#### **ORIGINAL ARTICLE**



# Effect of environmental gradients on community structuring of aerial insectivorous bats in a continuous forest in Central Amazon

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#### Abstract

Biotic and abiotic environmental factors influence the abundance and spatial distribution of species and the structuring of communities along environmental gradients. Topography, vegetation structure and food availability have been identified as factors that directly and indirectly influence habitat selection by species in tropical forests. Although the factors that determine community structure in phyllostomid bats have received substantial attention, aerial insectivorous bats have been largely neglected, and their responses to environmental gradients in continuous tropical forests remain poorly understood. In this study, we evaluated how aerial insectivorous bats respond to different environmental gradients in 25 km<sup>2</sup> of continuous preserved forest in Central Amazonia. Our hypothesis was that topography, vegetation structure and food availability influence aerial insectivorous bats. Insect biomass was shown to be the predictor variable with the greatest contribution to the bat species richness, abundance and assemblage composition. Bat activity and richness were positively related to insect biomass. Bat assemblage species composition was also related to terrain elevation and insect assemblage composition. Vegetation clutter did not influence the number of species, abundance and bat assemblage species composition. In contrast, vegetation clutter and terrain elevation influenced some bat species, indicating that the response to these variables was species-specific within the bat assemblage. Our study showed that the food availability, both the quantity and its distribution in the environment, was the main structuring factor of the bat community that occupy higher trophic levels, such as aerial insectivorous bats, in a continuous forest in Central Amazon.

Keywords Bat assemblages · Chiroptera · Ecological gradients · Food availability · Topography · Vegetation structure

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# Introduction

The spatial distribution of animal species in the environment does not occur at random, and individuals select the habitat according to their biological requirements (Rosenzwieg 1981; Stein et al. 2014). The preference for certain locations influences the abundance of populations and the structuring of assemblages (Doebeli and Dieckmann 2003; Michelot et al. 2019; Stein and Kreft 2015). Biotic and abiotic environmental factors determine assemblage structural patterns (Chesson 2000; Guo et al. 2013). At a local scale, the abiotic elements of the environment are represented by topographic and climatic gradients, while biotic components include vegetation structure, food availability and species interactions (Stein et al. 2014; Stein and Kreft 2015). As a result, environmental gradients may influence the abundance and distribution of species in a landscape (Tuomisto et al. 2014).

Topography, vegetation structure and food availability have been identified as factors that directly and indirectly influence habitat selection by species in tropical forests (Capaverde et al. 2018; Cintra and Naka 2012; Kinap et al. 2021). Changes in elevation can affect species distribution, at both wide scales of mountain ranges (>1000 m a.s.l.) and in locations with less pronounced topographic change (<100 m a.s.l.) (Carvalho et al. 2022; Dias-Terceiro et al. 2015; Willig and Presley 2016). In smaller elevation gradients (<100 m a.s.l.), terrain elevation is correlated with soil edaphic factors such as fertility, texture and water table depth, and this influences plant composition directly (Pansonato et al. 2013). Additionally, plant species distribution directly influences the assemblages of herbivorous animals that feed on leaves, sap, fruits and nectar (Jefferies et al. 1994). Changes in small elevation gradient can also influence the food chain, especially when carnivorous/ insectivorous animals respond to variation in prey distribution that also has its distribution associated with elevation (McCain 2007). Plant assemblage species composition also determines vegetation structure, which then influences the level of three-dimensional clutter and obstruction to animal movements (Capaverde et al. 2018; Oliveira et al. 2015). Habitat use by animal species will depend on their adaptive responses to the level of vegetation clutter, which consequently influences the movement of animals in a given forest (Bobrowiec and Tavares 2017; Fraga et al. 2018). In tropical forests, bottom lands and areas close to watercourses generally form corridors that are less obstructed, while neighboring elevated areas may have denser vegetation (Costa et al. 2009; Pansonato et al. 2013). Comparisons of such areas provide an understanding of how the configuration of different environmental gradients may structure local animal assemblages.

