

Diversity and activity patterns of aerial insectivorous bats along an altitudinal gradient in a tropical forest in Costa Rica

Type

Research paper

Keywords

species richness, weather conditions, elevation, acoustic monitoring, foraging activity, cloud forest

Abstract

Bat diversity and activity have been documented to change with elevation and to be correlated with temperature variation, especially in temperate regions. Acoustic elevational studies of insectivorous bat fauna in tropical mountains are scarce. Here, we investigated diversity, general and species-specific activity patterns of aerial insectivorous bats along an elevational gradient in Costa Rica and tested the hypothesis that on tropical wet mountains species richness of insectivorous bats follows a decreasing pattern with elevation. We expected a peak of species diversity and activity at lower elevations and higher temperatures and no major differences between months. With simultaneous acoustic monitoring on five elevations, we recorded 11 984 bat passes during approximately 550 recording hours and identified 15 species, two genera and one sonotype at the family level. We found the highest diversity and activity of bats at mid-elevations, besides elevational, temporal and species-specific differences that were partially explained by temperature. The fact that in our transect humidity does not change with elevation may explain observed differences from the expected patterns. Climate change in Monteverde could be one of the factors resulting in elevational movements of bats to mid-elevations, probably affecting the availability of food resources, and thus the foraging activity of aerial insectivorous bats.

Explanation letter

Porto Alegre, 05 March 2020

Dear Dr. Wauters

Please find enclosed a new revised version of our manuscript entitled "Diversity and activity patterns of aerial insectivorous bats along an elevational gradient in a tropical forest in Costa Rica".

We appreciate all the comments and suggestions made by the referees. We tried to address all their comments and hopefully improved the entire manuscript. Please find below a description of the modifications made.

We thank you once again for considering our manuscript for publication in Hystrix, the Italian Journal of Mammalogy and look forward to hearing from you.

Yours sincerely,

Main author.

Reviewer 1

My major concern with the study is related to the methods employed to identify species based on previous descriptions of bats' echolocation calls. While I acknowledge the value of previous studies in describing echolocation calls and the tremendous effort required to manually analyze so many recordings, I feel that the author(s) should at least provide an estimate of error rates in identifying species.

Since the entire study and the conclusions derived from it are primarily reliant of a correct identification of species, then it is important to include a measure of accuracy during this process. My suggestion would be to provide an estimated error of correct identification, which could be determined by manually identifying calls of known species (from acoustic libraries, for example). If authors have estimated this previously, then I would suggest that they include the correct/incorrect identification rates and acknowledge this in their methods or discussion.

R/ We appreciate the reviewer's suggestion and agree that ideally, identifications should include an estimate error. However, this rate of correct/incorrect identification will be possible only with the existence of complete acoustic libraries and automatic identification software that include those libraries. But for now, at least for Neotropical species, the identifications by an expert are the most accurate ones.

In our case, one of the authors realized all identifications and corroborated the species ID (blind-confirmation) with another of the authors who has a few decades of recording experience in the same area of the study and who has a vast knowledge of the species occurring there. We are conscious of the amazing acoustic variability and plasticity of some bat species, so when there was a doubt in the identification we classified at the genus or family level and not as a species.

Other small comments or suggestions follow.

Line 16: Do you mean transect?

R/Yes, word was corrected.

Line 37: Change "determined" to "determining" (or maybe "establishing" would be better).

R/ "determined" was eliminated as suggested by the other reviewer.

Line 86: Where is "Here"?

R/Site three was specified.

Line 104: Do you mean "altitudinally"?

R/ Yes, the word was corrected.

Line 129: Change "run" to "ran".

R/ Changed as suggested.

Line 146: Change "pattern" to "patterns".

R/ Changed as suggested.

Line 158: Change "reveal" to "reveals".

R/ Changed as suggested.

Line 165: Remove "the" before temperature.

R/ Changed as suggested.

Line 175: Change "show" to "shows".

R/ Changed as suggested.

Line 178: "That species"; which one are you referring to?

R/ We clarified the sentence.

Table 1: If I understand the table correctly, the last column should be bat

passes/night/species, not per site.
R/ Changed as suggested.

Table 2. You are only providing here the contrasts between one category within your variables with all other categories. My suggestion would be to compare all categories within variables.

R/ We have changed the table 2 for a new figure (New Figure 2) with predicted values by the model where the differences between groups can be easily observed.

Figure 1: I do not see the variable species represented in the graph, so what do you mean by bat passes/hour/species?

R/ This graph refers to total bat activity per site, it is the number of bat passes per hour for all the species at each site.

Figure 2: Same comment as for figure 1 (where is the variable species represented?); also, since the trends are difficult to understand I suggest that you remove this graph, or else remove the outlier at 1160 masl and stretch your y-axis.

R/ In the figure 1, we have removed the outlier at 1160 (just for plotting). We have changed the Figure 2. The new figure plots the predicted values for each factor included in the model.

Table 3. Same comment as for table 2.

R/ We changed the content in Table 3 and included only the likelihood ratio tests for the generalized linear models and we included the contrasts in supplementary material. We consider contrasts are not relevant but the factors affecting activity of bats.

Figure 3: This graph could substitute figure 1 and even table 1.

R/ This graph represents the activity of only six species (those with the highest activity) and figure one represents the total bat activity (all species together).

Reviewer 2

Introduction

Replace with "elevational" throughout the text.

For example: "elevational gradients"

R/ Changed as suggested.

After e.g. comma is used, not colon.

R/ Changed as suggested.

Correct for m a.s.l.

e.g., 1560 m a.s.l.

R/ Changed as suggested.

Material and Methods

It would be best for authors to separate site descriptions into topics to improve text flow. Also, adding a map made with a shapefile or layer with altitudinal variation would help in visualizing the sites.

Thus, the sites must be indicated on the map.

R/ We try to improve text flow but kept the description of sites within the same paragraph.

We also included a map as a supplementary figure, showing the sampling sites, elevation curves and weather stations.

Here it is better to put in degrees, minutes and seconds. It was missing to insert who is the north and the west.

R/ Coordinates were corrected.

Authors can insert a map even in supplementary material. On the map, indicate the altitude variation according to the altitudes considered.

R/ The map was included as suggested.

Where annual precipitation from? Why above you indicate the precipitation of the first site. Specify here which site you are talking about.

R/We referred to site three. We clarified it.

Perhaps the description of each altitudinal band can be done in topic or in a table. This would improve reading.

R/ Within the paragraph each altitudinal band is already characterize. It is specified as site one and its description, site two, site three and site four and five together.

Are the sites located on the same face of the mountain? If not, do the faces receive rainfall differently?

R/ Yes. It is mentioned in the previous paragraph that the study site is in the Caribbean slope of the Cordillera of Tilarán.

In fact, it would be only "temperature data", not "weather data" (temperature, atmospheric pressure, rainfall, wind speed, etc.). So maybe it would be better to put here "Temperature data". Hence in the text you will describe that you took this data from weather stations.

R/ "Weather data" was changed to "Temperature data".

Indicate on the map the location of the weather stations.

R/ Indicated.

This variation is based on a mountain range located at the same latitude as those found in Monteverde Cloud Forest Reserve. If not, authors may consider using data from WorldClim, for example (<https://www.worldclim.org/bioclimate>). Thus, they would not need to make transformations.

R/This variation is the average moist adiabatic lapse rate: 0.6°C per 100 m in elevation.

This variation was previously reported for La Selva- volcán Barva elevational gradient (also for the Caribbean slope) in north-eastern Costa Rica.

In the item about weather stations and temperature data, you did not mention that these stations have hourly data.

R/ We included this information.

Why was the temperature nested with elevation only?

What does it mean to be nested within?

R/ We have removed nested factors in the models after asses the multicollinearity of the factors as suggested by the reviewer.

The temperature decreases as altitude increases. Also, depending on latitude, there may be greater variation in temperature between the months of the year. The authors do not describe in the material and methods in which season of the year the months analyzed correspond. Are the months in the dry or rainy season, cold or hot? Are they in transitional periods?

R/ Now we specified to which seasons the sampling months corresponded.

