide baseline information that will allow us to document changes in the composition and diversity of Neotropical bat assemblages in the future. Therefore, the aims of this study were (1) to analyze the spatio-temporal distributional patterns of bat assemblages along a Neotropical elevational gradient, and (2) to investigate how climatic variables, specifically precipitation, are related to observed elevational patterns of species distribution.

Materials and Methods

Study Site

The study was conducted along an elevational gradient in Braulio Carrillo National Park (BCNP) and private reserves located in Área de Conservación Cordillera Volcánica Central (ACCVC), Costa Rica (Fig. 1). This elevational gradient is located in the northeast part of the Caribbean slope of Costa Rica (San José and Heredia Provinces) and includes a continuous forest track from 30 m a.s.l. around La Selva Biological Station (OET) to 2,906 m a.s.l. at Barva Volcano in Braulio Carrillo National Park (Timm *et al*., 1989). Forest types include lowland Tropical Wet Forest and Tropical Wet Forest cool transition in the lowlands, Tropical Premontane Rain Forest in the middle elevations and Tropical Lower Montane Rain Forest and Upper Montane Cloud Forest in the highlands (SINAC, 2005; Clark *et al*., 2015). The elevational gradient protects almost intact old-growth forest areas with some areas of secondary forests resulting from natural disturbances (landslides and earthquakes) and previous deforestation in the 1970s and 1980s at some elevations (Schelhas and Sánchez-Azofeifa, 2006; Clark *et al*., 2015), especially in the lowlands of the buffer zone that lies outside the national park (Schelhas and Sánchez-Azofeifa, 2006). In the area outside the Braulio Carrillo National Park several private reserves have been established since the 1980's (Selva Verde Reserve, Tirimbina Reserve, Bijagual Reserve, Albergue el Socorro Reserve) that focus their activities in conservation, research, education and ecotourism (Fig. 1 and Table 1). Annual rainfall varies from ca. 4,000 mm at the base to as much as 9,000 mm at intermediate elevations, diminishing to ca. 3,000 mm at the summit. Temperature averages 25°C in the lowlands, decreasing at roughly 0.54°C/100 m elevation to ca. 10°C at the summit (Clark *et al*., 2015). The protected area encompasses 52,000 ha and includes four life zones and two transition zones (Timm *et al*., 1989; Fig. 1). A list of plant species recorded in the gradient can be found in SINAC (2005).

Along this elevational transect we established four elevational bands (m a.s.l.): low (50–150), mid-low (375–500), mid-high (975–1,050) and high (1,950–2,050 — Table 1); they include the majority of elevations represented within the gradient, and each band is located in a different life zone or transition zone (Fig. 1). At each elevational transect we established two or three study sites (Table 1), some within the Braulio Carrillo National Park (BCNP) and some sites within privates preserves outside the BCNP, and in each site from two to four sampling locations were used depending on the topographic conditions. This allowed us to include and sample the spatial and structural heterogeneity of the elevational bands while avoiding oversampling at the same location, pseudoreplication, and 'trap-shy' behavior (Marques *et al*., 2013). Sampling at the highest elevations of the gradient (2,100 to 2,900 m a.s.l.) was not possible for logistical constraints and time limitations; however,

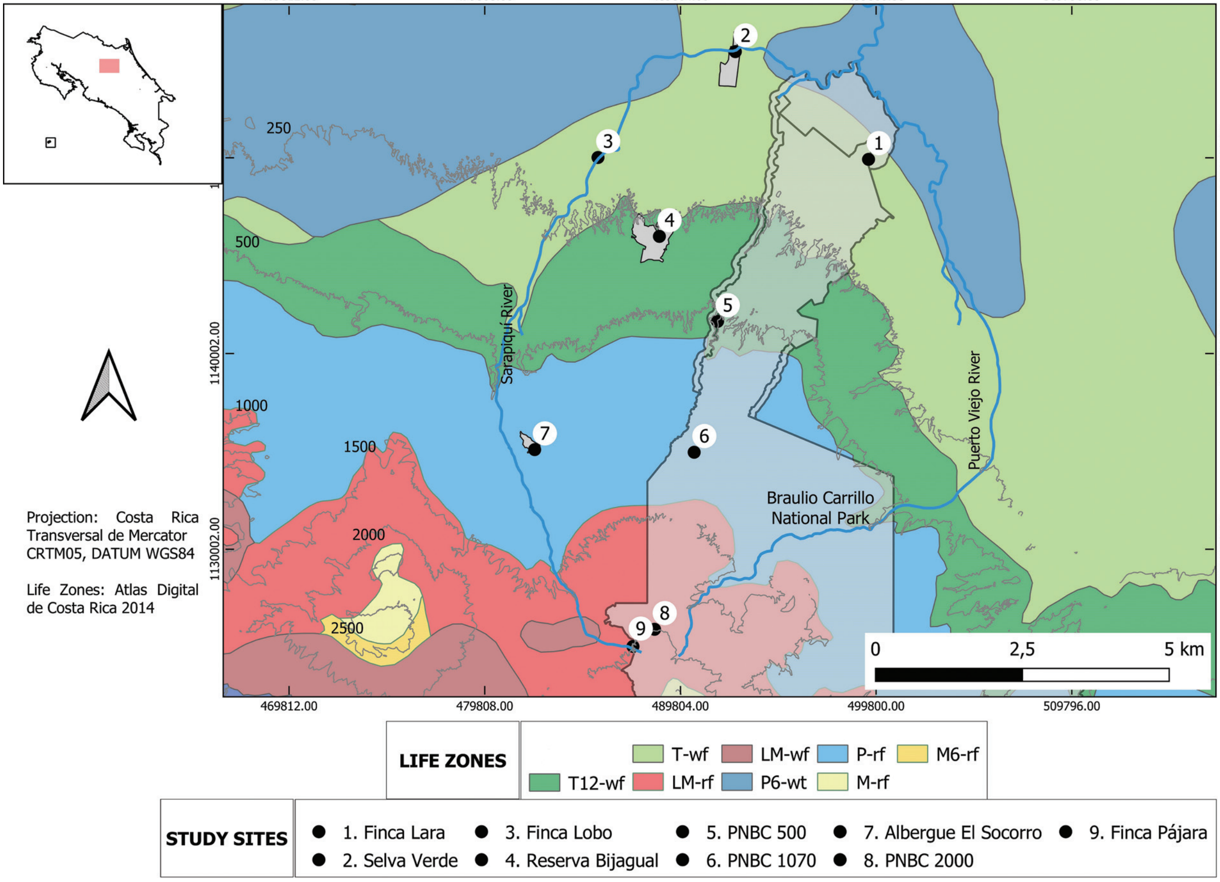

FIG. 1. Sampling sites for elevational bands (symbology: sites 1, 2 and 3 = low band, sites 4 and 5 = mid-low band, sites 7 and 8 = mid-high band, and sites 8 and 9 = high band), and life zones in the study site of Braulio Carrillo National Park, and private reserves, Costa Rica (symbology of life zones: T-wt: Tropical wet forest, T12-wf: Tropical wet forest Premontane belt Transition, P-rf: Tropical Premontane rain forest, LM-rf: Tropical Lower Montane rain forest, LM-wf: Tropical Lower montane wet forest, P6-wt: Premontane wet forest basal belt transition, M-rf: Montane rain forest, and M6-rf: Montane rain forest Lower Montane belt transition)

