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Exploring the effects of climatic and environmental heterogeneity on the spatial activity of Patagonian bats

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Abstract

Background The Patagonian region hosts endemic bat species and represents the southernmost distribution limit for several vespertilionids and molossids species. In cold temperate regions, insectivorous bats are more active during summer. However, during this period, the activity of bats can also vary spatially, depending on climatic and environmental factors (e.g., temperature, humidity, vegetation cover, productivity, elevation, proximity to water). The objective of this study was to analyze how the spatial activity of phonic groups is affected by climatic and environmental variables in a large, heterogeneous area of Patagonia, Argentina, using bioacoustic methods. Acoustic monitoring was conducted during the austral summer of 2020, at 100 points located at ten sites, in three ecoregions of Chubut Province (Patagonian Forest, Patagonian Steppe and Low Monte). Bat passes were classified into four phonic groups (PGs), each representing species with similar echolocation call structures. This classification was based on foraging habits and bioacoustic characteristics of species commonly recorded in the study area (PG1 = *Myotis chiloensis*, *M. levis*; PG2 = *Lasiurus varius*, *L. villosissimus*, *Histiotus magellanicus*; PG3 = *H. macrotus*, *H. montanus*; PG4 = *Tadarida brasiliensis*). The values of eleven variables were obtained for each point (e.g., temperature, relative humidity, vegetation cover, productivity, elevation, and proximity to water). Using generalized linear mixed-effects models (GLMMs), we analyzed how climatic and environmental variables influenced the spatial activity of Patagonian bat phonic groups.

Results Our results showed that spatial activity of four phonic groups analyzed in summer is driven by environmental (vegetation cover, elevation and proximity to water) and climatic variables (temperature and relative humidity). Nevertheless, the spatial activity of each specific phonic group was mainly influenced by vegetation cover variables and by their preference for each ecoregion, reflecting the habitat structure in which they forage.

Conclusions The spatial activity of four phonic groups from Central Patagonia in summer is governed jointly by climatic and environmental variables, with vegetation structure being the dominant driver. In the context of climate change, habitat loss and reduced water availability (especially in arid and semi-arid environments) could impact the populations of Patagonian bats, considering the importance of these factors in influencing their spatial activity.

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Keywords Chiroptera, Argentinian patagonia, Bioacoustic, Vegetation cover, Climatic variables, Elevation, Proximity to water

Introduction

The order Chiroptera is the second most diverse among mammals, with more than 1400 species currently recognized [88]. Bats as a group are most diverse in tropical regions of the world [3, 29, 30]; however, they have also spread into temperate and boreal zones, albeit to a lesser extent [3, 47]. A relevant example in temperate zones are the insectivorous bats that inhabit the Patagonian region [70]. This environmentally heterogeneous region is home to endemic bats and represents the southern distribution limit for several vespertilionid and molossid species. Currently, nine species of insectivorous bats have been recorded in Argentine Patagonia: seven vespertilionids (*Histiotus macrotus*, *H. magellanicus*, *H. montanus*, *Lasiurus varius*, *L. villosissimus*, *Myotis chiloensis*, and *M. levis*) and two molossids (*Eumops patagonicus*, with a single record in Patagonia; and *Tadarida brasiliensis*) [7, 36, 37]. The Patagonia region is characterized by a cold temperate climate, strong westerly winds, and a marked precipitation gradient from west to east [33]. It also exhibits significant environmental heterogeneity, ranging from humid forests to arid steppes [12, 50].

In temperate regions, insectivorous bats are more active during the warmest seasons of the year because of the greater and more stable availability of food (arthropods prey, primarily insects; [8, 14, 54, 87]). Consequently, gestation, birth, and lactation occur during this period [70]. However, during this time, bat activity can also vary spatially in relation to climatic and environmental factors such as temperature, humidity, water availability, vegetation structure, elevation and food resources. There is an extensive bibliography that supports these patterns in different regions of the world. Some authors have shown that favorable weather conditions (e.g., temperature and humidity) can increase the likelihood of insect activity and reduce energetic costs, thus favoring the activity of bats [4, 8, 14, 26, 41, 71]. Other studies indicate that because bodies of water can favor the presence of insects in addition to being a source of hydration, these are areas that would benefit from increased bat feeding activity [1, 46, 51, 54, 76, 86, 91, 92, 97]. Furthermore, it has been shown that vegetation cover can also indirectly affect bat spatial activity by influencing the density and distribution of insect prey [9, 10, 49, 62, 65]. An increase in vegetation cover could lead to greater abundance of phytophagous insects that serve as prey for bats, favoring their foraging activity [65]. Likewise, the habitat structure given by the vegetation cover can affect the spatial activity of bats, conditioning the foraging spaces in relation to their wing and bioacoustic characteristics [21, 22, 27,49]. In relation to elevation, several studies have shown that bat activity varies over an elevation gradient, being greater at middle elevations because, at those elevations, insect richness is also higher [55, 58, 91, 104]. Finally, another factor often considered is environmental productivity as a proxy for plant biomass available to primary consumers (e.g., insects). Given that insect's density could be affected by available nutrients, insectivorous bats could be potentially sensitive to habitat productivity [95, 96]. Therefore, greater bat activity is expected to occur in areas with greater environmental productivity [79]. Unfortunately, there are no studies that jointly analyze how these factors influence the spatial activity of Patagonian bats. However, this information can provide insight into the limitations of bat distributions, especially in regions with extreme and variable environmental conditions [26], such as those of Patagonia.

Studies on habitat use provide essential information for monitoring bat populations and are crucial for developing conservation policies [47, 51], especially for bat communities that inhabit little-explored areas with poorly known species (e.g., Patagonian vespertilionids). In this sense, all of these species that inhabit Patagonia have been listed as least concern (LC) for the IUCN Red List of Threatened Species; however, except for the molossid species and *M. levis*, the remaining species show completely unknown population trends, including the endemic species of the region (e.g., *H. magellanicus* and *M. chiloensis*). Studies of this type could contribute relevant information for the conservation of species, monitoring the status of their populations in the current context of climate change in the southernmost areas of their distribution. Recent advances in bioacoustic methods have allowed the development of many studies on the biodiversity, distribution, biology, ecology, and conservation of bat species [5, 28, 40, 56, 83, 85]. Since many bats use echolocation for orientation and prey detection, acoustic surveys are widely used for monitoring bat populations, and their use is essential for biodiversity studies and monitoring plans in different types of environments [6, 54, 77, 80].