Even being four months, there may be a variation in temperature between months. Thus, this makes me think about the autocorrelation between the variables analyzed. The authors enter the same model altitude and temperature, but they vary together. Didn't you do an autocorrelation test? In addition, authors must provide a strong justification for keeping months as a variable in the tests. My suggestion is that they maintain only altitude and temperature if they are not autocorrelated, or make a model that contains the interaction between the two.

R/ The reviewer made a good observation. We have assessed multicollinearity using the score of the model for the variance inflation factor, as implemented in the vif function from the R package car. We have simplified the models when the vif function indicated that the vif value exceeds 5 as

recommended (James et al 2014).

James, G., Witten, D., Hastie, T., and R. Tibshirani. 2014. *An Introduction to Statistical Learning: With Applications in R*. Springer Publishing Company.

The first goal was to estimate and compare wealth and diversity, so this part should come before the activity part.

R/ Changed as suggested.

Explain what each of these indexes mean in practice.

R/Explained as suggested.

“Activity patterns along the gradient” This part must be after richness and diversity.

R/Changed as suggested.

Results

I believe you are concluding this based on overlap or not of the confidence interval when considering the Hill Numbers, as described in Chao and Chiu (2016). However, you do not describe this in the material and methods.

In addition, overlapping confidence intervals do not reject the alternative hypothesis, that is, there may be significant difference even when there is overlap of intervals. When there is no overlap, the difference is guaranteed. See Schenker and Gentleman (2012) for more details and how to take the comparative test.

R/We thank the reviewer for this clarification and references.

Yes, our conclusions are based on overlap or not of the confidence intervals. Now we described it in the methods.

Which test was used to check for difference and significance? Checking the confidence interval overlap does not mean that there is a significant difference. To say that, you need to do some testing. You should check this throughout the text for Hill Numbers.

R/We decided to follow the method of Chao et al. (2014) considering the guaranteed significant differences if the 95% confidence intervals do not overlap.

After seen the references mentioned by the reviewer and knowing about nonsignificance of partially overlapping intervals, we modified the text.

Is this the value of standard deviation? Perhaps it is better to indicate what this is in the material and methods.

R/ It is the SD. We specified it as suggested.

When you write "frequently", it is understood that there is a percentage that indicates how often the species is. However, this is not indicated in Tabela 1. You can change the text of the results or enter the frequency of each species by sampling site in Table 1.

In the text, the most correct would be to say that this species presented higher average bat passes.

R/ We changed the text of the results as suggested.

Discussion

To state this, wouldn't it be better to do a test and check if there is no mid-domain effect?

Effectively, you did not text whether or not there is a peak in the middle altitudes.

See, for example: <https://www.journals.uchicago.edu/doi/10.1086/382056>

If the authors take this test, they should take into account in their discussion that their elevational gradient is not considering the entire gradient of the region, that is, starting from sea level elevation.

You are actually taking a part of the total gradient. What is the face of the gradient? The most continental or the sea-facing? Is this face drier or wetter? Is there a difference between the sample sites? This should be described in the material and methods.

Take a closer look at McCain and Grytnes (2010) for more details.

R/ We thank the reviewer for its suggestions about the mid-domain effect. However, we wanted to test the predictions of the McCain's climate model and to investigate the relationship between species richness and the temperature gradient, and also between species activity and temperature. We consider that our data do not meet the requirements to test for the MDE.

McCain CM (2007) Could temperature and water availability drive elevational species richness? A global case study for bats. *Global Ecology and Biogeography* 16: 1–13.

So your mountain is wet too? Then you should describe it in the material and methods.

R/ All the sites are described in methods. The descriptions include data about precipitation.

The temperature variation along the gradient? You should check the autocorrelation of the variables or think about modifying how you did the GLM analysis.

R/ The multicollinearity of the variables was assessed using variance inflation factors as described in methods.

However, you did not use precipitation or make a correlation.

R/ We reformulated the sentence and changed it as a possible explanation.

Did you measure this dependence?

R/ We removed the sentence.

These studies only evaluated the temperature, right? It would not be better to make comparisons with studies that were performed on altitudinal gradients. There are differences in species responses regarding temperature and temperature ~ altitude. Other factors may be involved in these responses.

R/ We agreed with the reviewer that other factors may be involved. However; we wanted to focus on the effects of temperature.

But in the results you indicate that activity was similar over the months.

However, you mention in the results: "The pattern of activity per site was very similar during all months...". Thus, their results would not support this discussion of migration. In fact, months-only evaluation would not support this.

Perhaps this is not the best explanation to justify that at medium altitudes there is greater activity and species richness. Authors should look for information in studies that have found similar patterns to explain their results. It makes little sense to say that bats simply migrate from lower or higher altitudes to medium altitudes. Migrating from high to low altitudes has been very well described for different species, either for breeding or simply feeding. Again, the authors studied a portion of the altitudinal gradient. Therefore, you should take this into account in your discussion.

R/ We modified the sentence but kept the idea that changes in climatic conditions may partially explain the altitudinal movements of species.

We included information from other studies and mentioned the limitations of our study..

Conclusions

The conclusion should be updated after the authors verified my comments on the data analysis. In addition, they should consider testing for evidence of the mid-domain effect, which will better support the results.

R/ We updated the conclusion but as previously explained we discarded testing the MDE.

Why didn't the authors add these variables to this manuscript? Do weather stations not provide this data?

R/ Unfortunately, some of the weather stations instruments were in poor condition or did not work properly during our sampling campaigns.

[Explanation letter.doc](#)

1 1 **Diversity and activity patterns of aerial insectivorous bats along an elevational**
2 2 **gradient in a tropical forest in Costa Rica**

3 3 **Abstract**

4 4 Bat diversity and activity have been documented to change with elevation and to be
5 5 correlated with temperature variation, especially in temperate regions. Acoustic elevational
6 6 studies of insectivorous bat fauna in tropical mountains are scarce. Here, we investigated
7 7 diversity, general and species-specific activity patterns of aerial insectivorous bats along an
8 8 elevational gradient in Costa Rica and tested the hypothesis that on tropical wet mountains
9 9 species richness of insectivorous bats follows a decreasing pattern with elevation. We
10 10 expected a peak of species diversity and activity at lower elevations and higher
11 11 temperatures and no major differences between months. With simultaneous acoustic
12 12 monitoring on five elevations, we recorded 11 984 bat passes during approximately 550
13 13 recording hours and identified 15 species, two genera and one sonotype at the family level.
14 14 We found the highest diversity and activity of bats at mid-elevations, besides elevational,
15 15 temporal and species-specific differences that were partially explained by temperature. The
16 16 fact that in our transect humidity does not change with elevation may explain observed
17 17 differences from the expected patterns. Climate change in Monteverde could be one of the
18 18 factors resulting in elevational movements of bats to mid-elevations, probably affecting the
19 19 availability of food resources, and thus the foraging activity of aerial insectivorous bats.

20 20
21 21 **Keywords:** acoustic monitoring, elevation, foraging activity, species richness, weather
22 22 conditions, cloud forest

23 23 **Running title:** Neotropical insectivorous bats along an elevational gradient

Introduction

Understanding patterns of biological diversity and activity along elevational gradients provides valuable insights for conservation at small geographical scales but yet for many mountain ecosystems these patterns are not well documented (Patterson et al. 1989, Lomolino 2001, Sánchez-Cordero 2001, Bender and Hartman 2015). Small mammals like bats are particularly useful in the study of diversity along elevational gradients because they are key organisms in the structure, composition, and dynamics of tropical ecosystems; generally, they have high diversity and abundance, and participate in multiple biological processes such as pollination, seed dispersal, insect predation and food webs (Fleming et al. 1972, McNab 1982, Fleming 1986, Fenton 1997, Mena et al. 2011). By understanding patterns and correlates of variation in activity of bats, the design of research and monitoring programs can be improved (Hayes 1997).