previous observations made by one of the authors (WPL) at those altitudes in the gradient showed very low species richness and capture success (an average of one individual per 10 hours of mist netting). We take into consideration this limitation (partial sampling throughout the entire elevational range) when inferring and discussing our results while also acknowledging that limited sampling at the highest elevations in a elevation gradient is less critical since diversity always decreases monotonically above some threshold intermediate elevation (McCain and Grytnes, 2010).

Field Work

Each elevational band was sampled during 17 consecutive months from August 2013 to December 2014, with the exception of the mid-low band in June 2014 given the excessive

TABLE 1. Elevational band name and range (m a.s.l.), life zone, sampling effort (number of mist-nets × number of hours open × length of mist-nets), study site, and elevation (m a.s.l.)

Elevational band and range	Life zone	Sampling effort	Study sites	Elevation
Low (50–150)	Tropical Wet Forest	16238	Finca Lara	50
			Selva Verde Reserve	73
			Finca Lobo	80
Mid-low (375–500)	Tropical Wet Forest Premontane transition	15732	Bijagual Reserve	375
			PNBC 500	500
Mid-high (975–1,050)	Tropical Premontane Rain Forest	14448	El Socorro Reserve	975
			PNBC 1070	1,070
High (1,950–2,050)	Tropical Lower Montane Rain Forest	16884	Pájara Reserve	1,950
			PNBC 2000	2,000

amount of precipitation that prevented us from accessing the site. Sampling at the elevational bands each month was made in a random order. At each sampling site we used 8 to 10 mist-nets (both polyester and monofilament, 12 m × 2.5 m; mesh 40 mm, Avinet Ltd.) positioned at ground level along trails within the forest, forest edges, forest gaps, rivers, and streams from 17:30 to 05:00 h in one night (when possible) or from 17:30 to 23:00 h in two consecutive nights because of weather conditions, rainfall, storms, or for security reasons. This methodology was used because even if it is known that sampling throughout the night increases the probability of capturing rare species and the representation of bat assemblages (Esbérard, 2009; Trevelin, *et al*., 2017), there is also high similarity on the abundance of bat species between the first and second half of the night (Esbérard and Bergallo, 2005) as well as high similarity of the bat assemblage composition between half-night and full night schedules (Trevelin *et al*., 2017). Therefore, more sampling nights can produce a higher number of species than more hours of nocturnal sampling because a great number of bats are active mainly after sunset (Morrison, 1980). In the two consecutive nights scheme we also moved mist-nets' position because this is known to increase capture success (Simmons and Voss, 1998; Bergallo *et al*., 2003; Marques *et al*., 2013). Because monitoring projects that seek to reliably detect trends in species richness require a sufficient number of temporal replicate observations on the same plot (Meyer *et al*., 2011), our sampling protocol of 17 consecutive months with 72 sampling nights followed the recommendations of Meyer *et al*. (2011) of conducting at least four replicate surveys per sampling unit within a given year because this should considerably reduce bias in estimates of species richness and ensure relatively high mean detection probability overall (Meyer *et al*., 2011). The sample effort per band per month was calculated multiplying the number of mist-nets used by the number of hours they were open and by the length of the mist-net, following Medellín (1993). After capture, each bat was placed in an individual cloth bag and processed within 15 minutes in average after being captured. We identified species based on Timm *et al*. (1999), Velazco and Patterson (2013), Mantilla-Meluk and Muñoz-Garay (2014) and York *et al*. (2019). We do not follow Carrión-Bonilla and Cook (2020) until more studies are conducted in the country that help elucidate the identity of the *Myotis pilosatibialis* (or *M. armiensis*) species in the country. Sex was determined by inspection of external genitalia and body mass (± 0.5 g) was obtained with a spring scale (Pesola Ltd). Each bat was then released as soon as possible. All research permits (ACCVCR-R-INV-0013, 060-2012-ACCVCR-PI, and 021-2013- ACCVCR-PI) were obtained at Ministerio de Ambiente y Energía (MINAET), Sistema de Área de Conservación (SINAC), Área de Conservación Cordillera Volcánica Central (ACCVC), Costa Rica. We follow the guidelines of animal care and live capture for bats as described in Sikes and Gannon (2011) and Sikes *et al*. (2016).

Climatic Variables

For each elevational band we obtained monthly precipitation (mm) and temperature (°C) data from meteorological stations located within the area. For the low and mid-low elevational bands, data were obtained from Organization of Tropical Studies' (OTS) stations located at 50 and 500 m a.s.l. For the mid-high and high elevational bands, we used data recorded by the meteorological stations of Instituto Costarricense de Electricidad (ICE) located at Ujarras de Cariblanco (930 m a.s.l.), and San Rafael de Varablanca (2,150 m a.s.l.), Rara Avis EcoLodge (700 m a.s.l.) located at El Plástico, Horquetas, and La Paz Waterfall Lodge San Rafael de Varablanca (1,800 m a.s.l.). All measurements were averaged daily, and monthly averages were used in all analyses. Based on the precipitation data, we established three periods: low from January to April, high from May to July, and mid from August to December (Supplementary Fig. S1). Given the high correlation (r = -0.97) between elevation and temperature, we assumed temperature is implicitly included in the elevational dimension.