Therefore, the objective of this study was to explore how bat spatial activity (at the phonic groups level) can be affected by climatic and environmental variables in an environmentally heterogeneous area of Central Patagonia from Argentina, using bioacoustic methods to generate useful information for the conservation of its populations. To address this, we tested five hypotheses based on the patterns described above: Hypothesis 1(Effect of vegetation structure): vegetation cover type (forest vs.

steppe) may differentially influence bat spatial activity based on their foraging characteristics. Activity of clutter-adapted species (PG1–2) will positively correlate with forest density, while open-space foragers (PG3–4) will show greater activity in steppe habitats [20]. Hypothesis 2 (Effect of microclimate): bat activity patterns will be significantly influenced by temperature and humidity, with optimal ranges varying by phonic group [41]. Hypothesize 3 (Effect of elevation): bat spatial activity will peak at intermediate elevations, where insect availability is higher [55, 91]. Hypothesis 4 (Effect of proximity to water): bat spatial activity will be greater near water sources due to increased insect availability [46]. Hypothesis 5 (Effect of environmental productivity): bat spatial activity will increase in areas with higher environmental productivity [79].

Methods

Study area

The study was conducted in Central Patagonia, Argentina, within Chubut Province, covering an extensive area of approximately 600 km in length and encompassing sites ranging from the Andean Mountain range to the Atlantic coast. Ten sites were selected along the province, partially following the course of the Chubut River and covering the three representative ecoregions of Patagonia. These included three sites in the Patagonian Forest (1 = Parque Nacional Los Alerces [PNLA], 2 = Área Natural Protegida Baguilt [ANPB], 3 = Nant y Fall [NyF]), five sites in the Patagonian Steppe (4 = Camino Los Rifleros [CLR], 5 = Piedra Parada [PP], 6 = Los Altares [LA], 7 = El Sombrero [ES], 10 = Área Natural Protegida Península Valdes [ANPPV]), and two sites in Low Monte (sensu [66]; 8 = Las Plumas [LP], 9 = Dique Florentino Ameghino [DFA]; see Fig. 1). The climate in Central Patagonia is cold [68], with an average annual temperature ranging from 5 °C to 13 °C [11], and a marked gradient of annual precipitation from west to east (3000 mm to 180 mm, respectively; [50, 57, 60]). This gradient is clearly reflected in the vegetation distribution. The Patagonian Forest ecoregion is located to the west of the province and has dense vegetation with trees up to 30–40 m high (e.g., *Austrocedrus chilensis*, *Fitzroya cupressoides*, *Nothofagus* spp; [73]), in combination with a dense understory

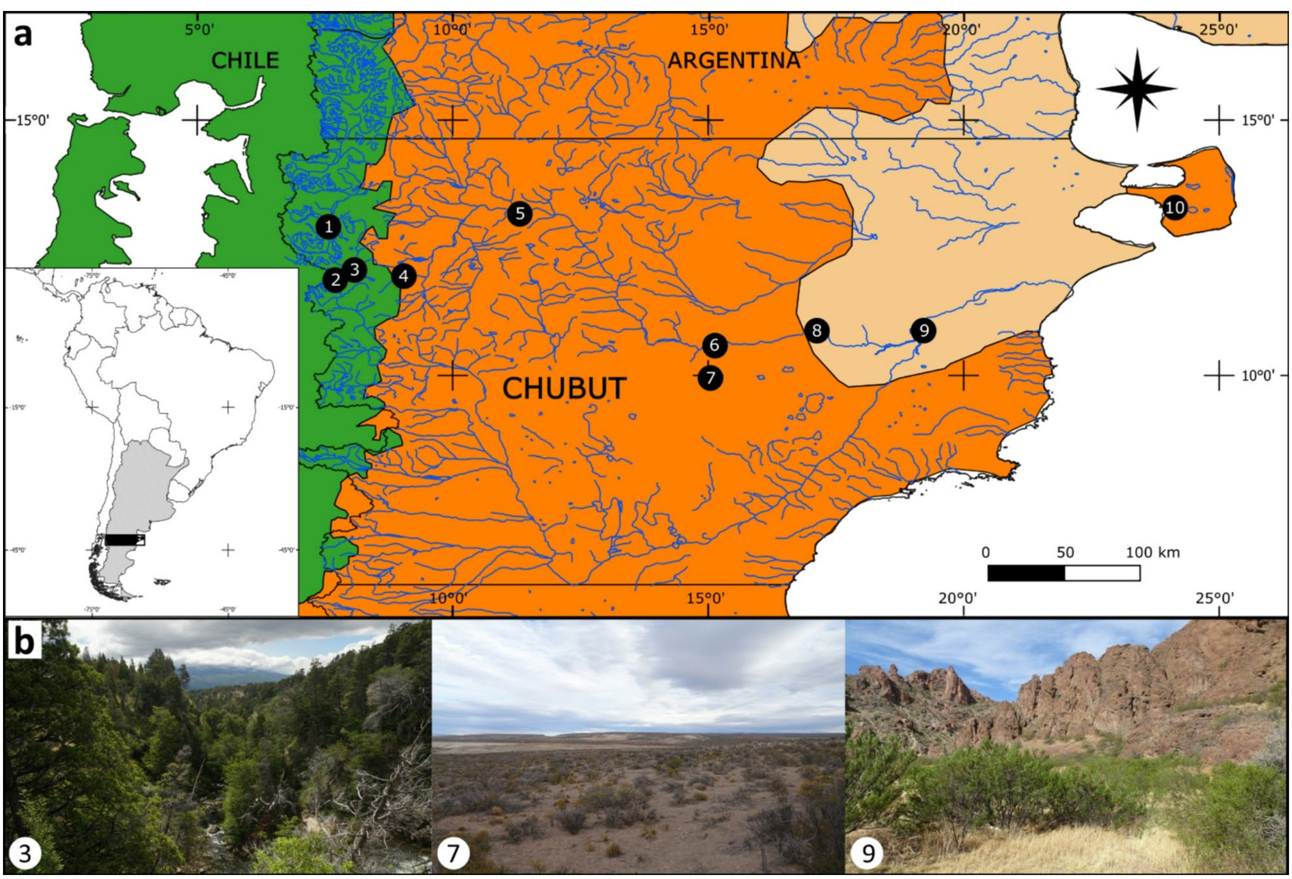

Fig. 1 Study Area. **a**) Acoustic monitoring sites of bats in the Central Patagonia from Argentina. Ecoregions are indicated in different colors: Patagonian Forest (green), Patagonian Steppe (orange) and Low Monte (yellow). Blue lines indicate the main water courses. **b**) Representative sites of each ecoregion: 3) ANP Nat y Fall (Patagonian Forest), 7) El Sombrero (Patagonian Steppe) and 9) Dique Florentino Ameghino (Low Monte). The names of the rest of the sites are indicated in the text

