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Aerial insectivorous bats in the Brazilian-Uruguayan savanna: Modelling the occupancy through acoustic detection

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The Pampa is the least protected and one of the least sampled for bats among the Brazilian domains. This leads to significant Linnean and Wallacean shortfalls for bats in the Brazilian-Uruguayan savanna ecoregion. Here, we aimed to model the occupancy of aerial insectivorous bats in response to landscape structure at different scales, considering the influence of microclimate on bat detection. We acoustically monitored 68 locations during the spring and summer of 2019/2020, gathering data on temperature and humidity associated with each acoustic record using data loggers. We detected at least 11 species of the Molossidae and the Vespertilionidae families, of which 9 were used in the model. The response to landscape structure was species-specific: the occupancy probability of *Eptesicus brasiliensis* and *Molossus cf. currentium* increased with landscape connectivity at the 500 m scale while *Eptesicus furinalis* and *Histiotus cf. velatus* were negatively affected by landscape connectivity at the 5.0 km scale. *Molossus* occupancy probability responded negatively to landscape heterogeneity at the 3.0 km scale, while *Promops centralis* responded positively to landscape heterogeneity at the 5.0 km scale. *Molossus rufus* responded negatively to native vegetation cover and positively to landscape heterogeneity at the 5.0 km scale. *Myotis albescens* and *Molossops temminckii* did not respond significantly to any of the evaluated landscape metrics. Our results show that different bat species perceive the landscape differently, regardless of the guild of use of space – edge- or open-space forager. Our estimate of projected occupancy for the areas contiguous to those sampled ranged from 0.45 to 0.70 for the whole of the bat taxa, suggesting that the landscape, particularly where it still maintains its native elements, is reasonably favourable to aerial insectivores.

KEYWORDS

acoustic monitoring, Chiroptera, landscape structure, microclimate, site occupancy

Introduction

Habitat loss, fragmentation, and degradation are the most cited causes of species extinction and biodiversity decline globally (Taubert et al., 2018). Intensive land use changes alter the structure of the landscape and limit the potential occurrence, dispersal, and colonisation by different species (Fahrig, 2003; Jetz et al., 2007; Crooks and Sanjayan, 2010). The conversion of open habitats into monoculture plantations of fast-growing trees or their degradation through intensive use for agriculture and livestock production has changed the dynamics and structure of the landscape (Ellis et al., 2010; de Oliveira et al., 2017; Souza et al., 2020). Such landscape changes are of particular concern in tropical countries (Phalan et al., 2013), like Brazil, which despite being a megadiverse, is also one of the world's largest producers of agricultural commodities (Myers et al., 2000; de Sousa-Neto et al., 2018).

The main consequence of intense land use change is habitat homogenisation. This is of particular concern as heterogeneous and complex environments are drivers of diversification, governing species turnover (Tews et al., 2004). Indeed, patches and networks of distinct natural elements provide increased resource availability, including food, roosts and shelters, and niche space for other activities throughout the animals' life histories, favouring increased coexistence, persistence, and species diversification (Stein et al., 2014). The diversity of natural elements between different habitats is also paramount for landscape connectivity (Bennett et al., 2006). Indeed, connectivity is a key element in landscape structure and can be defined as the degree to which the landscape facilitates or restricts the movement of organisms between fragments (Calabrese and Fagan, 2004; Taylor et al., 2010). The smaller the distance between patches of similar habitat, the more connected they are. Patches that are more connected to each other facilitate exchanges between subpopulations, reducing the risk of population decline and local extinction (Bennett et al., 2006).

In addition to connectivity and heterogeneity, the amount of available habitat is another factor explaining species richness and diversity across landscapes and is usually a better predictor of these biodiversity dimensions than the size or isolation of a given fragment, as proposed in the habitat amount hypothesis (Fahrig, 2013). Furthermore, different animal species respond differently to landscape structure and this response may be affected both by spatial and temporal scales (Wiens, 1989; Chave, 2013). However, our understanding is still poor of how changes in the landscape, especially those resulting from anthropogenic action, affect the components of biodiversity, including different taxa, different diversity facets, and different environmental and landscape scenarios.