Data Analysis

Diversity and sampling

We used the unified framework proposed by Chao *et al*. (2014) of the combined measurement and estimation of species diversity, rarefaction/extrapolation and Hill's numbers. Hill numbers are a mathematically unified family of diversity indexes with a different exponent q that incorporates species richness and relative abundance (Chao *et al*., 2014), where species richness is Hill number with q = 0, Shannon diversity index is Hill number with q = 1, and Simpson diversity index is Hill number q = 2 (Chao *et al*., 2014). With an increase in Hill numbers (q0, q1 and q2) there is a decrease in the weight or contribution of rare species to estimates of diversity (Chao *et al*., 2014). This approach is particularly useful for comparison of species diversity of different assemblages in time and space and provide reliable statistical inferences about these comparisons (Chao *et al*., 2014). Sampling robustness was measured with sample-size-based diversity accumulation curves that plot the expected diversity as a function of sample size using the number of individuals. The use of number of individuals is considered the best measure of sampling effort (Willott, 2001) given that this allows us to make a direct comparison of species richness among the elevational bands assuming equal sampling effort while avoiding biases created by net positioning and efficiency (Chaves-Ramírez *et al*., 2021). We also used coverage-based diversity curves to plot expected diversity as a function of interpolated (observed) and extrapolated (expected) coverage. All analysis were performed with the software iNext (Chao *et al*., 2016). To test whether there are differences in sampling effort among elevational bands, we performed an ANOVA test with elevation as a categorical variable, and Tukey's post-hoc test. There were no significant differences in sampling effort among the elevational bands ($F_{3,\ 67}$ = 0.66, P = 0.57).

Response variables

We estimated overall species richness and captures per species, and also richness and captures of feeding ensembles (sensu Fauth *et al*., 1996): frugivorous, nectarivorous, omnivorous, animalivorous, insectivorous, and hematophagous (vampire) bats, in addition to sex ratio (number of females/number of males), and biomass (sum of body mass of all bats captured, in g). All variables were recorded every month at each elevational band, and results were divided by the sampling effort (the number of mist-nets used by the number of hours they were opened for and by the length of the mist-net) of every month in each elevational band, as this provides a robust standardized sampling and it will allow comparison with future studies (Medellín, 1993). Species were assigned to feeding ensembles following Kalko *et al*. (1996). With these data, we tested the effect of elevation and precipitation period on all variables by using general linear models. We use a normal distribution for species richness, captures per species, richness of nectarivorous and frugivorous bats, and captures of frugivorous bats; a negative binomial distribution for richness of animalivorous, insectivorous, omnivorous and hematophagous bats, captures of nectarivorous, animalivorous, omnivorous, and hematophagous bats; and a Gumbell distribution for captures of insectivorous bats and biomass, all distributions were determined by tests of fit. We fitted all models with the interaction terms between elevation and precipitation period. All analyses were performed in InfoStat (Di Rienzo *et al*., 2020).

RESULTS

We recorded 1,834 individuals of 54 bat species in all bands (Table 2), with 33 species and 428 individuals in the low band, 27 species and 385 individuals in the mid-low band, 32 species and 453 individuals in the mid-high band, and 16 species and 568 individuals in the high band (Table 3). Frugivorous bats of the genera *Sturnira*, *Carollia* and *Dermanura* were the most abundant in the study area (Table 2). Hill numbers with q = 0 showed higher values on the low and mid-low elevational bands, followed by the mid-low and low bands. Similarly, Hill numbers q = 1 and q = 2 showed higher values in the low and mid-high elevational bands, with lower values in the mid-low band and the lowest values in the low range (Fig. 2). Sample coverage for all Hill numbers reached an asymptote with the sample effort employed in all elevational bands. Sample coverage on all Hill numbers (q = 0, q = 1 and q = 2) at the observed sample size was of 97.4% for the low elevational band, 97.9% for the mid-low band, 97.8% for the mid-high band and 99.1% for the high band (Fig. 2).

There was an effect of elevation, precipitation period and their interaction on species richness but not on species captures, sex ratios, and biomass (Table 4). Species richness was higher in the mid-high and low elevational bands during the high precipitation period than any other elevational band. This trend of higher species richness at the mid-high and low elevational bands was similar for other precipitation periods, although not significantly so. Species richness was highest in the mid-low band during the mid-precipitation period, and lowest when it rained the most. Finally, species richness was low for the high band throughout the year (Fig. 3).

There was an effect of elevation on species richness of nectarivorous and animalivorous bats (Table 4). Richness of nectarivorous bats was higher at the mid-high and high elevational bands; in contrast, richness of animalivorous bats was higher at the mid-low elevational band (Fig. 4). There was an

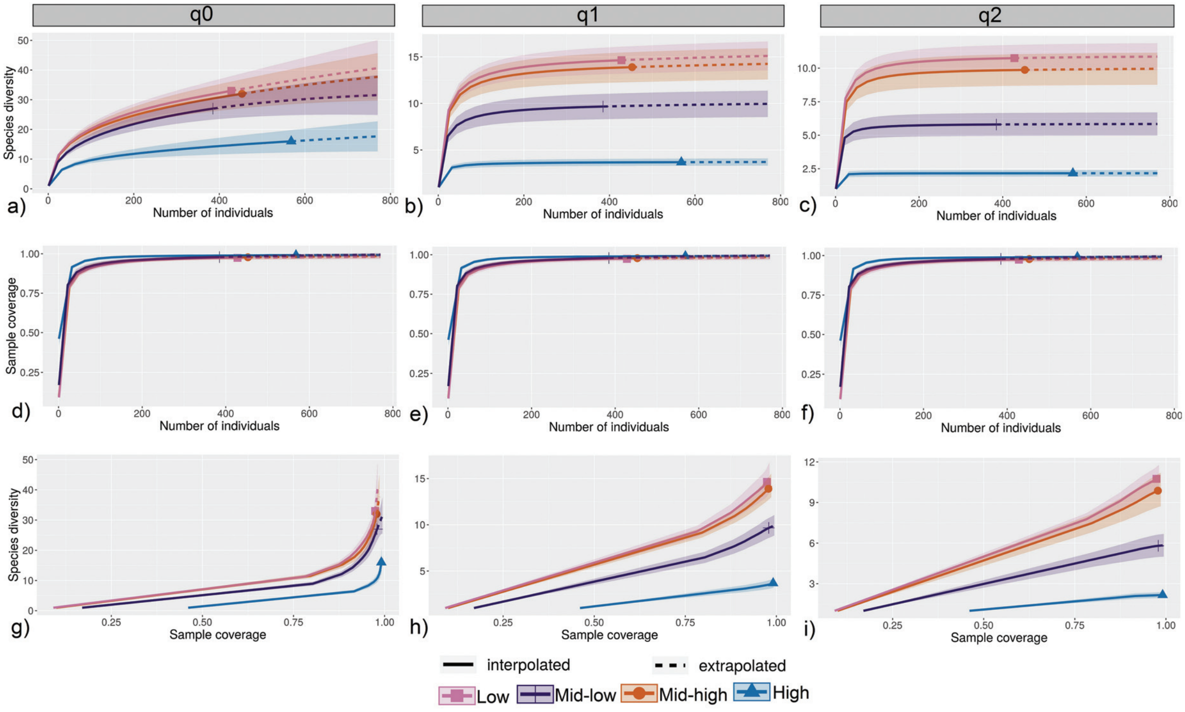

FIG. 2. Interpolated (continuous line) and extrapolated (dashed line) Hill numbers (q0, q1 and q2) with number of individuals (a, b, c), sample coverage accumulation curves with number of individuals (d, e, f) and sample coverage with species diversity (g, h, i) for each elevational band: low, mid-low, mid-high and high