The diversity of physical forms, morphological adaptations and feeding habits means that bats respond to processes structuring assemblages at the local scale (Capaverde et al. 2018; Bobrowiec et al. 2022; Colombo et al. 2022; Ferreira et al. 2023). Knowledge of the relationship between bats and abiotic and biotic variables has been most thoroughly studied in bats of the family Phyllostomidae, members of which are mostly frugivores, nectarivores or gleaning insectivores (the latter hunting insects perched on solid surfaces) (Bobrowiec et al. 2014; Capaverde et al. 2018; Marciente et al. 2015). The distribution of frugivorous and nectarivorous bats is directly associated with plant composition and vegetation structure, as they fly long distances to find the plant resources they consume (Jung et al. 2012; Lobova et al. 2009). Such bats are more common in areas with open vegetation and close to streams (Bobrowiec et al. 2014; Marciente et al. 2015; Pereira et al. 2019), while gleaning insectivores are indirectly influenced by the composition of insects associated with the closed vegetation structure away

from streams (Dechmann et al. 2011; Schnitzler and Kalko 2001), an association facilitated by adaptation for more highly maneuverable flight patterns (Capaverde et al. 2018; Marciente et al. 2015).

However, neotropical aerial insectivorous bats have been largely neglected, and the few studies that evaluated how environmental factors explain their distribution and abundance have been conducted in impacted environments (Colombo et al. 2022; Estrada-Villegas et al. 2010; Núñez et al. 2019). These bats have echolocation calls specialized for in-flight hunting of insects and so easily detect and avoid mist nets, which makes their capture difficult (Denzinger and Schnitzler 2013; MacSwiney et al. 2008). The use of ultrasound recorders has been recommended for sampling these bats in tropical forests (Appel et al. 2021a). Although the use of ultrasound recorders and the capacity to train personnel to identify bat species in the tropics has increased in recent years, knowledge of the factors determining the structuring of the aerial insectivorous bat species assemblage remains poor.

In this study, we evaluate how aerial insectivorous bats respond to different environmental gradients in 25 km<sup>2</sup> of continuous forest in Central Amazonia. Our hypothesis is that topography, vegetation structure and food availability influence aerial insectivorous bats. We propose that vegetation clutter and insect availability are the factors that most strongly determine the species composition of aerial insectivorous bat assemblages. We also expect that both the number of species and bat activity will be higher in upland areas where vegetation is more cluttered, and where the abundance and mass of insects is consequently higher (Oliveira et al. 2015) than in low-lying areas with more open vegetation.

## **Materials and methods**

#### Study area

The study was conducted in the Adolpho Ducke Forest Reserve (2°58' S; 59°55' W), located at Km 26 on the AM-110 highway, north of the city of Manaus, Amazonas State, Brazil (Fig. 1). The reserve is included in the Long-Term Ecological Research Program of the National Council for Scientific and Technological Development (PELD/ CNPq), and contains some 10,000 ha of *terra firme* forest. The dry season occurs from June to October and the rainy season from November to May. The average annual local temperature is 26 °C and rainfall varies between 1750 and 2500 mm (Ribeiro et al. 2002). The forest canopy varies from 30 to 35 m in height, with emergent trees reaching 50 m. The relief is irregular, with elevation variation from 45 to 140 m a.s.l. (76.67  $\pm$  20.56 m a.s.l., mean $\pm$  Standard Deviation).



Fig. 1 Location of the Adolpho Ducke Forest Reserve, and distribution of sampling plots within the PELD grid. Black circles on the PELD grid indicate riparian plots, and black squares indicate non-riparian plots

Bat sampling and the collection of predictor variables was carried out on the trail system that forms a grid of 25  $\text{km}^2$  (5×5 km) within the area of the reserve, which follows the RAPELD (Rapid Survey of Biological and Long-Term Ecological Survey) system (Magnusson et al. 2005) (Fig. 1). The grid has 30 permanent plots systematically spaced at 1 km intervals, and a further 19 riparian plots that follow the contours of local streams. Each plot is 250 m long and 40 m wide and follows local topographic contours to minimize internal heterogeneity of the physical, chemical and drainage properties of the soil (Magnusson et al. 2005). A total of 17 plots were sampled (seven riparian and 10 nonriparian) (Fig. 1). The distance between plots varied from 0.4 to 8.1 km. The recorders were installed in a temporal sequence to avoid proximity to each other (<1 km) and thus guarantee the independence of the recordings.