Brazil harbours a rich bat fauna, with 182 species recognised to date (Garbino et al., 2020, 2022). Insectivorous species constitute half of this diversity and are, in general, poorly

sampled throughout Brazil, since most studies on neotropical bats have been carried out on species more easily captured by mist nets (but see Arias-Aguilar et al., 2018; Hintze et al., 2020; Falcão et al., 2021). Species of this guild have great potential as bioindicators of environmental quality (Jones et al., 2009), playing an important role as biological control agents in altered landscapes, acting in the suppression of insect populations, including pests of agricultural crops (Cleveland et al., 2006; Rodríguez-San Pedro et al., 2018; Cohen et al., 2020; Kolkert et al., 2020; Aguiar et al., 2021). Despite this, bats may have different sensitivities to changes in landscape composition and structure. Such sensitivity depends on intrinsic factors that include body size, diet, flight, and dispersal abilities (Schnitzler et al., 2003; Lino et al., 2019). Undeniably, species with greater ability to fly and disperse are more likely to persist in altered landscapes, because they can search for favourable habitats within a less favorable matrix, while less vagile species may not be able to do the same, becoming restricted to suboptimal habitat conditions, with potentially severe consequences for their genetic diversity (Lino et al., 2019) and, ultimately, for their persistence.

Climate, habitat, and biotic interactions seem to be the factors most contributing to differences in bat composition, activity, and diversity (Estrada-Villegas et al., 2012; Appel et al., 2021; da Costa et al., 2021; Smith et al., 2021; Ramos Pereira et al., 2022). Climatic conditions are responsible for determining the temporal and spatial availability of resources at large scales and, at small scales may impose activity restrictions associated with metabolic costs, for instance, those associated with maintaining high and stable body temperatures when the ambient temperature is low. Moreover, the effects of temperature and relative humidity influence, in a complex and non-linear way, the propagation and attenuation of sounds emitted by echolocating bat species (Snell-Rood, 2012; Mutumi et al., 2016; Chaverri and Quirós, 2017). In terms of spatial resolution, different bat guilds perceive their habitat in different ways, both in terms of scale and landscape pattern (Bellamy et al., 2013; Ducci et al., 2015; Mendes et al., 2017; Falcão et al., 2021). So, due to the specificity of bat responses to the landscape, it is important to understand how different species and guilds respond to different habitat changes and configurations, considering the matrix and its quality.

The Uruguayan savanna ecoregion extends from the extreme south of Brazil, throughout Uruguay and a small section of the Argentinean province of Entre Ríos. In Brazil, this ecoregion is represented by the Pampa, characterised by extensive natural grasslands with shrubs and rocky outcrops (Pillar et al., 2009). In recent decades, the Pampean landscape has suffered with the conversion of natural areas into monocultures and the introduction of exotic species in silviculture (Roesch et al., 2009). Recent estimates indicate that the Pampa lost 21.4% of the remaining native vegetation cover between 1985 and 2020, remaining only 46% of the

original landscape (Souza et al., 2020). Although the Pampa is widely studied from the floristic point of view and in what concerns past and present human occupation (Guido et al., 2016; Leidinger et al., 2017), it remains largely understudied about the geographic distribution and patterns of occupancy of many animals (Konze, 2015; Queirolo, 2016; Tirelli et al., 2018). Bats are no exception to this pattern (Bernard et al., 2011), while it is known that most species occurring here are aerial insectivores, either open-space or edge-space foragers (Noronha, 2016).

Here, we use the history of acoustic detection and non-detection of bats to investigate the influence of landscape structure and microclimate on the occupancy and detection of aerial insectivores in the Brazilian Pampa. We hypothesise that the detection of all species should be influenced by microclimatic variables, and we predict that bat activity and, consequently bat detection, will increase positively with temperature, due to increased activity of their ectothermic prey, flying arthropods, and humidity, due to increased airborne sound propagation. Extremely low or high temperatures or humidity levels should negatively influence bat detection due to increased costs with thermal balance and reduced sound propagation or unpredictable echo behaviour in the lower and upper extremes of the humidity, respectively. We also hypothesise that species occupancy is influenced by the structure of the landscape, and we predict that (i) connectivity between patches of the same habitat positively affects the occupancy of edge-space foraging bats, as this guild should be favoured by forest patches offering extra roosts, perches, and food resources; (ii) heterogeneity should affect positively the occupancy of open-space bats, by favouring a more diverse and abundant prey community at different times of the night; and (iii) a greater amount of native vegetation cover should positively affect all species occurrences, as it offers greater carrying capacity, but potentially influencing, even more, the occupation of edge foragers.