Studies of bats along elevational gradients in the Neotropics have been mainly focused on patterns of distribution and composition of species principally through the use of mist nets as the main capture technique (e.g., Patterson et al. 1996, Sánchez-Cordero 2001, Echeverría-Tello 2013, Refulio 2015) and in a very few cases with acoustic methods (e.g., Ortiz-Badillo 2015). As a result, aerial insectivorous bats have usually been underestimated (O'Farrel and Gannon 1999, Ochoa et al. 2000). For this group, which may comprise about one-third of all bat species in the region (Jung and Kalko 2010), it is feasible to monitor echolocation calls through the use of acoustic detectors because they allow species identification as well as the assessment of distributional patterns and habitat use (Fenton 1997, Kalko and Schnitzler 1998, Ochoa et al. 2000). Studies of the insectivorous bat fauna activity using acoustic detectors along elevational gradients are common in the Palearctic (e.g., Piksa et al. 2007, Müller et al. 2012) and Nearctic realms (e.g., Grindal et al. 1999,

50 48 Wolbert et al. 2014), but scarce in the Afrotropic (e.g., Linden et al. 2014) and, to our
51 49 knowledge, almost none exist for the Neotropic.

52 50 Bat diversity and richness have been documented to vary with elevation, been strongly
53 51 correlated with temperature (McCain 2007) and usually showing a decrease pattern with
54 52 increasing altitude (Patterson et al. 1996, Heany 2001, Sánchez-Cordero 2001, Curran et al.
55 53 2012, Linden et al. 2014). Commonly, in temperate regions, the pattern of species richness
56 54 peaks at mid-elevations, while in the tropics, species richness declines with elevation
57 55 (McCain 2007). Meanwhile, bat activity shows a general decreasing pattern with elevation
58 56 (Thomas 1988, Barclay 1991, Linden et al. 2014, Wolbert et al. 2014), probably as a result
59 57 of higher temperatures favouring some reproductive and thermoregulatory strategies of bats
60 58 as well as higher insect densities (Grindal et al. 1999, Cryan et al. 2000, Weier et al. 2016).
61 59 Bat activity has been documented to be affected by weather factors, varying with habitat,
62 60 region or season but this influence is poorly understood (Bender and Hartman 2015).

63 61 Here, we investigated the patterns of diversity and activity of aerial insectivorous bats along
64 62 an elevational gradient within a continuous forest in the mountainous region of
65 63 Monteverde, Costa Rica. Using acoustic surveys we aimed to determine the pattern of
66 64 species diversity along the elevational gradient and to evaluate how the activity of aerial
67 65 insectivorous bats responds to temperature variation between months at different
68 66 elevations. As proposed by McCain (2007), species richness of bats on tropical wet
69 67 mountains follows a decreasing pattern with elevation, so we expected a peak of species
70 68 diversity and activity at lower elevations where higher temperatures occur. As the sampling
71 69 campaigns occurred during a short, almost non-seasonal period, we expected no major
72 70 differences in bat activity between months.

71 Material and Methods**72 Study site**

73 The study was conducted in the Monteverde Cloud Forest Reserve, and the Children's
74 Eternal Rainforest (10°18'33.3"N 84°47'45.8"W) on the Caribbean slope of the Cordillera
75 de Tilarán, Puntarenas and Alajuela provinces, Costa Rica (Fig. S1). The full description of
76 climate and vegetation characteristics of the region could be found in Nadkarni and
77 Wheelwright (2014). Based on those authors we described our sampling area.

78 The highest elevation, site one (1560 meters above sea level –m a.s.l.–) at the continental
79 divide holds a dense cloud forest, with an annual rainfall of 2500-3500 mm. In wind
80 exposed hills, the canopy height varies between 5-10 m, characteristics of the dwarf forest.
81 At site two (1360 m a.s.l.) the forest is composed of abundant and dense epiphytes and
82 understory with a canopy height that varies between 20-30 m. At site three (1160 m a.s.l.)
83 and lower elevations, the rainforest is essentially aseasonal; with annual precipitation of
84 3500 mm to 7000 mm and an almost imperceptible dry period in March and April. At site
85 three, in exposed steep hills, the forest is reduced to 15-20 m height, with a more
86 fragmented canopy, disordered structure, and little diversity. Sites four and five (960 and
87 760 m a.s.l.) include protected valleys and slight slopes, where the natural vegetation is
88 dense, with abundant epiphytes and high biodiversity. The canopy is more uniform (30-40
89 m) and trees frequently exceed 50 m in height.

90 Sampling design

91 We conducted acoustic surveys at five sampling sites along a transect of continuous forest
92 spanning 800 m altitude and a distance of approximately 14 km in a straight line. The

97 93 minimum distance between sites was 2.0 km. The top of the gradient was at the continental
98 94 divide -1560 m a.s.l.- down to 760 m in elevation where the forest was still well preserved.
99 95 Ideally, lower elevations would have been surveyed, but no large fragments of intact forest
100 96 exist below 600 m a.s.l. in this region of Costa Rica (McCain 2004). We performed
101 97 monthly sampling campaigns of seven consecutive nights, during the dry season from
102 98 February to April and early rainy season during May of 2014.

103 99 **Temperature data**

104 100 We obtained hourly temperature data from four weather stations (Davis Vantage Pro2™ &
105 101 Vantage Pro2 Plus™) located through the gradient at 1560 m, 1300 m, 950 m and 820 m
106 102 a.s.l. As weather stations and sampling points differed altitudinally, we used climatic data
107 103 from the nearest weather station and estimated temperature according to the moist adiabatic
108 104 cooling rate, average increases 0.6°C per 100 m in elevation (Barry 1992).

109 105 **Acoustic sampling of bats and identification**

110 106 Acoustic sampling was simultaneously carried out at each of five sites with one bat detector
111 107 (Song Meter SM2Bat or SM2Bat+ by Wildlife Acoustics) per site, programmed to record
112 108 in real time for 6.5 hours from sunset, in lapses of 10 minutes each 10 minutes. When
113 109 topographic conditions allowed it, we located the detectors along the trail and/or clearings
114 110 within the forest, alternating places between sampling campaigns.

115 111 Bat calls were analysed using Avisoft Saslab Pro, Version 5.0.24 (Raimund Specht, Avisoft
116 112 Bioacoustics, Berlin, Germany). Call duration, pulse interval, start and end frequencies and
117 113 peak frequency were registered. Bat echolocation calls were manually identified using
118 114 previous literature as a reference (e.g. O'Farrell and Miller 1999, Ochoa et al. 2000, Rydell

120 115 et al. 2002, Jung et al. 2007, 2014). All species identifications were corroborated by an
121 116 expert (blind confirmations).

122 117 **Data analyses**

123 118 We display the acoustic data by elevation and species (Table 1). Variables were
124 119 summarized by hour \pm standard deviation; mean air temperature was estimated as the
125 120 average of the temperatures by hour. Bat activity was quantified as the sum of the bat
126 121 passes within each hour. Following Fenton et al. (1998), we consider a bat pass as a
127 122 recorded sequence of ≥ 6 echolocation calls separated by at least four times the prevailing
128 123 interpulse intervals from other echolocation calls produced by a bat.

129 124 Using Hill numbers based on relative incidence in the assemblage (Chao et al. 2014), we
130 125 constructed sampling-based (occurrence data) and coverage-based rarefaction and
131 126 extrapolation sampling curves to investigate species diversity among sites. We estimated
132 127 species richness (order $q = 0$), Shannon (“typical” species) diversity (order $q = 1$, the
133 128 exponential of Shannon entropy), and Simpson (“dominant species) diversity (order $q = 2$,
134 129 the inverse of Simpson index) (sensu Jost 2006) with the “iNext” package (Hsieh et al.
135 130 2016) for each elevation. Significant differences at a level of 5% among the expected
136 131 diversities were considered if the 95% confidence intervals do not overlap (Chao et al.
137 132 2014). Nevertheless, partially overlapping intervals do not guarantee nonsignificance
138 133 (Schenker and Gentleman 2001). All analyses were run in R 3.3.1 (R Development Core
139 134 Team, 2016).

140 135 We evaluated which variables had an effect on the general activity of bats. We ran a
141 136 generalised linear model assuming a negative binomial distribution of the response variable
142 137 (bat passes / hour / species). The model includes elevation and month as factors and the

144 138 mean temperature as a predictor. We tested multicollinearity of factors assessing the
145 139 variance inflation factor with *vif* function of the R package "car" (Fox and Weisberg 2019).
146 140 We removed a factor if *vif* score was greater than 2 (Fox and Weisberg 2019). We ran the
147 141 model using a stepwise regression including one factor at a time and evaluate the
148 142 performance of the model in respect of the previous model using the Akaike's Information
149 143 Criterion. The statistical significance of regression terms was assessed by likelihood ratio
150 144 tests. For each species with more than 500 records, we evaluated the effect of the site
151 145 (elevation), period (month) and temperature in the activity (bat passes) by hour using
152 146 generalised linear models assuming a negative binomial distribution and with the same
153 147 procedure as we made with all the data. For all the models, the assumptions were evaluated
154 148 by qq-plots of the residuals.