TABLE 2. Captures of bat species at four elevational bands at the study site

Family/Species	Elevational band				Total
	Low	Mid-low	Mid-high	High	
Emballonuridae					
Rhynchonycteris naso	1	0	0	0	1
Saccopteryx bilineata	1	0	0	0	1
Mormoopidae					
Pteronotus mesoamericanus	1	21	2	0	24
Phyllostomidae					
Glyphonycteris sylvestris	0	1	1	0	2
Lampronycteris brachyotis	0	2	1	0	3
Micronycteris hirsuta	3	7	0	0	10
M. microtis	6	3	4	1	14
M. minuta	0	1	0	0	1
M. schmidtorum	0	0	1	0	1
Phylloderma stenops	1	0	0	0	1
Phyllostomus discolor	9	1	0	0	10
P. hastatus	1	0	0	0	1
Lophostoma brasiliensis	8	0	0	0	8
L. silvicolum	5	2	0	0	7
Tonatia saurophila	0	8	0	0	8
Trachops cirrhosus	3	2	0	0	5
Anoura cultrata	0	0	20	10	30
A. geoffroyi	0	0	3	9	12
Choeroniscus godmani	0	0	3	2	5
Glossophaga commissarisi	5	0	0	0	5
G. soricina	0	0	1	0	1
Hylonycteris underwoodi	3	2	15	17	37
Lonchophylla mordax	0	0	1	0	1
L. robusta	0	1	0	0	1
Carollia castanea	55	38	35	0	128
C. perspicillata	51	135	25	0	211
C. sowelli	33	55	60	0	148
Artibeus jamaicensis	68	26	5	0	99
A. lituratus	16	7	0	0	23
Centurio senex	0	1	1	0	2
Dermanura azteca	0	0	1	23	24
D. phaeotis	21	6	8	0	35
D. tolteca	0	0	42	60	102
D. watsoni	30	34	16	0	80
Ectophylla alba	29	0	0	0	29
Mesophylla macconnelli	2	0	1	0	3
Platyrrhinus helleri	1	2	2	0	5
P. vittatus	0	1	3	3	7
Uroderma convexum	54	0	0	0	54
Vampyressa thyone	1	1	17	0	19
Vampyriscus nymphaea	3	4	0	0	7
Sturnira hondurensis	0	1	72	377	450
S. parvidens	1	0	2	0	3
S. mordax	0	6	82	45	133
Desmodus rotundus	6	17	5	1	29
Diphylla ecaudata	0	0	1	1	2
Thyropteridae					
Thyroptera tricolor	1	0	0	0	1
Vespertilionidae					
Eptesicus brasiliensis	1	0	0	0	1
E. furinalis	5	0	5	1	11
E. fuscus	0	0	0	1	1
Lasiurus blossevillii	0	0	0	3	3
Myotis pilosatibialis	0	0	17	14	31
M. nigricans	2	0	1	0	3
M. riparius	1	0	0	0	1

TABLE 3. Overview of bat species richness (Spp) and captures (Ind) of different ensembles at the study site

Ensemble	Elevational band							
	Low		Mid-low		Mid-high		High	
	Spp	Ind	Spp	Ind	Spp	Ind	Spp	Ind
Frugivores	14	365	14	317	16	372	5	508
Nectarivores	2	8	2	3	6	43	4	38
Omnivores	3	11	1	1	0	0	0	0
Animalivores	5	8	8	12	4	0	1	0
Insectivores	8	30	1	35	4	32	4	20
Sanguinivores	1	6	1	17	2	6	2	2
Total	33	428	27	385	32	453	16	568

effect of elevation and precipitation period on species richness of frugivorous bats (Table 4), which was higher at mid-high (975–1,050 m a.s.l.) and low elevational bands (50–150 m a.s.l.). In relation to precipitation, species richness of frugivorous bats was higher during period of high and mid precipitation periods (Fig. 5). There was no effect of elevation on species richness of aerial insectivorous, omnivorous, and hematophagous bats (Table 4 and Supplementary Fig. S2). There was an effect of elevation on captures of nectarivorous and animalivorous bats (Fig. 6), but not on captures of frugivorous, omnivorous, aerial insectivorous and hematophagous species (Table 4 and Supplementary Fig. S3).