(e.g., *Chusquea culeou*, *Fuchsia magellanica* and *Berberis microphylla*; [16, 73]). The Patagonian Steppe ecoregion is located toward the center of the province and includes the Peninsula Valdés. This ecoregion with semidesert characteristics presents low vegetation cover [16, 50, 60], with a predominance of scrubby bushes, adapted to conditions of humidity deficit, low temperatures, frosts and strong winds (e.g., *Mulinum spinosum*, *Senecio bracteolatus*, *Adesmia volckmannii*; [16, 60, 69, 100]. The Low Monte ecoregion with a semiarid climate is located toward the northeast of the province including the Atlantic coast [60]. The vegetation is dominated by shrubs (e.g., the genera *Larrea*, *Prosopis*, *Chiquiraga*, *Ephedra*, and *Verberna*) and subshrub layers (e.g., *Cassia aphylla*, *Acantholyppia seriphiodes*, *Perezia recurvata*, and *Baccharis darwini*; [50]), whereas herbaceous cover is scarce [50, 60].

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Acoustic sampling

Passive acoustic monitoring was conducted during austral summer (January-February 2020). Each site simultaneously included 10 points (listening stations), thus, a total of 100 listening stations were analyzed across the study area. The listening stations were separated from each other by distances greater than 1.5 km (only five detectors were placed less than 1 km apart due to terrain characteristics and limited accessibility). At each listening station, an AudioMoth 1.0.0 ultrasonic detector (Silicon Labs) was placed at an approximate height of 2 m from the ground level whenever possible. In steppe areas where there are no tall trees or shrubs, the detectors were placed on the ground. Each AudioMoth 1.0.0 was programmed to record at a 192 kHz sample rate in a frequency range of 8 to 120 kHz [94] with medium gain. Each AudioMoth recorded in 20 s cycles followed by 5 s pauses, from sunset to sunrise for three consecutive nights under favorable weather conditions (i.e., no rain, no full moon, no strong wind).

All calls were recorded as full-spectrum calls in WAV format. First, we filtered out background noise from the recordings using Kaleidoscope software [103]. The filter settings specified a signal of interest between 8 and 120 kHz and 2 to 500 ms and with a 2-minimum number of calls per sequence, and we batch split each sequence to a maximum duration of 5 s to standardize bat activity ([94]; see below). Each sequence of 5 s (noise file classified by Kaleidoscope) was filtered again with SonoBat Batch Scrubber 5.1 (2012) to delete false negatives. Finally, only passes with a quality greater than or equal to 0.8 were selected with Sonobat 3.1 (2012) [90], to ensure high-quality call data [40].

We estimated bat activity as the number of passes during the sampling nights, and a bat pass was defined as one or more bat echolocation calls during an interval of 5 s [59, 94]. Because there is no acoustic library for Patagonian species that allows precise species-level identification; and taking into account that the echolocation calls of each species can vary structurally according to the habitat structure, ambient noise, geographic variation, and the existence of sympatry of close species [84], we classified the bat passes into four phonic groups (PGs), including species with similar call structures [9, 32]. This classification was made based on foraging habits, use of foraging space and bioacoustic characteristics [9, 20, 22, 32] of all species widely recorded in the study area (not including *Eumops patagonicus*). We then manually confirmed these classifications based on the following bioacoustics parameters of each call: Call structure (CS, frequence modulate quasi-constant frequency, FM-QCF, or quasi-constant frequency, QFC), lowest frequency (LF, kHz), highest frequency (HF, kHz), frequency of maximum energy (FME, kHz), bandwidth (BW, kHz), and call duration (CD, ms). Phonic group 1 (PG1) comprises edge-space aerial hawkers that emit short-duration (2–5 ms), high frequency (FME > 40 kHz), broadband (> 10 kHz) calls (FM-QCF; e.g., *Myotis* [27, 35]). Phonic group 2 (PG2) comprises edge and open spaces aerial hawkers that emit mid frequency (FME > 25 kHz), broadband (> 7 kHz) and duration less than 5 ms calls (FM-QCF; e.g., *Lasiurus*, *Histiotus magellanicus* [35, 40]). Phonic group 3 (PG3) comprises edge and open space aerial hawkers/gleaners that emit low frequency (FME < 22 kHz), bandwidth greater than 5 kHz, duration greater than 5ms calls (FM-QCF; e.g., *Histiotus macrotus*, *H. montanus* [35, 40]). Phonic group 4 (PG4) comprises open space aerial hawkers that emit low frequency (FME < 25 kHz), narrowband (< 5 kHz), and long duration (> 10 ms) calls (QCF; e.g., *Tadarida brasiliensis*; [9, 20]). Calls outside these ranges were not included in the analysis.

Variable selection

For each georeferenced sampling point (listening station), we obtained values for 11 climatic and environmental variables that were hypothesized to be related to Patagonian bat activity. We select two climatic variables, Night Mean Temperature (T in °C; MOD21A2, [43]) and Relative Humidity (HR as %; L2, AIRS2RET_NRT), with an average value of the three sampling nights for each of them. We included five variables related to vegetation cover, % non-tree vegetation (NTV; mean value of the sampling year 2020; MOD44B, [25]), % non-vegetated (NV; soil without vegetation cover, mean value of the sampling year 2020; MOD44B), % tree cover (TC; mean value of the sampling year 2020; MOD44B), normalized difference vegetation index (NDVI, 250 m; mean value of the sampling year 2020; MOD13Q1; [24]), and enhanced vegetation index (EVI, 250 m; monthly average value for the sampling month and year; MOD13Q1; [24]). As proxies for environmental energy availability, we obtained values of net primary productivity (NPP, kg C/m^2/year, 500 m; mean value of the sampling year 2020; MOD17A3HGF; [81]), and gross primary productivity (GPP, kg C/m^2/year, 500 m; monthly average value for the sampling month and year; MOD17A2H; [82]). Finally, we included elevation (E, mals) as a complementary variable of climatic events which can affect bat occurrence [93], and proximity to bodies of fresh water (PW = linear distance in kilometers from the detector location point to the nearest freshwater body), as a proxy for water availability. MODIS data products were obtained from the Terrestrial Ecology Subsetting & Visualization Services (TESViS) Global Subsets Tool [67]. The values of relative humidity were obtained from the AIRS project (2019, https://worldview.earthdata.nasa.gov/) [2], whereas the elevation and proximity to bodies of fresh water data were obtained for each georeferenced point via a satellite imagery layer. Finally, we included the qualitative variable ECO, according to the belonging of each site to one of the three ecoregions analyzed (Patagonian Forest, Patagonian Steppe and Low Monte).