Materials and methods

Study area

We sampled five areas in the Brazilian Pampa (within the Brazilian-Uruguayan savanna ecoregion; Figure 1) in the municipalities of Alegrete, Cacequi, and Quaraí, spanning a wide range of pristine habitats, including native grasslands, meadows, gallery forests, shrub formations, and rock outcrops, as well as areas that harbour different levels of cattle raising on natural grasslands and agriculture performed in converted areas. Sampling sites were classified into one of the two main physiognomies occurring in the region: (i) shallow soil fields, mostly composed of undergrowth vegetation, with a predominance of grasses, legumes, and composite plants that

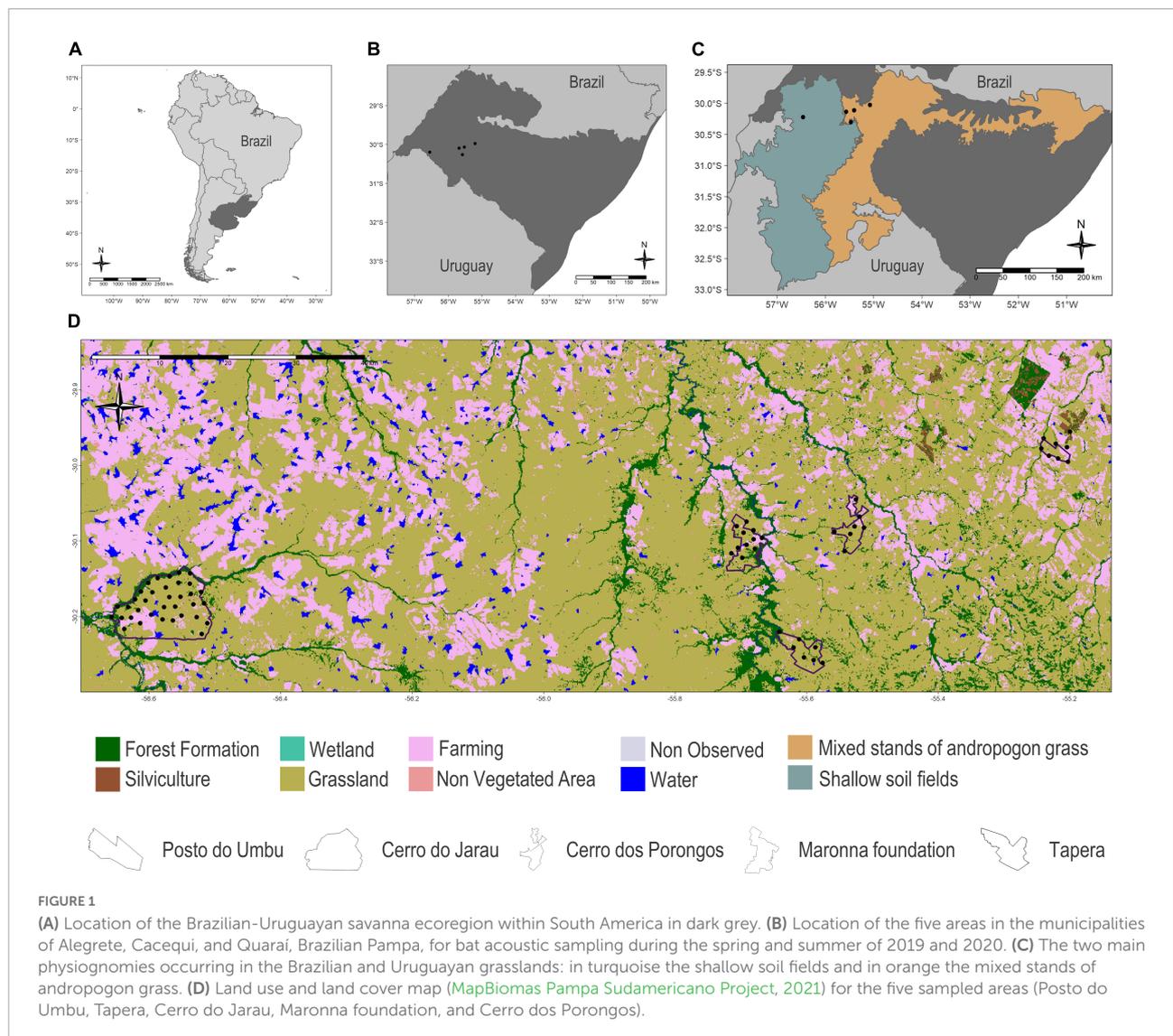
grow from basalt formations with low moisture retention and (ii) mixed stands of andropogon grass, where most of the area has already been transformed into rice and soybean crops; in pastures with overgrazing, the proportion of bare soil increases, benefiting the development of composite vegetation, such as plants of the genera *Soliva*, *Vernonia*, and *Senecio* (Boldrini, 2009).