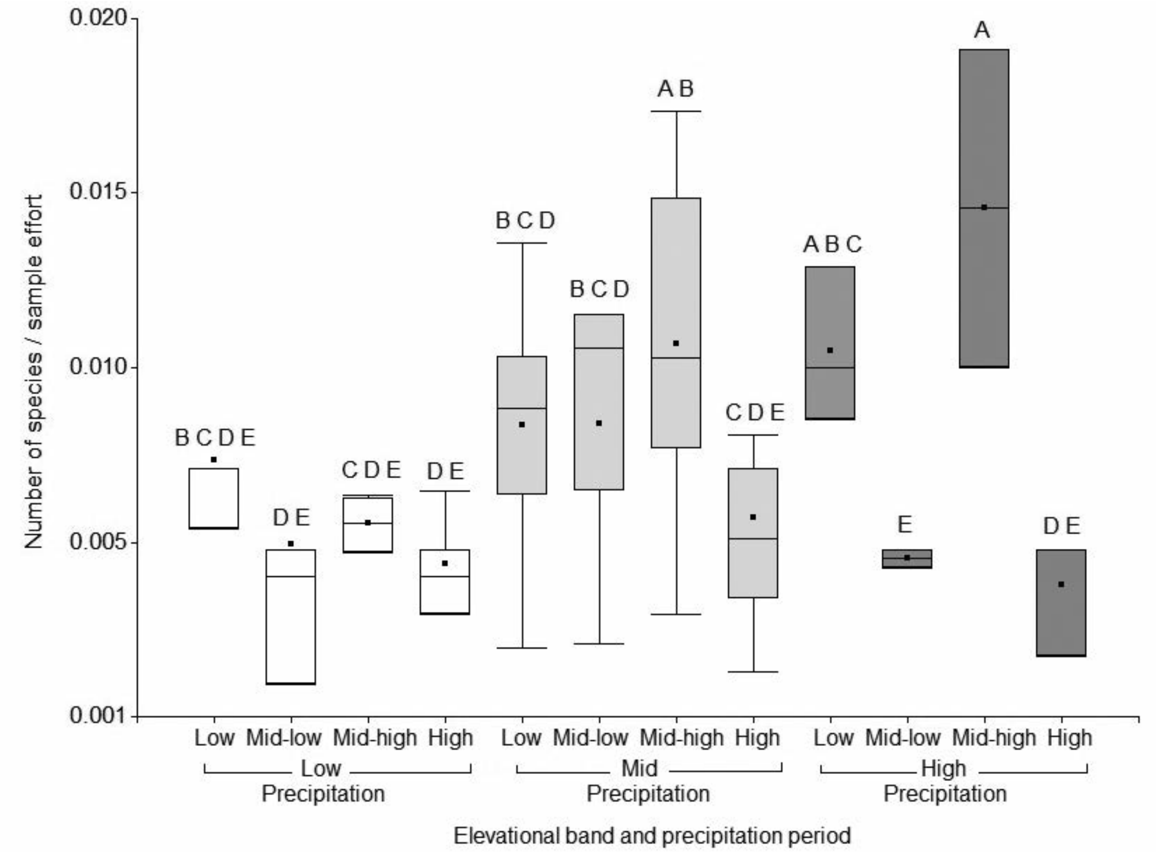

FIG. 3. Species richness/sample effort per period (according to precipitation: low, mid and high) and elevational band (low: 50–150, mid-low: 375–500, mid-high: 950–1,050, and high: 1,950–2,050 m a.s.l.). Different letters denote significant differences among elevational bands based on a posteriori Tukey-Kramer test; for example, the letter A at the Mid-high elevational band and High precipitation shows that this average is significantly different from all other categories that do not include the letter A, but is not significantly different from those that include this letter (i.e., mid-high elevational band*mid precipitation and low elevational band*high precipitation). Sample effort is the number of mist-nets used by the number of hours they were opened for and by the length of the mist-net

TABLE 4. Results of general linear models testing the effects of elevation, precipitation, and their interaction on species richness, captures per species, richness and captures of nectarivores, frugivores, insectivores, animalivores, omnivores and sanguinivores (hematophagous) species, sex ratio and biomass. Significant effects after Bonferroni correction ($P < 0.05$) are printed in bold

Variable	Predictive variable	*d.f.*	*F*	*P*
Species richness	Elevation	3, 56	7.60	< **0.001**
	Precipitation period	2, 56	3.49	**0.037**
	Interaction	6, 56	2.31	**0.046**
Captures per species	Elevation	3, 56	1.18	0.327
	Precipitation period	2, 56	1.44	0.247
	Interaction	6, 56	1.45	0.213
Nectarivore richness	Elevation	3, 56	7.87	< **0.001**
	Precipitation period	2, 56	0.49	0.614
	Interaction	6, 56	0.79	0.580
Frugivore richness	Elevation	3, 56	5.12	**0.003**
	Precipitation period	2, 56	4.87	**0.011**
	Interaction	6, 56	1.43	0.221
Insectivore richness	Elevation	3, 56	1.18	0.325
	Precipitation period	2, 56	1.33	0.273
	Interaction	6, 56	0.60	0.732
Animalivore richness	Elevation	3, 56	3.25	**0.029**
	Precipitation period	2, 56	0.13	0.877
	Interaction	6, 56	0.11	0.995
Omnivore richness	Elevation	3, 56	2.29	0.088
	Precipitation period	2, 56	0.34	0.712
	Interaction	6, 56	0.16	0.986
Sanguinivore richness	Elevation	3, 56	2.45	0.073
	Precipitation period	2, 56	2.09	0.134
	Interaction	6, 56	2.30	0.047
Captures of nectarivores	Elevation	3, 56	6.49	< **0.001**
	Precipitation period	2, 56	0.18	0.832
	Interaction	6, 56	0.23	0.966
Captures of frugivores	Elevation	3, 56	1.35	0.268
	Precipitation period	2, 56	1.27	0.289
	Interaction	6, 56	1.53	0.186
Captures of insectivores	Elevation	3, 56	0.82	0.488
	Precipitation period	2, 56	1.15	0.324
	Interaction	6, 56	0.62	0.714
Captures of animalivores	Elevation	3, 56	4.15	**0.010**
	Precipitation period	2, 56	0.26	0.776
	Interaction	6, 56	0.45	0.843
Captures of omnivores	Elevation	3, 56	1.85	0.148
	Precipitation period	2, 56	0.49	0.613
	Interaction	6, 56	0.34	0.912
Captures of sanguinivores	Elevation	3, 56	0.37	0.775
	Precipitation period	2, 56	0.51	0.602
	Interaction	6, 56	1.00	0.432
Sex ratio	Elevation	3, 56	1.08	0.367
	Precipitation period	2, 56	0.26	0.775
	Interaction	6, 56	1.74	0.128
Biomass	Elevation	3, 56	0.38	0.770
	Precipitation period	2, 56	0.84	0.435
	Interaction	6, 56	0.96	0.458

DISCUSSION

The elevational pattern of species richness registered in the present study corresponds to the low plateau and mid-peak pattern (McCain and Grytnes, 2010), given that species richness is higher at the mid-high band than at mid-low and high bands, but not significantly different from the low band. This pattern has been found for non-volant mammals (McCain, 2005), birds (McCain, 2009) and reptiles (McCain and Grytnes, 2010), but not for bats until this study. The elevational patterns recorded in several studies in the Neotropical region are either a decline with elevation in bat assemblages in Brazil