Statistical analysis

Descriptive summary statistics were calculated to assess the variation in climatic and environmental variables for each sampling site (mean ± standard error, $n = 10$). Generalized linear mixed-effects models (GLMM) were fitted to analyze the effect of climatic and environmental variables on bat activity by phonic group (PG). The response variables were the number of passes of PG1, PG2, PG3, and PG4, and were modeled with a negative binomial distribution and a log link function. The random effect of the factor site (ten levels) was included to consider the nested structure due to the multiple detectors per site (the number of passes at detectors on the same site are likely to be more similar to each other than to values from different sites). We employed an information theoretic approach for model comparison, allowing multiple model comparisons to be made, and the most parsimonious of these models to be identified [17]. Two sets of a priori models for each phonic group were determined: one that included all non-collinear explanatory variables, and the other that included vegetation structure variables (Supplementary Material Table 1). Collinearity was assessed using pairwise correlations, and a correlation coefficient (r) with an absolute value > 0.7 was used as a threshold (Supplementary Material Fig. 1). Akaike's information criterion (AIC) was calculated for each model, and model comparisons were made with ΔAIC (difference between the AIC for model *i* and the best model with the lowest AIC value). The AIC weight of a model (W*i*) was used as a measure that model *i* is the best model in the set of all models considered. To evaluate the relative importance of predictor variables (RIW*i*), AIC model weights were summed across all models that contained the parameter being considered and then divided the cumulative model weights for a particular variable by the number of models containing that variable to get an average variable weight per model [45]. Pearson residual plots were examined for model validation following the protocol described by Zuur et al. [106]. Additionally, simulated scaled residuals from the DHARMa package [42] were used for model validation. Specifically, we evaluated residual dispersion, zero-inflation and spatial autocorrelation. Analyses were performed in R software version 4.1.0 [74] via RStudio software version 2024.4.2.764 [72], using glmmTMB [15] and tidyverse [102] packages.

Results

A total of 18,958 bat passes were recorded over three nights, including ten sampling sites and 100 listening stations. As results of the classification, 12,335 bat passes were assigned to PG1, 4,414 to PG2, 573 to PG3, and 1,636 to PG4. The number of passes per site varied according to the phonetic group analyzed (Table 1). For PG1, the greatest activity was recorded at site 3 ($n = 6{,}259$ passes, in Patagonian Forest), and the lowest at site 8 ($n = 31$ passes, in Patagonian Steppe). Similarly, for PG2, the greatest activity was recorded at site 1 ($n = 1{,}517$ passes, in Patagonian Forest), and the lowest at site 10 ($n = 2$ passes, in Patagonia Steppe). While for PG3, the greatest activity was recorded at site 9 ($n = 173$, in Low Monte), and the lowest at site 2 ($n = 7$ passes, in Patagonia Forest). Finally, for PG4, the greatest activity was recorded at site 9 ($n = 714$ passes, in Low Monte), and the lowest at site 8 ($n = 15$ passes, in Low Monte). Although bat passes were detected at all sites, only PG2 was recorded at site 7, and only PG2 and PG4 at site 10.

Several models were plausible in explaining the variation in the spatial activity of four analyzed phonic groups, based on the criterion of ΔAIC < 2 (Table 2). All the most plausible models for the four phonic groups selected the variables temperature (T), relative humidity (RH), elevation (E), proximity to water (PW), and ECO (ecoregion). However, the variables that had the greatest influence on the spatial activity of phonic groups were vegetation cover, which varied according to the group analyzed (Supplementary Material Table 2).

Table 1 Median and interquartile range (IQR) of pass number, and mean ± standard error values of climatic and environmental variables analyzed for each site. See the abbreviations of the variables in the text. The median (IQR) provides a more appropriate summary of Bat pass data, as it better captures its zero-inflated and overdispersed nature

Site	N° Pass	PG1	PG2	PG3	PG4	NDVI	EVI	NPP (kg C/m²/year)	GPP (kg C/m²/year)	NTV (%)	NV (%)	TC (%)	T (°C)	HR (%)	E (masl)	PW (km)
1	51 (374)	18 (179)	26.5 (112)	2 (4.75)	0 (1.5)	0.751±0.02	0.339±0.02	0.772±0.02	0.046±0.002	22±1	8±2	70±2	14.1±0.2	49±0.6	558.8±7	0.35±0.39
2	67 (159)	32.5 (17.4)	45.5 (36)	0 (0.75)	6.5 (12.5)	0.720±0.02	0.393±0.01	0.674±0.03	0.044±0.001	36±3	13±2	51±3	6.3±0.4	46±0.00	870.6±58	0.44 ± 0.15
3	128 (119)	17.4 (43.8)	57 (48.5)	7.5 (2.5)	2.5 (11.5)	0.642±0.01	0.352±0.01	0.659±0.01	0.036±7e^{-4}	59±2	12±1	29±2	13.8±0.1	32±0.00	414.5±23	0.31 ± 0.49
4	4.5 (4)	0.5 (2.75)	0.5 (2)	1 (1.5)	0.58 (1)	0.313±0.02	0.155±0.01	0.290±0.03	0.014±0.001	56±2	36±2	8±1	8.3±0.3	54±0.8	762.1±27	1.28 ± 1.47
5	98.5 (124)	13 (30.8)	28.5 (48)	8.5 (22.2)	37 (60)	0.142±0.004	0.088±0.003	0.140±0.004	0.007±3e^{-4}	39±2	60±1	2±0.1	13.6±0.2	39±0.02	438.9±3	0.60 ± 0.28
6	6.5 (12)	1.5 (17)	4 (26.8)	0.5 (3.25)	0 (7)	0.129±0.002	0.078±0.002	0.116±0.003	0.006±2e^{-4}	52±1	46±0.4	3±0.4	18.1±0.3	32±0.1	243.3±4	0.70 ± 0.54
7	0 (1.75)	0 (0)	0 (1.75)	0 (0)	0 (0)	0.129±0.001	0.075±0.002	0.120±0.002	0.006±2e^{-4}	50±1	47±1	3±0.1	15.3±0.3	38±0.2	498.5±10	26.90 ± 9.70
8	11.5 (5.75)	0 (0)	2 (2.5)	8 (5)	0 (1.5)	0.139±0.001	0.093±0.001	0.125±0.0004	0.006±6e^{-5}	50±0.4	48±0.4	2±0.1	12.9±0.1	18±0.00	181.3±4	0.71 ± 0.48
9	146 (185)	42.5 (78.5)	20.5 (25.8)	9 (14)	12 (65.5)	0.148±0.004	0.092±0.003	0.129±0.002	0.006±1e^{-4}	55±1	42±0.3	2±0.2	14.3±0.2	23±0.02	205.9±25	2.35 ± 2.70
10	0 (1.5)	0 (0)	0 (0)	0 (0)	0(0)	0.210±0.004	0.123±0.002	0.265±0.003	0.011±2e^{-4}	63±1	32±0.4	4±0.2	12.8±0.1	53±0.5	78.7±1	108.63 ± 2.74