#### Sampling of aerial insectivorous bats

Aerial insectivorous bat activity was recorded using standalone recorders (Song Meter SM2BAT +), each with an SMX-US omnidirectional ultrasonic microphone (Wildlife Acoustics, Maynard, Massachusetts, USA). Recorders were installed in the center of the plots with microphones placed at a height of 1.5 m above the ground. Each recorder was programmed to passively record real-time bat activity via a16-bit full spectrum resolution with 1-s pre-trigger and 0.1-s post-trigger, "High Filter Pass" set to fs/32 (12 kHz) and a Trigger level of 18SNR. The SM2Bat + units were configured to record bats between 18:00 h and 06:00 h, giving a 12-h recording period per night during the 2013 rainy season (January to May). Each plot was sampled for four consecutive nights, a total of 53 sampling nights and 636 h of recording.

Bat passes were used as the sample units to quantify individual activity levels. A single pass was considered as any 5 s recording where two or more pulses characteristic of a bat species/sonotype were identified (Oliveira et al. 2015). Recordings were visualized using the Kaleidoscope 3.1.1 program (Wildlife Acoustics, Maynard, Massachusetts, USA). All species/sonotypes were identified by comparing the structure and frequency parameters of the echolocation pulses to the of bat ultrasounds reference library recorded by the Biological Dynamics of Forest Fragments Project (López-Baucells et al. 2016), located 40 km from the Ducke reserve, and also with data from the literature (Barataud et al. 2013; Briones-Salas et al. 2013; Jung et al. 2007; 2014). For sonotypes (species difficult to distinguish from only the calls), we used the same groups described by López-Baucells et al. (2016): Molossus II represent *Molossus currentium/rufus*; Vespertilionidae I represent *Lasiurus castaneus/ega/egregius*; Vespertilionidae II represent *Rhogeessa io/Lasiurus blossevillii* (Table S1). *Pteronotus rubiginosus* (identified as *P. parnellii* in Ducke Reserve by de Oliveira et al. 2015) was identified by the taxonomic and acoustic description proposed by Pavan et al. (2018) (calls with frequency peak of 55 kHz). Bat activity per plot was estimated from the sum of the number of passes per night (Oliveira et al. 2015).

#### Estimates of insect prey availability

Insects were sampled using light traps, that consisted of 20 cm diameter cones inserted into 100 ml plastic pots containing a 70% alcohol solution and detergent. To attract the insects, a flashlight with ten white LED bulbs was placed above the cone and pointed at it. Attracted insects were trapped in the plastic pot. Two light traps were installed in each plot, positioned along the plot centerline at 65 and 130 m from the recorder and placed at a height of 1.5 m from the ground. To estimate the total mass of insects collected in each plot, we combined six insect samples from each plot and identified the insects to Order (Capaverde et al. 2018). Insects were dried with filter paper to remove excess alcohol and individually weighed on a precision balance (reading limit 0.0001 g; Ohaus Discovery, Pine Brook, New Jersey) to estimate the total mass of insects captured in grams in each plot. We only included in the analyzes insect families consumed by aerial insectivorous bats such as Blattodea, Coleoptera, Diptera, Ephemeroptera, Homoptera, Hymenoptera, Isoptera, Lepidoptera, Mantodea, Orthoptera, Plecoptera and Trichoptera.

#### Measurement of understory-vegetation clutter

Vegetation clutter was estimated with the method proposed by Marsden et al. (2002), with the modifications suggested by Oliveira et al. (2015). Digital photographs were taken of a  $3 \times 3$  m white panel placed at 10 m intervals along a 250 m stretch of plot centerline (N=25 vegetation photographs per plot). The camera was positioned eight meters from the panel and perpendicular to it. The resulting photographs were converted to black (vegetation) and white, and the vegetation portion of the 25 photographs was estimated using Sidelook 1.1.01 software (Zehm et al. 2003). The vegetation clutter of each plot was calculated as the percentage of vegetation from the sum of all 25 photographic images.

#### Measurement of the topography

For each plot, elevation of the terrain was extracted using the Shuttle Radar Topographic Mission (SRTM) with 30 m resolution raster images provided by the Global Land Cover Facility (http://www.landcover.org). The geographic coordinates used to obtain the terrain elevation were measured at the midpoint of each plot, and the "Point Sampling Tool" of the Quantum Geographic Information System software version 2.2.0 (QGIS) was used to extract the terrain elevation values.