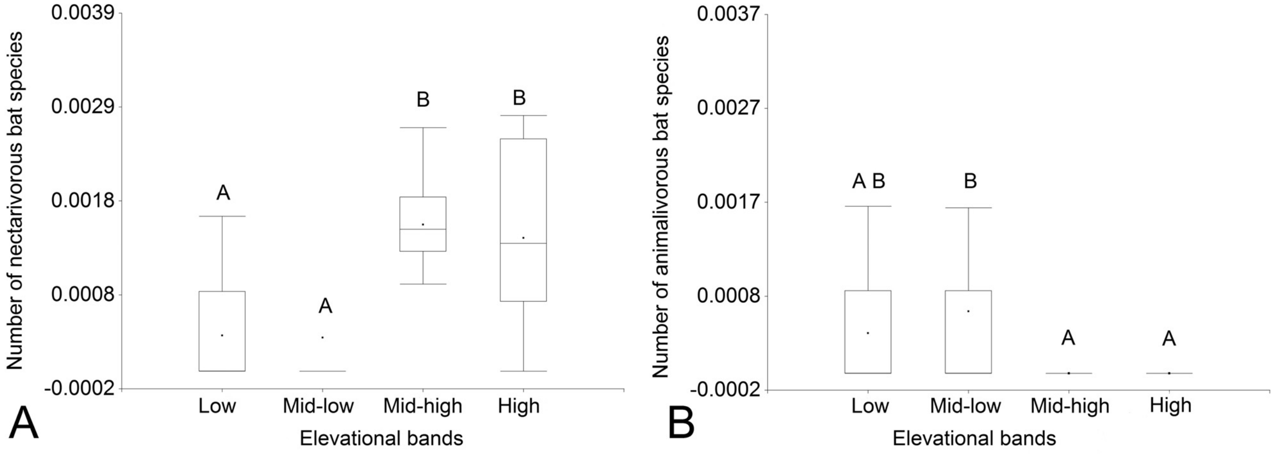

FIG. 4. Species richness/sample effort of (A) nectarivorous and (B) animalivorous bat species in the elevational gradient of the study site. Different letters denote significant differences among elevational bands based on a posteriori Tukey-Kramer test. Sample effort is the number of mist-nets used by the number of hours they were opened for and by the length of the mist-net

(Martins *et al*., 2015; Mello *et al*., 2016; Lopes *et al*., 2017; Coelho *et al*., 2018; De Carvalho *et al*., 2019), Mexico (Navarro and León-Paniagua, 1995; Briones-Salas, *et al*., 2005), Peru (Pattersonet *et al*., 1996; Cisneros *et al*., 2014), and Costa Rica (Rodríguez-Herrera, 2004; Rodriguez-Rocha, 2017), or the pattern of mid-peak richness for bat assemblages in Colombia (Bejarano-Bonilla *et al*., 2007), and Brazil (Bordignon and Franca, 2009). Species richness peaking around mid-elevation has also been recorded in hibernating bats in the Palearctic region (Piksa *et al*., 2013). The present study is, to the best of our knowledge, the first time that the pattern of low plateau-mid peak has been recorded for bat assemblages, and this is indeed important to highlight since historically, bat elevational patterns have been evenly split into decreasing with elevation and mid-elevational peaks (McCain, 2007). Different hypotheses have been proposed to explain patterns in species richness, some based on climate (temperature, precipitation, humidity, productivity), space (species-area relationship, mid-domain effect) or biological processes (ecotone effect, competition) (McCain and Grytnes, 2010). In several studies, bat species richness has been recorded to be higher where both temperature and precipitation were high (McCain, 2007). A possible explanation to our novel result of low-plateau-mid peak in bat species diversity is the combined effects of relatively high temperature and precipitation conditions (Table 1 and Fig. 3) present at some elevational bands within the study site. In our elevational gradient, temperature is

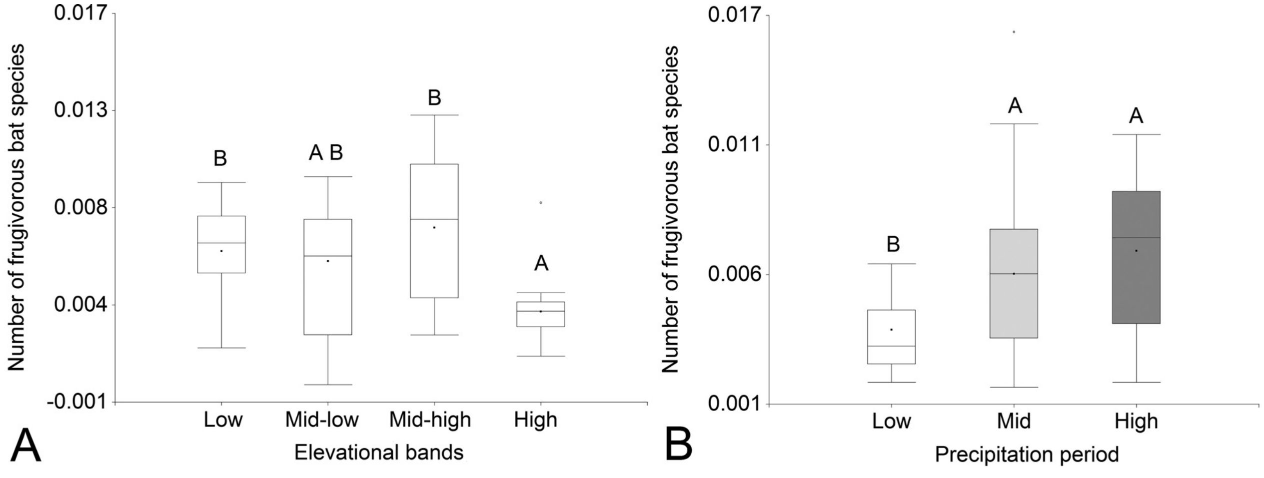

FIG. 5. Species richness/sample effort of frugivorous bats by (A) elevational band and (B) precipitation period. Different letters denote significant differences among elevational bands based on a posteriori Tukey-Kramer test. Sample effort is the number of mist-nets used by the number of hours they were opened for and by the length of the mist-net