Table 2 Generalized linear mixed-effects models explaining variation in Bat activity of phonic groups (PG). Models are provided in decreasing order of importance, and only best ranked models with $\Delta_i \leq 2$ are shown. Df: degrees of freedom; AIC: akaike's information criterion; ΔAIC: difference in AIC between the best model and the model indicated; W*i*: model weight. Explanatory variables: NDVI (normalized difference vegetation index), EVI (enhanced vegetation index), NPP (net primary productivity), GPP (gross primary productivity), NTV (% non-tree vegetation cover), NV (% soil without vegetation cover), TC (% tree vegetation cover), T (mean temperature), RH (mean relative humidity), E (elevation), PW (proximity to water body) and ECO (ecoregion: Patagonian Forest, Patagonian Steppe and Low Monte)

Phonic group	Model	Df	AIC	ΔAIC	W_i
PG 1	Model 6: TC + T + RH + E + PW + ECO	10	679.6	0.0	0.353
	Model1: NDVI + NTV + T + RH + E + PW + ECO	11	680.2	0.6	0.262
	Model 3: NPP + NTV + T + RH + E + PW + ECO	11	681	1.5	0.170
PG 2	Model 1: NDVI + NTV + T + RH + E + PW + ECO	11	758.3	0.0	0.246
	Model 6: TC + T + RH + E + PW + ECO	10	758.6	0.4	0.206
	Model 2: EVI + NTV + T + RH + E + PW + ECO	11	758.8	0.5	0.194
	Model 3: NPP + NTV + T + RH + E + PW + ECO	11	759.5	1.2	0.133
	Model 5: NV + NTV + T + RH + E + PW + ECO	11	759.8	1.5	0.114
	Model 4: GPP + NTV + T + RH + E + PW + ECO	11	759.9	1.6	0.108
PG 3	Model 2: EVI + NTV + T + RH + E + PW + ECO	11	463.1	0.0	0.367
	Model 1: NDVI + NTV + T + RH + E + PW + ECO	11	464	0.9	0.230
	Model 6: TC + T + RH + E + PW + ECO	10	464.9	1.8	0.149
	Model 3: NPP + NTV + T + RH + E + PW + ECO	11	465.1	1.9	0.136
PG 4	Model 6: TC + T + RH + E + PW + ECO	10	539.2	0.0	0.315
	Model 1: NDVI + NTV + T + RH + E + PW + ECO	11	540.6	1.5	0.152
	Model 5: NV + NTV + T + RH + E + PW + ECO	11	541	1.8	0.128
	Model 2: EVI + NTV + T + RH + E + PW + ECO	11	541.1	1.9	0.118

For PG1, the most important variable was TC (% tree cover) based on its W_i value (0.353) with a negative effect, indicating that the increase in tree cover generates a decrease in activity (Fig. 2a). The spatial activity of this group was positively associated with climatic variables (T and RH), indicating that higher temperature and humidity led to greater activity, whereas for E and PW the relationship was negative (Supplementary Material Fig. 2), showing that at higher elevations and greater distances from bodies of water, the activity of this group decreases.

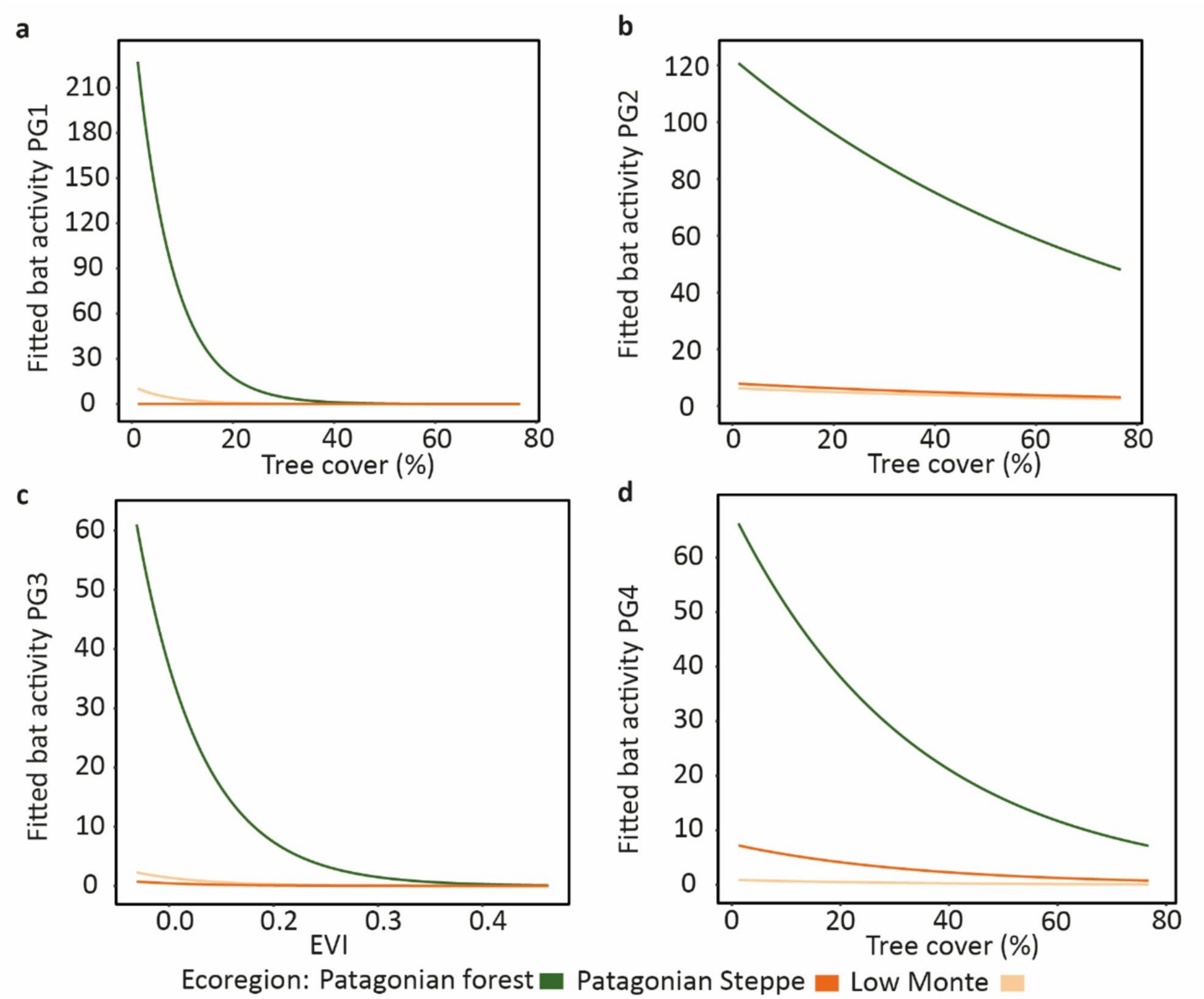

Fig. 2 Fitted values obtained by the GLMMs showing the effects of tree cover and enhanced vegetation index (variables with highest relative importance: RIW adjusted) on the number of passes of phonic groups **a**) PG 1, **b**) PG 2, **c**) PG 3 and **d**) PG 4. Fitted values were estimated from the full model while holding other variables at mean values