155 149 **Results**

156 150 *Sampling summary*

157 151 We recorded 11,984 bat passes during approximately 550 recording hours (for a total of 22-
158 152 28 sampled nights per site) and identified 15 species, plus sonotypes of two genera of
159 153 Molossidae and one sonotype of Vespertilionidae (Table 1). The number of species varied
160 154 among sites, being highest at 960 m a.s.l. (14 species) and lowest at 1560 m a.s.l. (six
161 155 species) (Table 1). The most common species recorded was *Myotis pilosatibialis* with
162 156 26.02 ± 4.81 bat passes/night/site. It was registered in all the elevations, but recurrently at
163 157 1160 m a.s.l. At that elevation and 960 m a.s.l., *M. pilosatibialis* was the species with
164 158 higher average bat passes recorded (Table 1). At elevations 760, 1360 and 1560 m a.s.l.,
165 159 *Pteronotus mesoamericanus*, *Myotis riparius* and *Centronycteris centralis*, respectively,

167 160 were the species with the highest activity. We recorded more than one bat pass/night for
168 161 seven species (Table 1).

169 162 *Species diversity among sites*

170 163 In general, all sites show similar diversities (Table 2, Fig. S2-S3). The sample coverage for
171 164 the five sites (760, 960, 1160, 1360 and 1560 m a.s.l.) was estimated as 99.47%, 100.00%,
172 165 99.91%, 99.84% and 95.67%, respectively, indicating that sampling is nearly complete for
173 166 all sites. Sample-based diversity of the sites for species richness ($q=0$); exponential of
174 167 Shannon entropy ($q=1$); and inverse Simpson index ($q=2$) decreased as follows: $q=0$:
175 168 1160>960>760>1360>1560 m a.s.l.; $q=1$: 1560>1360>1160>960>760 m a.s.l. and $q=2$:
176 169 1560>1160>1360>960>760 m a.s.l. (Fig. S2). Only the 95% confidence intervals for
177 170 species richness of sites 3 and 1 (1160 and 1560 m a.s.l., respectively) and Simpson
178 171 diversity of site 5 (760 m a.s.l.) were nonoverlapping, implying significant differences.

179 172 Coverage-based diversities for species richness ($q=0$); exponential of Shannon entropy
180 173 ($q=1$); and inverse Simpson index ($q=2$) decreased as follows: $q=0$:
181 174 960>1160>1360>760>1560 m a.s.l.; $q=1$: 1360>1160>960>1560>760 m a.s.l. and $q=2$:
182 175 1160>1360>1560>960>760 m a.s.l. (Fig. S3). For coverage values higher than 40% the
183 176 nonoverlapping of the 95% confidence intervals for site 4 (960 m a.s.l.) and site 5 (760 m
184 177 a.s.l.) imply that the diversities of order $q=0$ (species richness) and $q=2$ respectively, are
185 178 significantly different.

186 179 *Activity patterns along the gradient*

187 180 The summary of the adjusted model relating general bat activity with temperature,
188 181 elevation and period are presented in Table 3. The GLM reveals significant variation in the

190 182 number of bat passes / hour / species between the elevations and months (Table 3, Figs. 1
191 183 and 2). The site at 1160 m a.s.l. had the highest activity/hour/species during most of the
192 184 four months, while site 1560 m a.s.l. had the lowest activity (Fig. 2). The pattern of activity
193 185 per site was very similar during all months; however, in March, there was a general
194 186 increment in the activity and particularly for the site at 1360 m a.s.l. regarding the other
195 187 months (Fig. 1). Evaluating the overall range, we found temperature had a negative effect
196 188 on the activity (Table 3, Fig. 2).

197 189 *Activity patterns by species*

198 190 Only six species had more than 500 records: *Myotis albescens*, *Myotis nigricans*, *M.*
199 191 *pilosatibialis*, *M. riparius*, *P. mesoamericanus* and *C. centralis*. The activity patterns were
200 192 idiosyncratic among the species (Fig. 3). The summaries of the significant factors which
201 193 adjusted to the models relating activity for the six bat species with temperature, elevation
202 194 and period are presented in Table 4. The GLMs show that month was the factor affecting
203 195 all the species (Table 4). However, when the elevation was included, it was the factor with
204 196 more effect in the activity of the species except for *M. albescens* and *M. riparius*, for which
205 197 the period (month) was the factor explained more variance in the activity (Table 4, Fig. 3).
206 198 In general, all species had more activity at middle elevations, between 960 and 1360 m
207 199 a.s.l., and low activity in the lowest and the highest elevation analysed (Fig. 3). March was
208 200 the month with the highest activity for the species *M. pilosatibialis*, *M. nigricans* and *M.*
209 201 *riparius* and *P. mesoamericanus* (Fig. 3). When the temperature has an effect in the activity
210 202 of bats, it was negative (Table 4, Table S1).

203 Table 1. Mean \pm standard error of bat passes/night for species recorded along an elevation gradient in a tropical forest in Costa Rica.

Species	Mean bat passes/night Elevation (m)					General mean bat passes /night /species
	760 m	960 m	1160 m	1360 m	1560 m	
Emballonuridae						
<i>Centronycteris centralis</i>	0.05 \pm 0.04	1.39 \pm 0.71	14.32 \pm 4.22	5.21 \pm 1.86	0.33 \pm 0.33	4.35 \pm 1.04
<i>Peropteryx kappleri</i>		0.36 \pm .35				0.08 \pm .08
<i>Saccopteryx bilineata</i>	8.32 \pm 3.03	0.50 \pm 0.18				1.55 \pm 0.58
Mormoopidae						
<i>Pteronotus gymnonotus</i>	1.32 \pm 0.79	0.14 \pm 0.08	0.48 \pm 0.21	0.11 \pm 0.11		0.38 \pm 0.15
<i>Pteronotus mesoamericanus</i>	12.00 \pm 1.32	16.14 \pm 2.86	26.08 \pm 4.69	3.29 \pm 1.34	0.17 \pm 0.09	11.53 \pm 1.42
Molossidae						
<i>Eumops</i> sp. sonotype 1	0.32 \pm 0.32	0.32 \pm 0.13			0.29 \pm 0.17	0.18 \pm 0.07
<i>Molossus</i> sp. sonotype 1	0.27 \pm 0.23	0.25 \pm 0.21	0.08 \pm 0.06	0.04 \pm 0.04	0.08 \pm 0.08	0.14 \pm 0.07
<i>Tadarida brasiliensis</i>		0.29 \pm 0.22	0.52 \pm 0.52			0.17 \pm 0.11
Vespertilionidae						
<i>Eptesicus brasiliensis</i>	0.05 \pm 0.05	2.79 \pm 1.35	0.12 \pm 0.08	1.11 \pm 0.49		0.89 \pm 0.33
<i>Eptesicus furinalis</i>				0.21 \pm 0.14		0.05 \pm 0.03
<i>Eptesicus fuscus</i>			0.04 \pm 0.04	1.61 \pm 1.20		0.36 \pm 0.26
<i>Dasypterus ega</i>		0.14 \pm 0.09				0.03 \pm 0.02
<i>Myotis albescens</i>	4.41 \pm 2.1	29.11 \pm 8.12	37.72 \pm 10.60	16.68 \pm 6.42		18.28 \pm 3.32
<i>Myotis nigricans</i>	1.18 \pm 0.77	8.04 \pm 3.13	82.76 \pm 18.07	0.86 \pm 0.79	0.04 \pm 0.04	18.46 \pm 4.57
<i>Myotis pilosatibialis</i>	0.05 \pm 0.05	33.00 \pm 7.77	87.84 \pm 17.39	6.36 \pm 2.64	0.25 \pm 0.17	26.02 \pm 4.81
<i>Myotis riparius</i>	4.32 \pm 2.32	3.57 \pm 1.76	21.40 \pm 5.72	27.79 \pm 14.01		11.87 \pm 3.43
<i>Rhogeessa bickhami</i>			0.04 \pm 0.04			0.01 \pm 0.008
Vesp. sonotype 1			0.04 \pm 0.04			0.01 \pm 0.008
Nights sampled	22	28	25	28	24	
General mean bat passes / night / site	32.27 \pm 6.13	96.04 \pm 9.76	271.44 \pm 31.12	63.25 \pm 20.77	1.17 \pm 0.47	94.36 \pm 11.46

242

Species number per site

11

14

13

11

6

243

11

244 204 Table 2. Diversity of all species based on incidence data (${}^0\Delta$ = species richness), of
 245 205 “typical” species (${}^1\Delta$ = Shannon diversity), and of dominant species (${}^2\Delta$ = Simpson
 246 206 diversity) at each elevation and its respective sample coverage (SC).