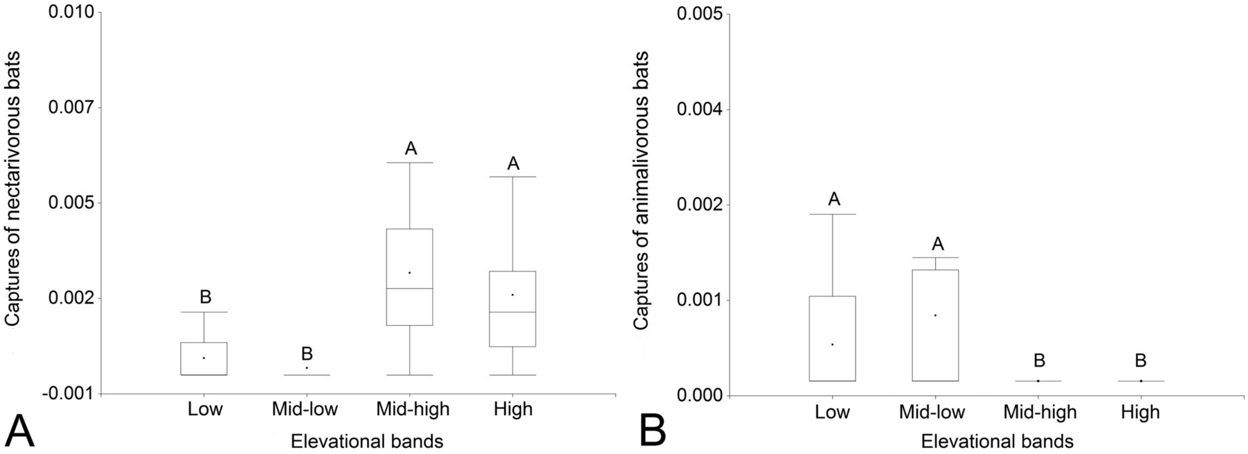

FIG. 6. Captures/sample effort of (A) nectarivorous and (B) animalivorous bats in the elevational gradient of the study site. Different letters denote significant differences among elevational bands based on a posteriori Tukey-Kramer test. Sample effort is the number of mist-nets used by the number of hours they were opened for and by the length of the mist-net

higher in the low elevational band (~25°C) and decreases with altitude at ~0.54°C/100 m in elevation, reaching ~19°C at the mid-high elevational band. Precipitation is higher at the mid-high elevational band (annual precipitation = ~9,000 mm), but it is still high at low elevations (~4,000 mm) (Clark *et al*., 2015). This combination of conditions might be prompting high bat species richness at these elevational bands, yet further studies in gradients with similar abiotic conditions are necessary to corroborate this hypothesis (McCain, 2007), especially because temperature and precipitation have been used as proxies of Net Primary Productivity (Sundqvist *et al*., 2013; Sun and Du, 2017), which might impact bat species richness. Finally it is important to include in future studies other biological and evolutionary explanations of species richness patterns on altitudinal gradients like source-sink dynamics, ecotone effects, competition, habitat heterogeneity and complexity (Lomolino, 2001; McCain and Grytnes, 2010), even if it is difficult to define these characteristics as well as to measure these traits for all species along large spatial (altitudinal) scales (McCain and Grytnes, 2010).

A second important finding of our study is the contrasting effect of precipitation on species richness in the elevational gradient. Most notably, we found a positive effect of the highest period of precipitation on species richness on the mid-high (975–1,000 m a.s.l.) elevational band, where tropical premontane forests are located in this latitude. These types of forests are predicted to be significantly affected by climate change, as there may be an increase in the elevation of cloud formation and a decrease in precipitation (Karmalkar *et al*., 2008). Therefore, a decrease in precipitation in tropical premontane forests will likely produce habitat shrinkage and local species extinction (Helmer *et al*., 2019). It remains to be tested whether a decline in precipitation in mid-high elevation may result in a decrease in bat species richness at our study site; however, what is more worrisome is the multitude of risks that these premontante forests currently face in light of their role in maintaining diverse tropical bat assemblages. These ecosystems, for example, have been heavily affected by land-use changes in the Neotropical region, as they are often subjected to logging, mining, road building and clearance for farming and grazing (Foster, 2001). Therefore, conservation efforts in this life zone are of critical importance for avoiding local extirpation of species, maintaining functional and ecological diversity of bat communities in elevational gradients, and preventing and managing species redistributions, especially because species band shifts have several implications across multiple temporal and spatial scales of biodiversity (Bonebrake *et al*., 2018).

We found no effect of elevation on the recorded captures of bats (a proxy of bats abundance), which is different from the pattern of decreasing abundance with increasing elevation registered in Costa Rica by Echeverría (2013), by Navarro and León-Paniagua (1995), and Briones-Salas *et al*. (2005) in México, by Lopes *et al*. (2017), Martins *et al*. (2015), Rodrigues Coelho *et al*., 2018, and De Carvalho *et al*. (2019) in Brazil. This is a novel result because a common explanation to the low abundance of bats in highland habitats is the low availability of feeding resources that contrasts with the high abundance of resources in lower habitats

(Navarro and León-Paniagua, 1995). Also, in contrast with previous studies which have observed a decrease in biomass with elevation (Navarro and León-Paniagua, 1995), we found no such effect, most likely given the relatively high number of frugivorous bats captured in the mid-high and high bands (Table 3 and Supplementary Fig. S3), especially the bats of the genus Sturnira, the most abundant species recorded in the gradient (Tables 2 and 3). Finally, we found no effect of elevation on sex ratio, which coincides with previous findings in other assemblages where the sex ratio is about 1:1 (Mares and Wilson, 1971).

We also found high species richness and abundance of nectarivorous bats in the mid-high and high elevational bands, which is different from the pattern found by Echeverria (2013) in Costa Rica (however this study did not include lowland sites), or by De Carvalho *et al*. (2019) in Brazil, where they found no effect of elevation. In our study, four out of 10 nectarivorous species registered overall are commonly found at high (*Anoura*) or middle elevational bands (*Lonchophylla*) (Table 2 — LaVal and Rodríguez-Herrera, 2002). At OTS's La Selva Station (lowland site) located in the study area, Tschapka (2004) recorded two nectarivorous species as residents (*Glossophaga commissarisi* and *Hylonycteris underwoodi*) and two species as seasonal (*Lichonycteris obscura* and *Lonchophylla robusta*), and he suggested the last one might commute daily from roosting sites at intermediate elevations (700 m a.s.l.) to lowlands in order to exploit temporarily rich resources. The elevational pattern found for nectar-eating bats in this study emphasizes the importance of the protection of tropical premontane and tropical lower montane rain forests for the conservation of bats of this ensemble and their ecological functions (pollination) for plants in those ecosystems.