PG1 showed a positive association with forested environments (Patagonian Forest), as reflected in the ECO variable (Patagonian Forest; Fig. 3a).

For PG2, the most important variable was TC according to its W_i value (0.206), and its effect was negative, indicating that the increase in tree cover generates a decrease in activity (Fig. 2b). Similarly, the NTV had a negative effect on spatial activity (Supplementary Material Fig. 3b). The relationships were negative for T, E, and PW, showing a decrease in the spatial activity of the group with increasing temperature, elevation, and distance to water bodies (Supplementary Material Fig. 3c, e, f). The relationship was positive for HR, indicating that the spatial activity of the group increases with higher HR (Supplementary Material Fig. 3 d). Regarding ECO, PG2 showed a greater association with Patagonian Forest environments (Fig. 3b).

For PG3, the variables that most influenced spatial activity were EVI and NDVI according to their W_i values (0.23, Fig. 2c). Both variables affected negatively the activity, showing that the spatial activity of the group decreases with higher EVI and NDVI values. The NTV, also was an important variable, and its relationship with spatial activity was positive, indicating that higher non-tree vegetation cover led to greater group spatial activity (Supplementary Material Fig. 4a). The relationship was negative for T and positive for RH, indicating that the decrease in temperature and the increase in relative humidity generate greater activity (Supplementary Material Fig. 4b, c). Regarding E and PW, the association was negative, showing that as elevation and distance to

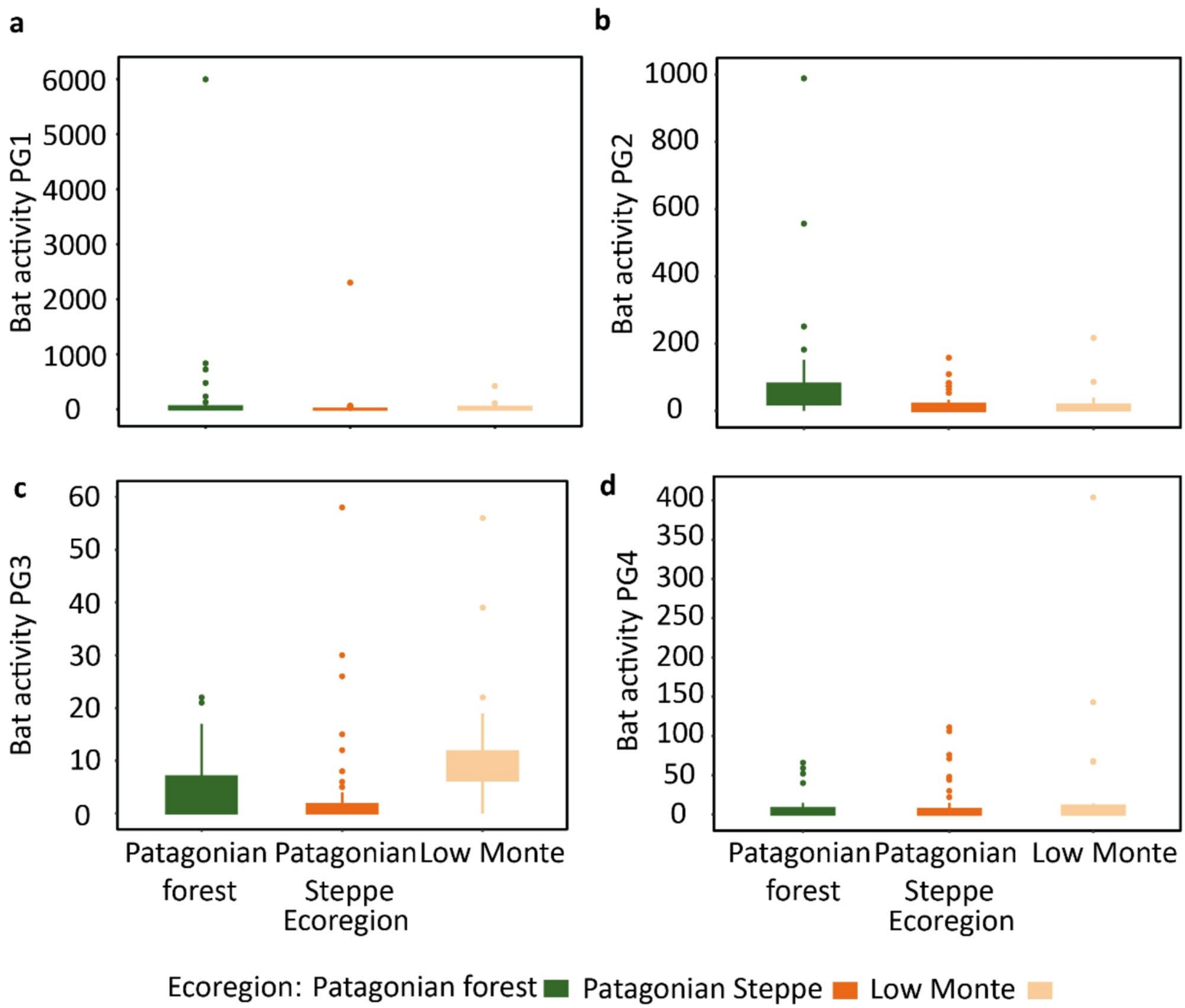

Fig. 3 Variation of number of passes of phonic groups **a**) PG 1, **b**) PG 2, **c**) PG 3 and **d**) PG 4 according to ecoregions

water bodies increased, the spatial activity of the group decreased (Supplementary Material Fig. 4d, e). This group was primarily related to Low Monte (Fig. 3c).