The climate is sub-tropical, with average annual temperatures ranging from 16 to 22°C and annual rainfall varying from 1,200 to 1,600 mm (Pillar and Lange, 2015). The geological formation is complex, including recent marine sedimentary deposits to ancient pre-Cambrian formations, in some areas of the South-Rio-Grandense Shield (Chernicoff and Zappettini, 2004). The relief is relatively homogeneous and flat, varying from sea level up to about 400 m elevation (Pillar and Lange, 2015). Currently, only 46% of Brazilian Pampa remains covered by native vegetation and only 2% is legally protected by conservation units; this makes the Pampa the least protected domain in Brazil (Souza et al., 2020). Still, many landowners subscribed the Alianza del Pastizal's initiative, aiming for the conservation of natural grasslands through the production of certified environmentally sustainable meat, an initiative led by BirdLife International and developed through local partners in Brazil, Uruguay, Argentina, and Paraguay (Save Brasil, Aves Uruguay, Aves Argentina, and Guyra Paraguay).

Acoustic monitoring and analysis

We monitored 68 sites located at least 1.5 km apart, during the spring and summer of 2019 and 2020 (Figure 1). Autumn and winter are rainy, windy, and cold, which deemed acoustic bat monitoring inefficient. We sampled bats using automated sound detectors – AudioMoths (Silicon Labs) – set at a sampling rate of 256 kHz, 16 bits, programmed to record cuts of 15 s every 2 min from sunset to sunrise, for at least five nights in each site. We also coupled automated temperature and humidity sensors to each active AudioMoth to obtain detailed information on the microclimatic conditions associated with each bat record.

Species identification was done through manual analysis of recordings in Raven Pro 1.6 Software (K. Lisa Yang Center for Conservation Bioacoustics, 2022) selecting a Hamming window with 1,024 Fast Fourier Transformation (FFT; overlap 93%) to minimise the effect of spectral dispersion. We evaluated the following parameters: the overall shape of the pulse (constant frequency, CF; modulated frequency, FM; quasi-constant frequency, qCF; and variations therein), frequency modulation (FM), number of harmonics (nH), peak frequency (PF), duration (D), inter-pulse interval (IPI), frequency of maximum energy (FME), maximum frequency (Fmax), minimum frequency (Fmin), and bandwidth (BW = Fmax – Fmin). Whenever possible, we identified bat recordings to the species level, following acoustic identification keys for



Neotropical and Brazilian bats (Barataud et al., 2013; López-Baucells et al., 2016; Arias-Aguilar et al., 2018). We quantified bat activity using sequences with at least three consecutive good quality (signal to noise ratio ≥ 12 dB; Jung et al., 2014) echolocation calls in a recording; each sequence that met this criterion was considered a “bat pass.” Species were classified as edge-space or open-space foragers according to Denzinger and Schnitzler (2013).

Landscape metrics

To test for spatial autocorrelation in our dataset, we calculated Moran’s I index (Supplementary Table 1) for each sampled area, using the “Moran.I” function from the R package *ape* (Paradis et al., 2019). We obtained the landscape metrics from a categorical land use raster of the Brazilian-Uruguayan

savanna ecoregion for 2019 (MapBiomias Pampa Sudamericano Project, 2021). We created circular buffers of seven sizes (500 m, 1.0 km, 1.5 km, 2.0 km, 3.0 km, 4.0 km, and 5.0 km in radius) using the location of the AudioMoth as a centroid in each sampling site to extract the landscape metrics. Smaller buffers do not reflect the nightly dispersal ability of most of the species that potentially occur in the area. We calculated six structural landscape metrics for all buffers sizes at Landscape and Class levels (Table 1), using a classification raster of eight categories: forest formation, silviculture, wetland, grassland, farming, non-vegetated area, non-observed, and water. For class-level metrics, we used eight directions (queen’s case) that correspond to the number of directions in which patches may be connected, as recommended in McGarigal et al. (2012). All metrics were extracted using the *landscapemetrics* package (Hesselbarth et al., 2019) in R Program version 4.0.4 (R Core Team, 2021).