In contrast to the patterns described by De Carvalho *et al*. (2019), of no effect of elevation on abundance of omnivorous or animalivorous bats, or by Capaverde *et al*. (2018) of a positive effect of elevation on richness of animalivorous bats, we found higher richness and abundance of animalivorous bats in mid-low elevational range similar to the pattern discovered by Patterson *et al*. (1998). These species correspond to bats of the genera *Lophostoma*, *Tonatia* and *Trachops*, species recorded in Costa Rica below 800 m a.s.l. (*Phylloderma*), below 1,000 m a.s.l. (*Phyllostomus*), or below 500 m a.s.l. (*Lophostoma*) (Timm *et al*., 1999; LaVal and Rodríguez-Herrera, 2002). We also found that elevation had no effect on species richness for hematophagous and insectivorous bats. Hematophagous bats had a wide distribution, most likely associated with the availability of domestic animals because cattle are a more predictable prey source than wildlife (Lee *et al.*, 2012). *Desmodus* is known to have a widespread distribution (Greenhall *et al.*, 1983) and it has been recorded as high as 3,800 m a.s.l. in the Andes (Greenhall *et al*., 1983; Soriano, 2000). A mid-peak richness of insectivorous bats has been found at an elevational gradient in Costa Rica (Arias-Aguilar *et al.*, 2020) that includes elevations ranging from 760 to 1,560 m a.s.l. based on acoustic monitoring, a technique not included in this study.

Our results also show that there is an effect of elevation and precipitation period on species richness of frugivorous bats (Table 4). Frugivorous bats showed higher species richness in the mid-high (975–1,000 m a.s.l.) and low bands (50–150 m a.s.l.), and during of high and mid precipitation periods (Fig. 5). In relation to elevation, frugivorous bats represent an important component of the bat assemblages captured at those elevations (42% and 50% of species recorded in low and mid-high assemblages, respectively — Tables 2 and 3). Precipitation possibly affects frugivorous bats through fruit production. The high precipitation period coincides with the high fruit production of understory trees in June–July recorded by Boyle and Bronstein (2012) at elevations of 300 and 750 m a.s.l. at the study site, whereas the mid precipitation period coincides with the highest fruit production recorded by the authors in September, October and November (Boyle and Bronstein, 2012). Peak production of fruits in the montane forest of Monteverde in Costa Rica also coincides with the high and mid precipitation periods (Dinerstein, 1986; Koptur *et al*., 1988). A predicted decrease in precipitation from both the horizontal and vertical processes in middle elevation areas because of climate change (Karmalkar *et al*., 2008), may affect not only the species richness of frugivorous bats, but also eventually the composition of bat communities in premontane and montane forests and their interactions with other species (e.g. fruit consumption and seed dispersal). It is known that shifts in species interactions lead to different ecological impacts on ecosystems as asynchronous migrations within communities, creation of novel assemblages, decoupling of trophic interactions, and mismatches in the phenology between consumers and their resources (Bonebrake *et al*., 2018), all affect ecosystemic function, integrity and resilience.

In conclusion, the high species richness recorded in the mid-high and low bands in the elevational gradient in Costa Rica adds a new trend to the known spatial patterns of species richness in Neotropical bats. This finding opens not only new perspectives on the fundamental ecological question of elevational distribution of life and its variation, but also highlights the high species richness of premontane tropical forests, particularly for nectarivorous and frugivorous bats, which are often considered good indicators of ecosystem health (Castro-Luna *et al*., 2007; Carrasco-Rueda and Loiselle, 2019). In addition, our finding of a significant effect of the high and mid precipitation periods on species richness as well as on species richness of two ensembles (nectarivorous and frugivorous bats) in the mid-high elevational band is to be underlined given the predicted future decrease in precipitation in the tropical premontane and montane habitats that may occur at that elevation. All this is of particular interest for conservation policy makers given the intense and persistent threats that this ecosystem and its species suffer. For example, Central American montane vertebrates including montane bats have showed high extirpation risks (~90% and ~50%, respectively) under different climate change scenarios (McCain and Colwell, 2011). Our results certainly provide baseline information on spatio-temporal distribution of assemblages and feeding ensembles of bats for comparison with future studies in elevational gradients. It is important not only to study how combined climatic variables affect natural populations but also to promote an agenda of increased funding for global and elevational monitoring of precipitation given the high increase (10-fold) in population extirpation risk associated with discordant changes in precipitation and temperature (McCain and Colwell, 2011). More research efforts on movements, composition and variation of species assemblages of bats are needed in tropical habitats, especially because of the scarcity of population-level monitoring in protected areas of tropical forest like in our study site (Beaudrot *et al*., 2016). In addition, more studies are needed in the northern Pacific slope of the country given its precipitation pattern is drastically different from the Caribbean slope and where future climatic change scenarios predict significant changes in precipitation amounts as well as an increase in the elevation of cloud formation (Karmalkar *et al*., 2008), affecting ecosystem function and stability. Other potentially fascinating results could arise if phylogenetic and functional diversity measures, not just taxonomic, are considered in future studies (Cisneros *et al*., 2014). Finally, our study shows the importance of continuous studies in montane ecosystems, a neglected habitat for research given the complex logistic, difficult access, and lower capture success, a paradigm that we must change if we still want to preserve its diversity and ecological integrity.

Supplementary Information

Contents: Supplementary Figures: Fig. S1. Monthly mean precipitation (mm) ± SD at the study site; Fig. S2. Species richness/sample effort of A) insectivorous, B) omnivorous, and C) hematophagous bats in the elevational gradient of the study site. Different letters denote significant differences among ranges based on a posteriori Tukey-Kramer test; Fig. S3. Captures/sample effort of A) frugivorous, B) omnivorous, C) insectivorous, and D) hematophagous bats in the elevational gradient of the study site. Different letters denote significant differences among ranges based on a posteriori Tukey-Kramer test. Supplementary Information is available exclusively on BioOne.

Acknowledgements

We thank two anonymous reviewers that provided comments that improved our manuscript. We thank Gaudy Ramírez, Santiago Pineda, Edwin Paniagua, Marco Ramírez and Henry Lara for their assistance during field work. We thank Guido Saborio for his assistance with the map. We acknowledge SINAC-ACCVC that issued research permits, OTS, ICE, and La Paz Waterfall Garden that provide access to climatic data. We also thank to Bijagual Reserve, Selva Verde Reserve, Finca Lara, Finca Pájara, Finca Lobo, and Albergue El Socorro for allowing access to field work. We also acknowledge funding provided by CONICIT-Ministerio de Ciencia y Tecnología of Costa Rica, Bat Conservation International through the Student Research Grant, Cleveland Metroparks Zoo through the Scott Neotropical Fund, and the American Society of Mammologists through the Latin American Student Field Research Award. WPL dedicates this research to the memory of Elizabeth Kalko.

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Received 20 October 2021, accepted 19 February 2022

Associate Editor: Wiesław Bogdanowicz