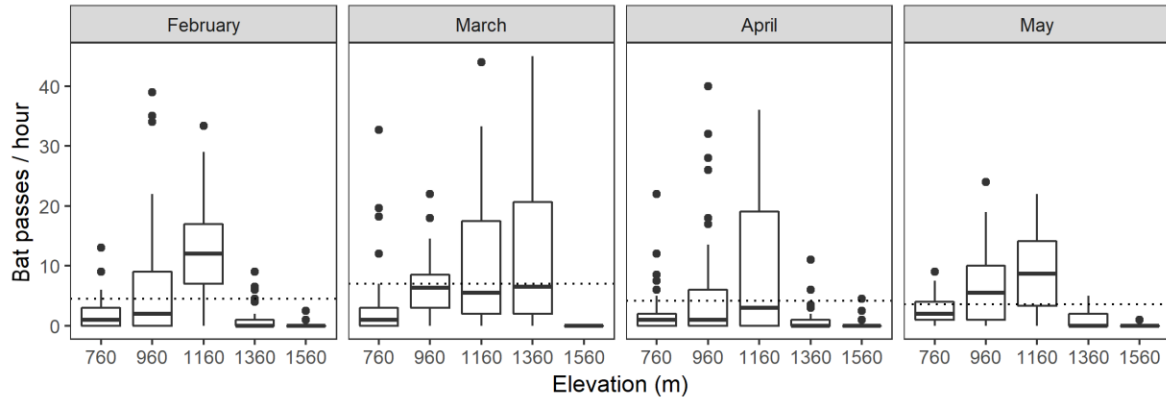
	Estimated diversity (SE)				
Elevation (m)	760	960	1160	1360	1560
${}^0\Delta$ (Richness)	14.00 (4.50)	14.00 (0.39)	15.25 (3.40)	11.50 (1.32)	6.48 (1.27)
${}^1\Delta$ (Shannon)	5.05 (0.19)	5.53 (0.12)	5.75 (0.06)	5.87 (0.18)	5.99 (0.93)
${}^2\Delta$ (Simpson)	3.88 (0.17)	4.47 (0.08)	5.21 (0.07)	4.77 (0.18)	5.68 (0.96)
SC	0.99	1.00	1.00	1.00	0.96

207

Table 3. Likelihood Ratio Test for the generalized linear model to explain the bat passes/hour/ species in an elevation gradient in a tropical forest in Costa Rica using as predictor period (months), elevation and temperature. The significance of the effects are represented with ** for $p < 0.01$ and *** for $p < 0.001$.

Factor	Deviance	df	Residual deviance	df	p
Null			1342.05	888	
Elevation	444.56	4	897.49	884	< 0.001***
Month	40.84	3	856.65	881	< 0.001***
Temperature	7.26	1	849.4	880	0.007**

212

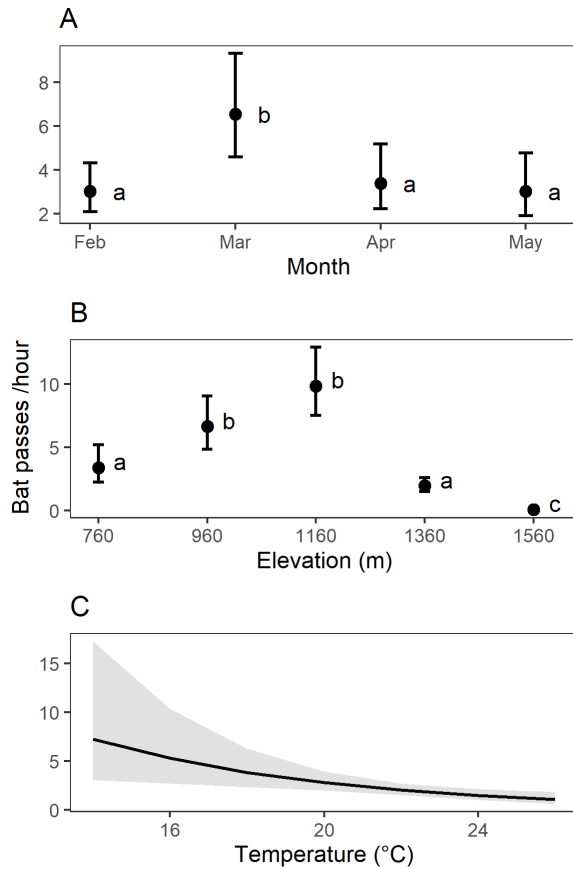


270 213

271 214 Fig.1. Bat passes / hour for each site (elevation) and month analysed. The dotted line

272 215 represents the mean of bat passes / hour for each month.