Finally, for PG4, TC was the most important predictive variable based on its W_i value (0.315) and had a negative effect on the spatial activity of this group (Fig. 2d). This relation showed that an increase in tree cover generates a decrease in the activity of PG4. The relationship was negative with T and positive with RH, showing increased activity with the decrease in temperature and the increase in relative humidity (Supplementary Material Fig. 5a, b). Like the other, the relationship was negative with E and PW, showing that with increasing elevation and distance to water bodies, the spatial activity of the PG4 decreased (Supplementary Material Fig. 4c, d). Regarding the ECO variable, this group was more closely related to the Low Monte (Fig. 3d).

Based on the most plausible models, the productivity variables exerted less influence on phonic group activity than other environmental variables. The results indicated that NPP was selected at least once by the most plausible models for PG1, PG2, and PG3, but not for PG4; while GPP was retained by a single model for PG2. The influence of NPP and GPP was negative, indicating a decrease in the spatial activity of phonic groups in environments with higher values for these variables.

In summary, vegetation structure consistently emerges as the most influential predictor across all phonic groups, showing negative effects on bat activity. While responses to microclimate varied by group (e.g., PG1 and PG2 favored warmer conditions, whereas PG3 and PG4 preferred cooler temperatures), all groups avoided higher elevations and distant water sources and exhibited strong ecoregion associations—PG1 and PG2 with the Patagonian Forest, and PG3 and PG4 with Low Monte.

Discussion

The main aspects of Patagonian bats that have been studied are morphology [34, 35, 40] and distribution [37, 38, 99], including occasional records for some species [7, 23]. In this context, our study provides unique information on spatial activity of phonic groups that inhabit an extensive and environmentally heterogeneous area in the Patagonia region via a passive monitoring network.

The most plausible models revealed that climatic and environmental variables jointly influenced the spatial activity of all phonic groups of Central Patagonia, supporting most of our hypotheses. We found that the spatial activity of phonic groups in summer, varied in relation to climatic and environmental characteristics. The spatial activity of all phonic group was associated with temperature, relative humidity, elevation, and proximity to water, but mainly responded to the structure of the habitat (cover vegetation variables and ecoregion). Each phonic group responded differently to these last variables. In contrast, the productivity variables had less influence than expected compared to the other variables analyzed.

Effect of vegetation cover

Each phonic group's association with different vegetation cover and ecoregions suggests preferences based on foraging style and spatial use, supporting our hypothesis 1. In this sense, PG1 (*Myotis*) spatial activity was influenced to a greater extent by the TC (% tree cover) in a negative way. In Patagonia, *M. chiloensis* and *M. levis* are adapted for aerial foraging in edge spaces due to their short, wide wings and small size [27, 35], which allow them greater maneuverability in edge spaces [35]. However, despite their high maneuverability, the activity of this group could also be reduced in highly cluttered environments since they lack echolocation calls adapted to environments with high background interference from vegetation [20, 22]. Therefore, this echolocation call structure (high-frequency, broadband, and short-duration FM-QCF) would allow these species to feed in edge spaces (and not so much in narrow spaces) in environments with greater plant structure compared to the other phonic groups [22, 27], explaining PG1's preference for forested areas like Patagonian Forest where activity was higher (e.g., site 3).

The PG2 (*Lasiurus* and *H. magellanicus*) spatial activity showed a negative association with TC (% tree vegetation) indicating decreased activity in environments with dense vegetation structure (e.g., cluttered spaces). This relationship may be due to the fact that the species included in this group (*Lasiurus* and *H. magellanicus*), have wing characteristics that allow them to hunt in the air and forage on edges (mainly *H. magellanicus*) and open spaces [35]. Likewise, the structure of the echolocation calls of these species is not adapted to navigate or feed in dense vegetation, but rather in edge spaces or forest clearings [20, 22]. *Lasiurus* in particular, probably has the most flexible behavior, alternating forested habitats and open space, due to its migratory capacity [35]. In addition, ecoregion variable was also selected by the most plausible models, showing a greater activity of PG2 in Patagonian Forest (e.g., site 1). This coincides with the fact that most of the records of these species in the study area are found in forest environments [23, 36, 37].

The spatial activity of PG3 (*Histiotus*) was negatively associated with the variable EVI and NDVI, and positively with NTV. EVI and NDVI are indexes that responds to structural variations in the canopy, so lowest values indicate low tree cover [105]. In combination, the association with both variables indicate that spatial activity of this group is greater in environments with less tree vegetation. Consistently, the model selected ECO variable, showed a higher spatial activity of PG3 in Low Monte (e.g., site 9). The PG3 include *Histiotus* species (*H. macrotus* and *H. montanus*) that are characterized by having longer ears (> 27 mm) and emitting low-frequency calls [40]. Such features are associated likely to foraging in edge or open space in different degree [35, 40], which is consistent with the environments where this group presented greater activity (Low Monte and Patagonian Steppe).

Finally, the spatial activity of PG4 was associated negatively with TC, indicating that an increase in tree cover generates a decrease in the activity of this group. In addition, PG4 showed a greater spatial activity in environments with low or sparce vegetation. This group included only *Tadarida brasiliensis*, due to its distinct echolocation call structure (QCF, [20]). This species is widely known to be an aerial hawker in open space, due to the combination of its wing morphology (long and narrow wing [35, 63]) and bioacoustic characteristics [20, 21]. Therefore, it is expected to observe greater spatial activity of this specie in open environments with less vegetal structure such as Low Monte (e.g., site 9).

Effect of microclimate

As mentioned initially, temperature and relative humidity also resulted in important predictive variables on spatial activity in summer for all phonic groups analyzed, supporting our hypothesis 2. The groups showed an increase in activity with decreasing temperature, except PG1, which showed an inverse association (greater activity at higher temperatures). In relation to relative humidity the spatial activity was positively associate with the four phonic groups, indicating an increase in activity with increasing relative humidity.

The climatic variables T and RH, have been widely associated with the activity of bats, for its effect on thermoregulation of these animals and probably because it affects insect densities [14, 41, 101]. Favorable weather conditions increase the flight probability of insect prey and reduce the energetic costs of flight and echolocation [14]. With respect to temperature, only PG1 showed a positive relationship with this variable, indicating that spatial activity for this group is, as expected, favored by higher temperatures. On the contrary, for the rest of groups, spatial activity decreased with increasing temperature. Reducing activity on warmer nights in summer may be a strategy to prevent water loss through evaporation and, thus avoid dehydration, especially in arid environments with less water availability [54, 61, 76], such as Low Monte and Patagonian Steppe [12, 33]. In relation to this, the increase in relative humidity favored the spatial activity of all phonic groups. Thus, our results suggest that relative humidity levels above 30% may enhance bat activity. However, these results should be studied in more depth to corroborate this relationship.