## **Data analysis**

The response variables number of species and activity of aerial insectivorous bats were related to the predictor variables terrain elevation, vegetation clutter, insect biomass and insect assemblage composition using Generalized Linear Mixed Model (GLMM) with Template Model Builder (TMB) in glmmTMB package (Brooks et al. 2017), with the distribution that best fit the regression models (Gaussian, Poisson or Negative Binomial). The types of plots (riparian and non-riparian) were used as a random variable in the GLMM to account for potential plot type effect. We compared the residual dispersion of GLMM to select for the family function with the best correction of the data dispersion in the DHARMa package (Hartig 2021). The most suitable model family of each GLMM are presented in Tables 1 and 2. Insect assemblage composition was represented by the first axis of a one-dimensional Non-Metric Multidimensional Scaling (NMDS) ordination using the 'metaMDS' function (k = 1, trymax = 5000) from the *vegan* package (Oksanen et al. 2014), with a Bray-Curtis dissimilarity index (variation explained of the species composition = 72%; Stress = 0.23). Total insect-abundance data were used for the NMDS ordination. Before running the GLMM, multicollinearity among the predictor variables was evaluated using the 'VIF' function of the *usdm* package (Naimi et al. 2014). No predictor variables had multicollinearity (VIF  $\geq 10$ , according to Naimi et al. 2014). We tested the residuals distribution, over/underdispersion and presence of outliers of each GLMM model using the 'simulateResiduals' function in the DHARMa package. No GLMM presented problems related to data dispersion. Species-specific GLMMs were undertaken for eight bat species as previously described: Centronycteris maximiliani, Cormura brevirostris, Myotis sp., Myotis riparius, Pteronotus rubiginosus, Saccopteryx bilineata, Saccopteryx leptura and Vespertilionidae I. To minimize potential detection problems, we selected only the species that had at least 200 records of ultrasound calls (Table S1). Species of the Molossidae family were excluded from the analysis, because they usually forage above the forest canopy, out of reach of recorders. The marginal

	$R^{2}m$						,	100		Р		2	P 050 0		
		I R <sup>2</sup> c	N	Р	HP (%)	2	Ч	(%) 'HH	N		HP (%)		0.000	HP (%)	
Activity Richness Species composition	0.49 0.35	0.35	1.60 -0.14 <b>6.54</b>	0.11 0.90 <b>0.001</b>	10.3 4.0	-1.90 -1.50 4.50	0.058 0.14 0.09	10.1 19.9	3.54 2.54 7.41	<pre>&lt; 0.000 &lt; 0.011 0.011</pre>	1 74.5 55.1	-1.82 1.20 <b>7.90</b>	0.24 0.001	5.2 21.0	NB2 Gaussian
$R^2$ m is the marginal tioning of the richne with $P < 0.05$ annear	variance ss and act	explained tivity are	by the fixed shown. As 1	d variable: the multiv	s and R <sup>2</sup> c is th ariate analyze	ne conditio s for speci	nal varian es compos	ce explained sition do not	l by the er generate	ntire model. I an explanati	Independent $\epsilon$ on of the vari	xplanator iance, thes	y power (HF e results are	) based on hi not presente	erarchical parti 1. Relationship
NB2 Negative binon	nial distril	bution: qu	adratic par	ameterizati	ion										
<b>Table 2</b> Result of thinsect assemblage spect	ne GLMN Decies con	1 for the 1 nposition	relationship	between	the activity o	f aerial in	sectivorou	is bat specie	s and the	predictor va	triables terrai	in elevatio	n, vegetation	n clutter, inse	et biomass and
Species	Varian explain	ce led	Terrain e	levation		Vegetatio	n clutter		Insect t	iomass		Insect ass	smblage con	aposition	Model family
	R <sup>2</sup> m	$R^2c$	N	Ρ	HP (%)	2	Р	HP (%)	N	Р	HP (%)	2	Ρ	HP (%)	
C. maximiliani	0.32	0.32	- 1.30	0.21	20.0	1.10	0.30	7.3	0.10	1.03	1.1	3.00	0.003	71.6	NB1
C. brevirostris	0.49	0.49	- 1.00	1.00	18.4	-0.50	0.62	1.0	1.92	0.054	6.1	-3.31	0.004	74.5	NB2
<i>Myotis</i> sp.	0.96	0.96	0.53	0.60	14.9	-1.00	0.40	1.5	0.14	1.00	0.5	-4.10	< 0.0001	83.1	NB2
M. riparius	0.56	0.56	4.21	0.005	42.5	-3.04	0.003	38.0	2.50	0.013	17.5	-1.20	0.25	2.0	NB2
P. rubiginosus	0.51	0.51	1.03	0.41	3.5	1.00	0.44	18.2	3.35	0.0002	76.5	-1.00	0.35	1.8	NB1
S. bilineata	0.34	0.34	2.02	0.10	8.9	-0.22	1.03	4.8	3.00	0.004	81.3	0.23	1.00	5.1	NB1
S. leptura	0.54	0.54	1.14	0.25	6.2	-2.20	0.05	7.1	1.03	0.30	1.8	-4.15	< 0.0001	84.8	NB2
Vesnertilionidae I	0.53	0.53	3.01	0.005	48.3	-2.60	0.001	26.5	4.00	0.000	23.2	-1.00	0.50	2.1	NB2