273 216

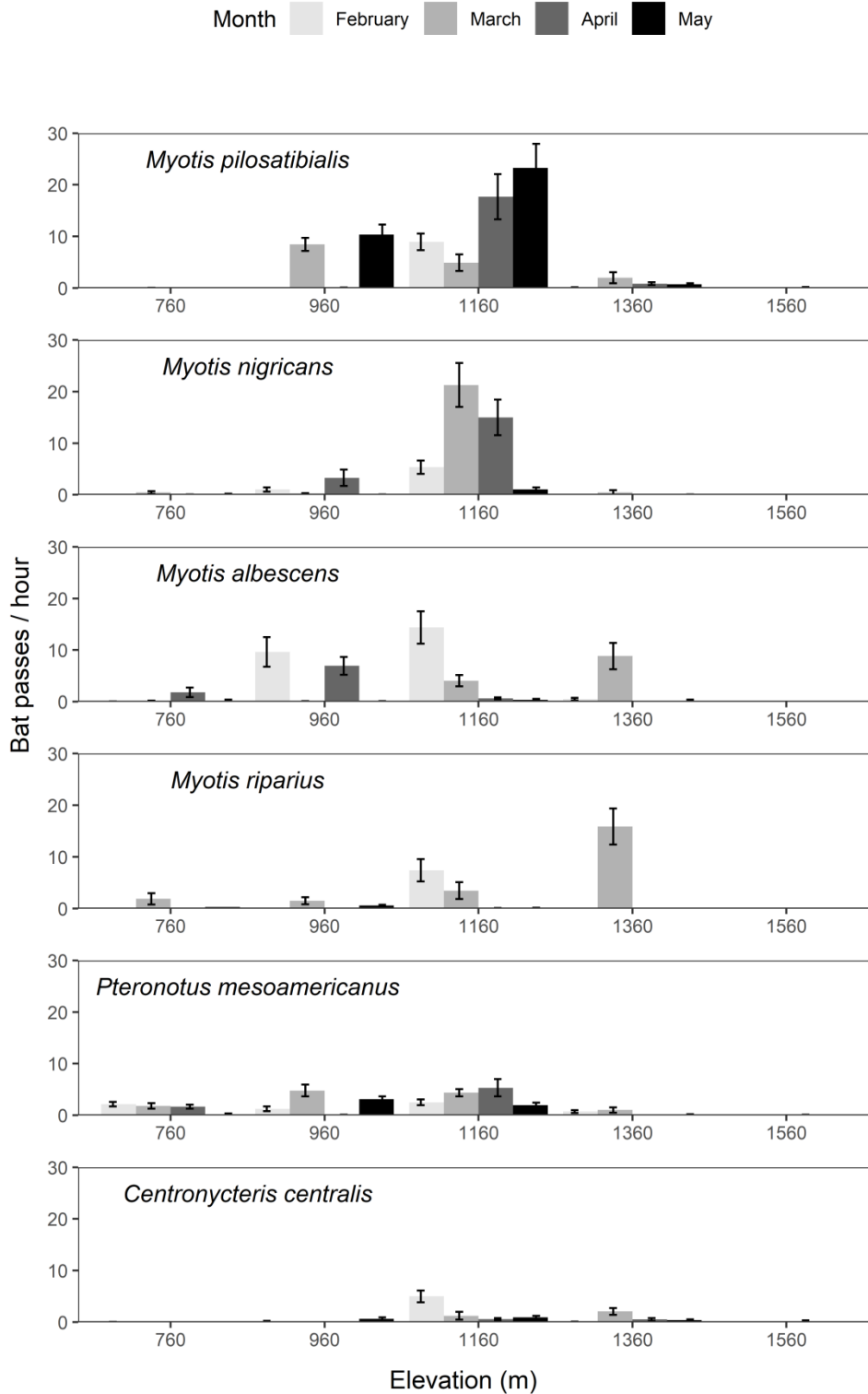


275 217
 218 Fig. 2. Predicted values of bat passes / hour for each period (month) (A), elevation (B) and
 276 219 temperature (C) according to the generalized linear model. In A and B, dots represent the
 277 220 mean expected for each group and whiskers the standard error. Letters represent groups
 278 221 which are different between them ($p < 0.05$). In C the line represents the fitted line and the
 279 222 gray shadow represents the standard error.

Table 4. Likelihood ratio tests for the generalized linear models with negative binomial distribution to explain the bat passes/hour for each species with more than 500 records. The models were constructed using the effect of period (months), elevations and temperature. Models were tested using step AIC (Akaike Information Criterion) and variables removed when the model was improved. Variables removed are marked with NI (not included). The significance of the effects are represented with * for $p < 0.05$, ** for $p < 0.01$ and *** for $p < 0.001$.

Species	Factor	Deviance	df	Residual Deviance	df	p
<i>Myotis pilosatibialis</i>	Null			888.16		
	Elevation	403.29	4	484.86	884	<0.001***
	Month	42.7	3	442.17	881	<0.001***
	Temperature	4.06	1	438.11	880	0.04*
<i>Myotis nigricans</i>	Null			716.64		
	Elevation	353.61	4	363.03	884	<0.001***
	Month	39.77	3	323.26	881	<0.001***
	Temperature					NI
<i>Myotis albescens</i>	Null			463.42		
	Month	60.6	3	402.82	717	<0.001***
	Temperature	15.57	1	387.25	716	<0.001***
	Elevation					NI
<i>Myotis riparius</i>	Null			363.45		
	Month	122.7	3	243.75	717	<0.001***
	Elevation	33.03	3	210.72	714	<0.001***

304		Temperature					NI
305	<i>Pteronotus</i>	Null			702.34		
306	<i>mesoamericanus</i>						
307		Elevation	90.47	3	611.87	717	<0.001***
308		Month	23.04	3	588.84	714	<0.001***
309		Temperature					NI
310	<i>Centronycteris centralis</i>	Null			515.31	888	
311		Elevation	174.38	4	340.93	884	<0.001***
312		Temperature	51.13	1	289.8	883	<0.001***
313		Month	9.02	3	280.78	880	0.03*



228

229

230

231

Fig. 3. Mean and standard error of the bat passes / hour for the six bat species in an elevation gradient of tropical forest in Costa Rica during four months.

239

Discussion

To our knowledge, this is the first study to describe diversity and general and species-specific patterns of activity of aerial insectivorous bats along an elevational gradient in a Neotropical rainforest, using exclusively acoustic methods.

General patterns along the gradient

Although the temperature decreased with elevation we found the highest richness, diversity and activity of the insectivorous bats in mid-elevations, and lower values at the lowest and highest site. These findings differ from previous results reported for other wet mountains in Mexico and South Africa (McCain 2007, Weier et al. 2016) where the warmest–wettest conditions are towards the base of the mountain and support the highest bat species richness. In contrast with what was previously thought, we found that the increase in temperature by itself did not explain a higher species richness or activity, and the deviations from the expected pattern of species distribution may be partially attributed to lack of correlation between temperature and precipitation patterns. Despite we did not test that correlation, it is suggested by the fact that, in Monteverde precipitation does not decrease with elevation, it is highest at midlands (McCain 2007) and by additional information from the weather stations (at 1560, 960 and 820 m a.s.l.) that revealed a higher average rainfall at site 960 m during our study period than at the other two elevations.

As an alternative explanation, despite the continuity of the forest along the gradient, the lowest species richness and lowest diversity at the site 760 m a.s.l. could be a consequence of habitat disturbance occurring at lower elevations (under 600 m a.s.l.). It has been argued, that montane communities adjoining areas of dense human settlement sustain lower species richness than within intact habitat (McCain and Grytnes 2010). However, we do not know

344 255 the magnitude of this effect on the community of insectivorous bats of Monteverde and as
345 256 we did not sample in the lowlands this may be biasing the observed patterns.

346 257 Overall foraging activity of bats along the gradient was slightly but negatively affected by
347 258 temperature. Precisely why bat activity diminished with higher temperatures is uncertain.

348 259 Previous studies from temperate regions revealed that the influence of temperature on bat
349 260 activity could be positive (e.g. Vaughan et al. 1997, O'Donnell 2000) or negative (e.g.

350 261 Boonman et al. 1998, Ciechanowski et al. 2007). On the Neotropical region, increases in
351 262 temperature due to climate change, besides other factors, has negatively impact insect

352 263 density and species richness (Janzen and Hallwachs 2019), so one has to wonder what has
353 264 been the effect on diversity, abundance, activity, and elevational distribution of bats here

354 265 due to drastic reduction of insect populations.

355 266 Our results also showed a temporal variation on bat activity. Temporal changes on local
356 267 levels of insectivorous bat activity may be related to local sampling conditions (Bender and

357 268 Hartman 2015) as unusually large hatches of insects or other factors area- and species-
358 269 specific (Hayes 1997). For example, horizontal, vertical or regional movements related (or

359 270 not) with migration could be linked to temporal variations on the abundance of some
360 271 species (Esbérard et al. 2011). Timm and LaVal (2014) reported that in Monteverde

361 272 abundance variation of some mammals was due to elevational migration in search of food.

362 273 Monthly variation in the activity of the insectivorous bats during our study period does not
363 274 necessarily represent migration but it may reflect changes in food resources. In fact, some

364 275 insects like butterflies, dragonflies, and wasps perform elevational migrations and in others,
365 276 like some nocturnal beetles, species richness and diversity varied with elevation (Hanson

366 277 2014).

367 278 *Species-specific patterns*

369 279 The activity of the most common insectivorous bats was differently affected by elevation,
370 280 temperature and sampling month. Besides, as occurred with the overall bat activity, species
371 281 responses to temperature varied along the gradient and within sites. Those differences could
372 282 explain the observed changes in the elevational distribution for some species (see LaVal
373 283 and Rodríguez 2002) in the Caribbean slope of Monteverde. *Myotis riparius*, *M. albescens*
374 284 and *E. furinalis* occurred above their known distribution (above 700 m a.s.l.), while *E.*
375 285 *fuscus* was found below their known distribution on the Caribbean slope (below 1650 m
376 286 a.s.l.). Recently Frank et al. (2018) also reported the presence of *M. riparius* at high
377 287 elevations (around 1400 m a.s.l.). For the first time, we reported the occurrence of
378 288 *Centronycteris centralis* in Monteverde as well as its presence at middle and high
379 289 elevations in Costa Rica. Our results support the hypothesis of LaVal (2004) that lowland
380 290 bat species in this region are moving upwards — colonizing mid-elevations and increasing
381 291 species richness, as also occurred with birds (Pounds et al. 1999).