Effect of elevation and proximity to water

Elevation and proximity to water also were important predictive variables in all most plausible models for each group, consistent with hypotheses 3 and 4. In this case, both variables affected negatively the summer spatial activity of four phonic groups. Within the range of 71 to 1,105 masl included in our study, higher spatial activity was observed in environments located in intermediate elevations. For PG1 and PG2 the greatest activity was recorded between 350 and 550 masl, reinforcing both groups' preferences for forested environments. A plausible explanation for these results is that, in environments with a marked elevational gradient (Patagonian Forest), the greatest insect species richness could be found at mid-elevations, resulting in greater food availability and enhanced bat activity. This same relationship has been observed in bat communities in other temperate regions [58, 91]. While that for PG3 and PG4, the spatial activity was higher in elevations between 200 and 440 mals. In this case, selection could be mainly due to the type of environment (with low vegetation structure, such as scrubland and steppe) due to its wing restrictions and foraging habits [35].

Our results show that increased distance to freshwater bodies is associated with reduced bat activity. Similar patterns have been observed in other studies, demonstrating how water sources can affect the structure of bat populations and communities [1, 13, 18, 46, 51, 54, 62, 86, 92]. Water bodies are expected to contain a high abundance of nocturnal insects (many of which have aquatic life stages) and constitute an important part of the bat insectivorous diet [46, 54, 92] and particularly of Patagonian bats [39]. In addition, bats use water sources for drinking, thus, even small, temporary or ephemeral ponds can be highly important for these animals [46, 54, 75, 92]. Likewise, the availability of free water has been considered an important conditioning factor in lactating female bats, because water loss during roosting is greater throughout lactation, thus generating a greater water requirement [1, 46].

Effect of environmental productivity

Among the variables analyzed in our study, the productivity variables (NPP and GPP) were those that had the least influence on the spatial activity of phonic groups. Notably, none of these variables were significant predictors for PG4. Similarly, GPP was only selected as a predictive variable by a single model for PG2. Both variables had a negative effect on the spatial activity of phonic groups, so they did not support our last hypothesis. This suggests that morphological traits that influence foraging style and space use may have a stronger effect on activity than food availability. It is evident that the environments that showed greater productivity also exhibited denser tree cover and, therefore, more closed or cluttered spaces, which would make navigation difficult for any of phonic groups analyzed since none of them are adapted to foraging in narrow spaces [20]. However, these results should be considered preliminary and analyzed in more detail at the microhabitat level for corroboration, since previous studies have demonstrated their importance in determining bat activity [79, 95, 96].

Final considerations

Because this study is the first in the analyzed area (without a prior basis for comparison), the sensitivity of the microphones used may represent a methodological limitation in our study. Although the use of AudioMoth detectors has significantly expanded in recent years in bioacoustic studies of bats (e.g., [53, 78]), their efficiency could be considered a limitation compared to similar equipment [48]. Therefore, it is necessary to continue acoustic monitoring, testing different equipment that can corroborate our results and deepen knowledge about the specific activity of Patagonian bats. We also consider it important to explore these studies at a smaller scale, or at the microhabitat level, to corroborate our results. It would also be interesting to evaluate whether these factors have the same impact, considering Patagonia's latitudinal gradient.

Nonetheless, despite these limitations, our findings provide valuable insights into the activity patterns of Patagonian bats. From a conservation perspective, and in the context of climate change, this information takes on greater relevance. Habitat loss due to anthropogenic activity (agricultural expansion, overgrazing, deforestation, fires, etc.) in Patagonia, coupled with the effects of climate change [52, 89], could affect the availability of shelters, food, and water for Patagonian bats, considering their association with these environments. While it is unknown how climate change may directly impact Patagonian bat populations, it has been demonstrated how this factor can impact the ecosystems in which these animals live. In this sense, both forested and semi-arid environments are highly vulnerable to climate change [19, 54, 64, 86]. A recent study projects a significant decrease in the extent of temperate deciduous forests (−30%) and the Patagonian Steppe (−20.6%; [98]). Relatedly, rising temperatures, loss of plant species, changes in precipitation, and the frequency of drought events are expected to increase the vulnerability of Patagonian ecosystems [31, 52, 98]. Therefore, Patagonian bats could be affected not only by habitat loss but also by water scarcity, with arid or semi-arid environments—e.g., Patagonian Steppe and undergrowth—being the most affected [46]. In this context, the population trends of most species inhabiting Patagonia are unknown, including the region's endemic species (e.g., *H. magellanicus* and *M. chiloensis*, sensu IUCN 2024). Although our analysis does not differentiate at a specific level, the trends in activity patterns for each bat group are clear and can be used as a basis for more detailed studies on this topic. From our results, it can be interpreted that the preservation of habitat (plant structure in both forest and steppe environments) and water bodies is essential for the protection of insectivorous bat populations in Patagonia. Therefore, our findings may be useful for implementing conservation policies for Patagonian bat populations in protected and unprotected areas in Patagonia.

Conclusion

Passive acoustic monitoring in Central Patagonia, Argentina, revealed that the summer spatial activity of four phonic groups is jointly governed by climatic (temperature and relative humidity) and environmental variables (elevation, proximity to water and ecoregion), with vegetation structure being the dominant driver. The differential association of each phonic group with specific vegetation cover variables and ecoregions may indicate a particular preference of each group for certain environments, depending on their foraging style and use of space. In relation to this, the PG1 (*Myotis*) and PG2 (*Lasiurus* and *Histiotus magellanicus*) showed greater spatial activity in forest environments (Patagonian Forest), while PG3 (*H. macrotus* and *H. montanus*) and PG4 (*T. brasiliensis*) showed greater spatial activity in steppe environments (Low Monte). In the context of climate change, the loss of habitat and water availability (mainly in arid and semi-arid environments) could affect the populations of Patagonian bats, considering the importance of these factors in influencing their spatial activity. Further research is still needed to fully understand the activity patterns of bats; however, our study is the basis for continuing in this line.

Supplementary Information

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Supplementary Material 1

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Author contributions

All the authors contributed to the conception of the study and the design of the manuscript. ALG and ODP conducted the fieldwork and bioacoustic data analyses; MGG performed the statistical analysis. All the authors contributed to the writing and editing of the manuscript.

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Data availability

The datasets generated and/or analyzed during the current study are not publicly available as they are currently under analysis but are available from the corresponding author on reasonable request. All R codes associated with this study are available from the Figshare Repository. https://figshare.com/s/6a9f52212e7d0684a273.

Declarations

Ethical approval

Not applicable.

Consent for publication

Not applicable.

Consent to participate

Not applicable.

Competing interests

The authors declare no competing interests.

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