(variance explained by the fixed variables) and conditional (variance explained by the entire model) variance explained by the predictor variables in a GLMM was calculated using 'r.squaredGLMM' function in *MuMIn* package (Walsh and MacNally 2013). The independent contributions of each explanatory variable were estimated using hierarchical partitioning as implemented in the *hier.part* package (MacNally and Walsh 2004).

To evaluate potential spatial autocorrelations between our sampling plots, we checked correlation between GLMM residuals using Moran's I statistics in SAM v4.0 software (Rangel et al. 2010). We adjusted the number of distance classes in the correlograms to the equal distance between sampling plots. Seven distance classes were used (0.58, 1.75, 2.91, 4.08, 5.24, 6.40, 7.57 km). Each Moran's I value was tested for significance by 1000 permutations. No response variable showed spatial autocorrelation of GLMM residuals.

The species composition of the aerial insectivorous bats was related to the predictor variables described above using a multivariate extension of the generalized linear models of the 'manyglm' function (Warton et al. 2012), using Negative Binomial distribution with quadratic parameterization in the mvabund package (Wang et al. 2012, 2020). This approach allowed hypotheses testing without confounding location with dispersion effects in a multivariate space, which could inflate type I and II errors (Warton et al. 2012). The effect of each predictor variable was evaluated using the 'anova. manyglm' function from the mvabund package, based in Monte-Carlo fitted model resampling and Wald test. P values were adjusted for multiple tests with 999 bootstrap iterations. The 'manyglm' and 'anova.manyglm' functions (or any other multivariate analysis for species composition) do not incorporate random variables like the GLMM tests used previously. All statistical analyzes, except spatial autocorrelation, were performed using R 4.2.2 (R Core Team 2022).

## Results

We recorded 10,019 calls of aerial insectivorous bats, belonging to 20 bat species and six bat families (Table S1). Most records and species came from to the family Emballonuridae (4916 records; 9 species), which represented 49% of all records and 45% of species. Four species had more than a thousand activity records each (*Pteronotus rubiginosus, Saccopteryx bilineata, Cormura brevirostris* and *Myotis riparius*). Seven species were recorded in more than half the plots, and three species occurred in all plots (*C. brevirostris, S. bilineata* and *P. rubiginosus*) (Table S1).

Insect biomass ranged from 0.017 to 0.778 g  $(0.23 \pm 0.20 \text{ g}, \text{mean} \pm \text{Standard Deviation})$ , terrain elevation ranged from 56.4 to 121.8 m  $(83.7 \pm 22.0 \text{ m})$ , and vegetation clutter values ranged from 50.7 to 69.2%  $(58.8 \pm 6.2\%)$ 

(Table S2). Insect biomass was the predictor variable with the greatest contribution to bat activity, species richness, and bat species composition (Table 1). Bat activity and species richness were positively related to insect biomass (Table 1; Fig. 2). Bat species composition was related to terrain elevation (Fig. 3) and insect assemblage composition (Table 1). *Centronycteris maximiliani, Peropteryx macrotis, P. trinitatis, Saccopteryx gymnura, S. bilineata, Furipterus horrens, P. rubiginosus* and *Eptesicus brasiliensis* showed greatest activity in the plots with greatest abundance of insects of the orders Homoptera, Coleoptera, Diptera and Hymenoptera (Fig. 4). Vegetation clutter influenced neither the activity, richness nor species composition of the sampled aerial insectivorous bats (Table 1).