382 292 Changes in Monteverde's climatic conditions could be one of the factors facilitating
383 293 elevational movements of bats, as the species move up or down the mountain attempting to
384 294 remain within the temperature and humidity limits to which they are adapted (Timm and
385 295 LaVal 2014). Nightly increases in minimum temperature within sites probably do not
386 296 impose a physiological limit for bat activity, at least for our most commonly recorded
387 297 species. However, tropical insects are relatively sensitive to temperature change and are
388 298 currently living very close to their optimal temperature (Deutsch et al. 2008). Particularly,
389 299 species found at middle elevations and on mountaintops are less tolerant to high
390 300 temperatures than species restricted to lowland (García-Robledo et al. 2016). Besides
391 301 temperature, insects may also be affected by vegetation density resulting in differences in
392 302 activity between bat species with different foraging strategies (Müller et al. 2012). In this
393

394 303 sense, further studies are therefore required to elucidate if the negative effects of
395 304 temperature on insects may cause a decreased in the activity of insectivorous bats and how
396 305 habitat structure affects its foraging behaviour in Monteverde.

397 306 **Conclusions**

398 307 We found that patterns of activity and diversity for aerial insectivorous bats in Monteverde
399 308 differed from other tropical mountains where the wettest-warmest conditions are inversely
400 309 correlated with elevation (McCain 2007). Highest activity and diversity of bats occurred at
401 310 mid-elevations and was partially explained by temperature with elevational, temporal and
402 311 species-specific differences. However due to habitat disturbances under 600 m a.s.l. we did
403 312 not sample lower elevations. Those differences, as previously suggested for temperate
404 313 regions (Hayes 1997, Bender and Hartman 2015) may be a result of changes in the
405 314 availability of food resources. However, it is unknown how local temperature changes
406 315 impact the insects consumed by bats in Monteverde. Studies with other animal groups (like
407 316 birds, lizards and frogs) showed that regional climate changes linked to changes on land use
408 317 (e.g. deforestation of lowlands) affect cloud formation and precipitation regimes with
409 318 negative ecological implications (Pounds et al. 1999, Nair et al. 2003). It will be necessary
410 319 to explore how cloud and precipitation regimes, as well as the effect of wind together with
411 320 air temperature, influence the activity and occurrence of aerial insectivorous bats in
412 321 Monteverde.

413 322 **Acknowledgements**

414 323 We thank the Tropical Science Center for all the support provided, especially to the Investigation
415 324 Program, and the Spanish Agency for International Development Cooperation (AECID) funding
416 325 projects D/027406/09, D/033858/10 and A1/039089/11. We are very grateful to Julio Madriz for his
417 326 field assistance.

419 327 **References**

420 328 Barclay R.M.R., 1991. Population structure of temperate zone insectivorous bats in relation
421 329 to foraging behavior and energy demand. *J. Anim. Ecol.* 60: 165–178.

422 330 Barry R.G., 1992. Mountain weather and climate. Routledge, London.

423 331 Bender M.J., Hartman G.D., 2015. Bat activity increases with barometric pressure and
424 332 temperature during autumn in Central Georgia. *Southeast. Nat.* 14: 231-242.
425 333 doi.org/10.1656/058.014.0203

426 334 Boonman A., Boonman M., Bretschneider F., van de Grind W., 1998. Prey detection in
427 335 trawling insectivorous bats: duckweed affects hunting behaviour in daubenton's bat,
428 336 *Myotis daubentonii*. *Behav. Ecol. Sociobiol.* 44(2): 99-107.

429 337 Chao A., Gotelli N., Hsieh T.C., Sander E.L., Ma K.H., Colwell R.K., Ellison A.M., 2014.
430 338 Rarefaction and extrapolation with Hill numbers: a framework for sampling and
431 339 estimation in species diversity studies. *Ecol. Monograph.* 84: 45-67.

432 340 Ciechanowski M., Zając T., Biłas A., Dunajski R., 2007. Spatiotemporal variation in
433 341 activity of bat species differing in hunting tactics: effects of weather, moonlight,
434 342 food abundance, and structural clutter. *Can. J. Zool.* 85: 1249-1263.
435 343 doi:10.1139/Z07-090

436 344 Cryan P.M., Bogan M.A., Altenbach J.S., 2000. Effect of elevation on the distribution of
437 345 female bats in the Black Hills, South Dakota. *J. Mammal.* 81: 719-725.

438 346 Curran M., Kopp M., Beck J., Fahr J., 2012. Species diversity of bats along an altitudinal
439 347 gradient on Mount Mulanje, southern Malawi. *J. Trop. Ecol.* 28: 243-253.

- 441 348 Echeverría-Tello J.L., 2013. Ensembles de murciélagos frugívoros y nectarívoros en un
442 349 gradiente altitudinal de Costa Rica y su potencial distribución bajo escenarios de
443 350 cambio climático. Tesis de maestría en ciencias, CATIE, Turrialba, Costa Rica.
- 444 351 Esbérard C.E.L., Lima I.P., Nobre P.H., Althoff S.L., Jordão-Nogueira T., Dias D.,
445 352 Carvalho F., Fabián M.E., Sekiama M.L., Sobrinho A.S., 2011. Evidence of vertical
446 353 migration in the Ipanema bat *Pygoderma bilabiatum* (Chiroptera: Phyllostomidae:
447 354 Stenodermatinae). *Zool.* 28: 717-724. doi.org/10.1590/S1984-46702011000600004
- 448 355 Fenton B.M., 1997. Science and the conservation of bats. *J. Mammal.* 78: 1-14.
- 449 356 Fenton B.M, Portfors C.V., Rautenbach I.L., Waterman J.M., 1998. Compromises: sound
450 357 frequencies used in echolocation by aerial-feeding bats. *Can. J. Zool.* 76: 1174-
451 358 1182.
- 452 359 Fleming T.H., 1986. Opportunism versus specialization: the evolution of feeding strategies
453 360 in frugivorous bats. In: Estrada A., Fleming T.H. (Eds.) *Frugivores and seed*
454 361 *dispersal*. Dr. W. Junk Publishers, Dordrecht, The Netherlands. 1105-1118.
- 455 362 Fleming T.H., Hooper E.T., Wilson D.E., 1972. Three central american bat communities:
456 363 structure, reproductive cycles and movement patterns. *Ecology* 4: 555-569.
- 457 364 Frank T.M., Gabbert W.C., Chaves-Campos J., LaVal R.K., 2018. Impact of artificial lights
458 365 on foraging of insectivorous bats in a Costa Rican cloud forest. *J. Trop. Ecol.*
459 366 <https://doi.org/10.1017/S0266467418000408>.
- 460 367 Fox, J., Weisberg, S., 2019. *Companion to Applied Regression*. Sage, Thousand Oaks,
461 368 Canada
- 462 369

- 464 370 Grindal S.D., Morissette J.L., Brigham R.M., 1999. Concentration of bat activity in riparian
465 371 habitats over an elevational gradient. *Can. J. Zool.* 77: 972-977.
- 466 372 Hanson P. 2014. Insects and spiders. In: Nadkarni N.M., Wheelwright N.T. (Eds.)
467 373 Monteverde: Ecology and conservation of a tropical cloud forest. Oxford University
468 374 Press, New York. 223-244.
- 469 375 Hayes J.P., 1997. Temporal variation in activity of bats and the design of echolocation-
470 376 monitoring studies. *J. Mammal.* 78(2): 514-524.
- 471 377 Heaney L.R., 2001. Small mammal diversity along elevational gradients in the Philippines:
472 378 an assessment of patterns and hypotheses. *Glob. Ecol. Biogeogr.* 10: 15-39.
- 473 379 Hsieh T.C., Ma K.H., Chao A., 2016. iNEXT: iNterpolation and EXTrapolation for species
474 380 diversity. R package version 2.0.12
475 381 URL: <http://chao.stat.nthu.edu.tw/blog/software-download/>.
- 476 382 Janzen D., Hallwachs W., 2019. Perspective: Where might be many tropical insects? *Biol.*
477 383 *Conserv.* 233: 102-108. <https://doi.org/10.1016/j.biocon.2019.02.030>.
- 478 384 Jost L., 2006. Entropy and diversity. *Oikos* 113(2): 363-375.
- 479 385 Jung K., Kalko E.K.V., 2010. Where forest meets urbanization: foraging plasticity of aerial
480 386 insectivorous bats in an anthropogenically altered environment. *J. Mammal.* 91:
481 387 144-153.
- 482 388 Jung K., Kalko E.K.V., Helversen O., 2007. Echolocation calls in Central American
483 389 emballonurid bats: signal design and call frequency alternation. *J. Zool.* 272: 125-
484 390 137

- 486 391 Jung K., Molinari J., Kalko E.K.V., 2014. Driving factors for the evolution of species-
487 392 specific echolocation call design in new world free-tailed bats (Molossidae).
488 393 PLoSONE 9(1): e85279.
- 489 394 Kalko E.K.V., Schnitzler H.U., 1998. How echolocating bats approach and acquire food.
490 395 In: Kunz T.H., Racey P.A. (Eds.) Bat. Biology and Conservation. Washington,
491 396 London: Smithsonian Institution Press. 197-204.
- 492 397 LaVal R.K., 2004. Impact of global warming and locally changing climate on tropical cloud
493 398 forest bats. *J. Mammal.* 85: 237-244. doi.org/10.1644/BWG-016
- 494 399 Laval R.K., Rodriguez-H B., 2002. Murciélagos de Costa Rica. 1st ed. Santo Domingo de
495 400 Heredia, Costa Rica (Instituto Nacional de Biodiversidad, INBIO). 320 p.
- 496 401 Linden V.M.G., Weier S.M., Gaigher I., Kuipers H.J., Weterings M.J.A., Taylor P.J., 2014.
497 402 Changes of bat activity, species richness, diversity and community composition
498 403 over an altitudinal gradient in the Soutpansberg range, South Africa.
499 404 *ActaChiropterol.* 16: 27-40. doi.org/10.3161/150811014X683246
- 500 405 Lomolino M.V., 2001. Elevation gradients of species-density: historical and prospective
501 406 views. *Glob. Ecol. Biogeogr.* 10: 3-13.
- 502 407 McCain C.M., 2004. The mid-domain effect applied to elevational gradients: species
503 408 richness of small mammals in Costa Rica. *J. Biogeogr.* 31: 19-31.
- 504 409 McCain C.M., 2007. Could temperature and water availability drive elevational species
505 410 richness patterns? A global case study for bats. *Glob. Ecol. Biogeogr.* 16: 1-13.

- 507 411 McCain C.M., Grytnes J.A., 2010. Elevational gradients in species richness. In:
508 412 Encyclopedia of Life Sciences. John Wiley & Sons, Ltd, Chichester, UK. 1-10.
509 413 doi.org/10.1002/9780470015902.a0022548
- 510 414 McNab B.K., 1982. Evolutionary alternatives in the physiological ecology of bats. In: Kunz
511 415 T.H. (Eds.) Ecology of bats. Plenum Publishing Corporation, New York. 151-196.
- 512 416 Mena J.L., Solari S., Carrera J.P., Aguirre L.F., Gómez H., 2011. Small mammal diversity
513 417 in the tropical Andes: an overview. In: Herzog S.K., Martínez R., Jørgensen P.M.,
514 418 Tiessen H. (Eds.) Climate change and biodiversity in the tropical Andes. Inter-
515 419 American Institute for Global Change Research (IAI) and Scientific Committee on
516 420 Problems of the Environment (SCOPE).260-275.
- 517 421 Müller J., Mehr M., Bässler C., Fenton M.B., Hothorn T., Pretzsch H., Klemmt H.J., Brandl
518 422 R., 2012. Aggregative response in bats: prey abundance versus habitat. *Oecologia*
519 423 169:673-84. doi: 10.1007/s00442-011-2247-y.
- 520 424 Nadkarni N.M., Wheelwright N.T., 2014. Monteverde: ecology and conservation of a
521 425 tropical cloud forest. Updated Chapters. Oxford University Press, New York.
- 522 426 O'Donnell C.F.J., 2000. Influence of season, habitat, temperature, and invertebrate
523 427 availability on nocturnal activity of the New Zealand Long-tailed Bat (*Chalinolobus*
524 428 *tuberculatus*). *New Zeal. J. Zool.* 27: 207-221.
- 525 429 Ochoa J., O'Farrell M.J., Miller B.W. 2000. Contribution of acoustic methods to the study
526 430 of insectivorous bat diversity in protected areas from northern Venezuela. *Acta*
527 431 *Chiropterol.* 2(2): 171-183.

- 529 432 O'Farrell M.J., Miller B.W., 1999. Use of vocal signatures for the inventory of free-flying
530 433 Neotropical bats. *Biotropica* 31(3): 507-516.
- 531 434 O'Farrell M.J., Gannon W.L., 1999. A comparison of acoustic versus capture techniques
532 435 for the inventory of bats. *J. Mammal.* 80: 24-30. doi.org/10.2307/1383204
- 533 436 Ortiz-Badillo R.M., 2015. Diversidad de murciélagos en un gradiente altitudinal en el
534 437 estado de Nuevo León, México. Tesis de Maestría, Facultad de Ciencias Forestales.
- 535 438 Patterson B.D., Meserve P.L., Lang B.K., 1989. Distribution and abundance of small
536 439 mammals along an elevational transect in temperate rainforests of Chile. *J.*
537 440 *Mammal.* 70: 67-78.
- 538 441 Patterson B.D., Pacheco V., Solari S., 1996. Distribution of bats along an elevational
539 442 gradient in the Andes of southeastern Peru. *J. Zool. (London).* 240: 637-658.
- 540 443 Piksa K., Bogdanowicz W., Tereba A., 2011. Swarming of bats at different elevations in
541 444 the Carpathian Mountains. *Acta Chiropterol.* 13: 113–122.
- 542 445 Pounds J.A., Fogden M.P.L., Campbell J.H., 1999. Biological response to climate change
543 446 on a tropical mountain. *Nature* 398: 611-615.
- 544 447 Refulio S.M., 2015. Diversidad de murciélagos a lo largo de una gradiente altitudinal en las
545 448 Yungas de la cuenca del río Pampa Hermosa Junín, Perú. Tesis para optar al título
546 449 profesional de Biólogo con mención en Zoología. Universidad Nacional Mayor de
547 450 San Marcos Facultad de Ciencias Biológicas.
- 548 451 Rydell J., Arita H.T., Santos M., Granados J., 2002. Acoustic identification of insectivorous
549 452 bats (Order Chiroptera) of Yucatan, Mexico. *J. Zool.* 257(1): 27-36.

- 551 453 Sánchez-Cordero V., 2001. Elevation gradients of diversity for rodents and bats in Oaxaca,
552 454 Mexico. *Glob. Ecol. Biogeogr.* 10: 63-76.
- 553 455 Schenker N., Gentleman J. 2001. On Judging the Significance of Differences by Examining
554 456 the Overlap Between Confidence Intervals. *Am. Stat.* 55: 182-186.
- 555 457 Timm R.M., LaVal R.K., 2014. Mammals. In: Nadkarni N.M., Wheelwright N.T. (Eds.)
556 458 Monteverde: Ecology and conservation of a tropical cloud forest. Oxford University
557 459 Press, New York. 223-244.
- 558 460 Thomas D.W., 1988. The distribution of bats in different ages of Douglas-fir forests. *J.*
559 461 *Wildl. Manage.* 52: 619-626.
- 560 462 Vaughan N., Jones G., Harris S., 1997. Habitat use by bats (Chiroptera) assessed by means
561 463 of a broad-band acoustic method. *J. Appl. Ecol.* 34: 716-730.
- 562 464 Weier S.M., Linden V.M.G., Gaigher I., White P.J.C., Taylor P.J., 2016. Changes of bat
563 465 species composition over altitudinal gradients on northern and southern aspects of
564 466 the Soutpansberg mountain range, South Africa. *Mammalia* 81: 49-60.
565 467 doi:10.1515/mammalia-2015-0055
- 566 468 Wolbert S.J., Zellner A.S., Whidden H.P., 2014. Bat activity, insect biomass, and
567 469 temperature along an elevational gradient. *Northeast. Nat.* 21: 72-85.
568 470 doi.org/10.1656/045.021.0106

Manuscript body

[Download source file \(388.5 kB\)](#)

Supplementary Online Material

File 1 - [Download source file \(2.21 MB\)](#)

File 2 - [Download source file \(20.8 kB\)](#)