Myotis riparius, P. rubiginosus and S. bilineata were positively influenced by insect biomass (Table 2). Altitude positively influenced M. riparius and Vespertilionidae I (Table 2). Vegetation clutter negatively influenced M. riparius, S. leptura and Vepertilionidae I (Table 2). Insect



Fig. 2 Relation between insect mass and species richness (A) and aerial insectivorous bat activity (search-phase calls per night) (B) in a continuous forest in Central Amazon. Grey areas around linear trend lines represent 95% confidence intervals



**Fig. 3** Distribution of aerial insectivorous bat species activity in relation to insect biomass gradient in a preserved continuous forest in Central Amazonian, Brazil. The columns represent the amount of activity of each bat species in the sampling plot. The horizontal order of the sampling plots was based on the insect biomass gradient. The vertical order of species was based on bat activity along the insect biomass gradient, in which the species with more activity in plots with the highest insect biomass are positioned near the top of the graph, while the species with more activity in plots with the lowest insect biomass are placed near the bottom. Once the activity value of each species is on a different scale, it is not possible to make a direct comparison among species

assemblage composition influenced the species *C. maximiliani*, *C. brevirostris*, *Myotis* sp. and *S. leptura* (Table 2).

### Discussion

Our results showed that in continuous forests the aerial insectivorous bat assemblage was structured mainly by food availability. Bats were more active and there were more species in areas with greater insect biomass. Bat assemblage species composition was also influenced by insect assemblage composition and terrain elevation. In contrast, vegetation clutter and terrain elevation influenced relatively few aerial insectivorous bat species, indicating that the response to these variables was species-specific within the bat assemblage.

Our findings mirror previous studies that also identified insect biomass as a determining factor in the spatial distribution of aerial insectivorous bats (Fukui et al. 2006; Hagen and Sabo 2011; Lloyd et al. 2006). Bats of the genus *Myotis* show greater foraging activity near streams where the abundance of adult aquatic insects is higher (Fukui et al. 2006), while the distribution of *M. evotis* and *M. thysanodes* has been shown to be associated with the abundance of larger, non-aquatic, insects (Lepidoptera, Coleoptera and Hemiptera) (Ober and Hayes 2008). The size of the insects, an attribute that is related to the overall biomass of insects recorded in a location, is also an important aspect in the diet





**Fig. 4** Distribution of aerial insectivorous bat species activity (**A**) and abundance of insect orders consumed by bats (**B**) in relation to the first NMDS axis of insect composition. The columns represent the amount of activity of each bat species and abundance of each insect order in the sampling plot. As the two distributions are ordered by the

same variable (NMDS 1 axis of insect composition), the horizontal order of the sampling modules is the same in both graphs. Thus, it is possible to verify whether the activity of bat species coincides with the abundance of insect orders

of bats. The larger the prey, the fewer individuals need to be consumed for the bat to meet the per night energy requirement (Akasaka et al. 2009; Pyke 1984). Greater size of individual prey also allows the selection of more nutritious items and of those sites with a greater energy return (Abreu et al. 2010; Schoener 1974).

As with a number of other studies, the current investigation demonstrated that insect assemblage species composition also acts as a factor that modulates the distribution and abundance of aerial insectivorous bats (Barclay 1991; Fukui et al. 2006; Gonçalves et al. 2013; O'Donnell 2000; Salvarina et al. 2018). Bat spatial distribution was linked to the locations of greatest preferred prey abundance, as in the species P. rubiginosus which mainly consumes Hemiptera, Diptera, Coleoptera and Hymenoptera (Emrich et al. 2014), forms which are more abundant in the plateau areas of Amazonian continuous forests (Oliveira et al. 2015). In the plots sampled in this study, bats such as P. rubiginosus and four species of the Vespertilionidae family (Vespertilionidae I, Vespertilionidae II, M. riparius and Eptesicus brasiliensis) were more active in plots with greater abundance of insects in the orders Diptera and Coleoptera. Although this does not guarantee that the insects sampled are those consumed by these bats, the observed relationship is an indication of an association between the distribution of bats and their potential prey. These four bat species are specialists on those insect orders (Brigham and Saunders 1990; Ober and Hayes 2008; Syme et al. 2001). For example, 65% of the diet of Eptesicus fuscus may consist of Coleoptera (Brigham and Saunders 1990), while species of the genus tropical Myotis have a diet concentrated in Diptera, Coleoptera and Lepidoptera (Whitaker 2004). Species of the family Emballonuridae P. macrotis and S. bilineata have a diet based on Coleoptera and Diptera (Bradbury and Vehrencamp 1976), while S. leptura consumes large volumes of Hymenoptera (Nogueira et al. 2002; Schnitzler and Kalko 2001).

Unlike aerial insectivorous bats, gleaning insectivorous bat assemblage structure in the same study area was not determined by insect biomass and insect assemblage composition (Capaverde et al. 2018). This indicates that the two insectivorous bat guilds respond differently to food distribution. The difference in foraging mode, wing morphology and characteristics of the echolocation call of these two groups of bats may influence their relationship with the distribution of prey insects (Capaverde et al. 2018; Oliveira et al. 2015). Gleaning insectivorous bats search for potential prey by listening to the sounds generated by arthropods on vegetation and on the ground, and the echolocation call is frequency modulated, a type which is effective in dense and cluttered vegetation (Arlettaz et al. 2001; Schnitzler and Kalko 2001). In contrast, aerial insectivorous bats capture their prey in mid-air during flight. Consequently, their echolocation signals are more variable, with most species having a constant or quasiconstant frequency signal (Kalko and Schnitzler 1998; López-Baucells et al. 2016). In addition, wings of aerial insectivores are adapted to more maneuverable forms of flight than gleaning insectivorous bats, possibly due to the greater maneuverability of their prey that are captured inflight (Marinello and Bernard 2014). Wing characteristic and echolocation forms provide aerial insectivorous bats with greater maneuverability in dense vegetation environments. As a result, the space distribution of the gleaning insectivorous bats is more influenced by vegetation clutter (Capaverde et al. 2018; Caras and Korine 2009; Marciente et al. 2015), while aerial insectivorous bats are more influenced by the quantity and distribution of prey (Hagen and Sabo 2014; Oliveira et al. 2015).

Areas with more cluttered vegetation may decrease the bats' ability to maneuver and forage for insects compared to less obstructed areas (Marciente et al. 2015). However, in the current study, between-plot variation in vegetation clutter (46.6–69.2%) was not enough to influence bat activity, or the number and composition of species present. Aerial insectivorous bats have a higher aspect ratio and relative wing loading resulting in greater maneuverability in flight than fruiteating and nectarivorous bats (Marinello and Bernard 2014), allowing them to use forests with a high level of vegetation clutter (Schnitzler and Kalko 2001). However, a response at assemblage-level may not be matched by the response at species level; in the current study, members of the Vespertilionidae family (especially Myotis. sp.) and S. leptura avoided areas of highly obstructed vegetation. However, our estimate of vegetation clutter is limited to the understory (up to 3 m in height) and measurements of canopy vegetation may provide new information on the effects of vertical forest structure on bats distribution.

Terrain elevation positively influenced the activity of three species of aerial insectivorous bats (*M. riparius* and Vespertilionidae I). *Myotis riparius* is identified as a slow-flying species (Norberg and Rayner 1987). Since plateau areas have a higher level of vegetation clutter than the vegetation in areas close to streams (Oliveira et al. 2015), it is possible that this species is avoiding more open areas and with it a greater risk of predation (Appel et al. 2021b). In addition, the elevation has a direct and positive relationship on insect biomass in Ducke reserve (Capaverde et al. 2018), creating habitats that favor foraging by these species (Tre-itler et al. 2016).

Our study showed that the aerial insectivorous bat community of a continuous tropical forest was structured by food availability. In addition, the variables terrain elevation and vegetation obstruction also influence the distribution and activity of aerial insectivorous bats at the species level. Future studies may include a functional approach to understand which species traits can explain their relationship with environmental variables (Colombo et al. 2022; Ferreira et al. 2023).

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Author contributions Conceptualization: PEDB; designed this study: PEDB, WEM; field data collection: LQO, PEDB; ultrasound data analysis: GA, AL-B; statistical analysis: PEDB, RCCC; writing—original draft preparation: RCCC, PEDB, GA; writing—review and editing: all authors; funding acquisition: WEM, PEDB; supervision: PEDB. All authors gave final approval for publication.

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**Data availability** The raw data used during this study are available upon request to corresponding author and study supervisor Paulo Estefano D. Bobrowiec.

#### Declarations

**Conflict of interest** On behalf of all authors, the corresponding authors states that there is no conflict of interest.

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