TABLE 1 Selected landscape metrics and respective level, code and raster reclassification, for bat acoustic sampled during the spring and summer of 2019 and 2020 in the Brazilian Pampa.

Landscape metric	Level	Code	Raster reclassification
Connectivity – mean euclidean nearest-neighbour distance	Class	Enn_mn	1 = Forest formation, wetland, and water; 0 = all other classes
Favourable landscape (percentage)	Class	Pland	1 = Forest formation, wetland, and water; 0 = all other classes
Native vegetation (percentage)	Class	Pland_nvc	1 = Forest formation, grassland, and wetland; 0 = all other classes
Landscape altered by anthropogenic action (percentage)	Class	Pland_antro	1 = Forest plantation, farming and non-vegetated area; 0 = all other classes
Native grassland (percentage)	Class	Pland_ng	1 = Grasslands; 0 = all other classes
Heterogeneity – Shannon's evenness index	Landscape	Shei	None

Single-season occupancy models and extrapolations

We used detection/non-detection records to build single-season occupancy models (MacKenzie et al., 2002, 2017). We treated each survey location as a sample unit and each night was halved to represent a survey occasion, resulting in two occasions per night per site. We used mean temperature and mean air relative humidity as detection covariates (p). We used the abovementioned landscape metrics as occupancy covariates (Ψ). All covariates were standardised by subtracting the mean and dividing by the standard deviation, resulting in mean $\mu = 0$ and standard deviation $\sigma = 1$. Multicollinearity was evaluated using the variance inflation factor (VIF), using the “vifstep” function from R package *usdm* (Naimi, 2017), and only variables with $VIF < 3$ were used for the modelling (Zuur et al., 2010). After the VIF analysis, our model included three landscape metrics at all selected scales (Enn_mn, Shei, and Pland_nvc), all showing a VIF value below 3 (Supplementary Table 2).

We fitted all models using the “occu” function in the *unmarked* R package (Fiske and Chandler, 2011). Detectability was modelled using the covariates mean relative humidity (humi) and mean temperature (temp), including the null model. Occupancy probability was modelled using the best detection model combined with landscape variables at each of the seven scales analysed, totalling 4 models for detection (Supplementary Table 3) and 21 models for occupancy by species (Supplementary Table 4). We ranked the models using the second-order Akaike Information Criterion (AICc) and the determination coefficient (r^2), and considered as the best-supported models for those with $\Delta AICc < 2$ (Burnham and Anderson, 2002). To evaluate models' goodness-of-fit (GoF), we used three discrepancy measures: sum of squared errors, Pearson's Chi-squared, and Freeman-Tukey Chi-squared, with at least 1,000 bootstraps. Additionally, to evaluate the model's fit based on the frequencies of the detection histories, we used the goodness-of-fit test recommended by MacKenzie and Bailey (2004), where well-fitted models should return a p -value > 0.05 . As a measure of dispersion, we used the c -hat value as follows: c -hat < 1 indicates underdispersion, we keep the value of c -hat at 1; $1 < c$ -hat < 3 indicates moderate

overdispersion, so we multiply the variance-covariance matrix of the estimates by c -hat, and as result, the SEs of the estimates are inflated, according to Burnham and Anderson (2002). This was done using the R package *AICcmodavg* (Mazerolle, 2020). To predict the probability of occupancy at each location, we used the “modavgPred” function in the *AICcmodavg* R package (Mazerolle, 2020), while considering the uncertainty of defining the best model using the averaged parameters across the best-ranked models ($AICc < 2$; Burnham and Anderson, 2002). In addition, we also used the average of the best models to see how occupancy changes with the covariates.

To spatially extrapolate our results, we used a raster of the MapBiomias at a scale of 1:250,000 (MapBiomias Pampa Sudamericano Project, 2021) and cropped it with the adapted shapefile of ecological systems from the Uruguayan Savanna Ecoregion at a scale of 1:500,000 (Hasenack et al., 2010). With the final raster on the scale of 1:250,000, we extracted the polygons representing the two mains sampled phytophysionomies (shallow soil fields and mixed stands of andropogon grass), covering areas of the Brazilian and Uruguayan Pampa for each modelled scale. We created a square grid for each scale modelled on the entire polygon, extracted the coordinates of each cell, and extracted the same landscape metrics used as occupancy covariates, creating a new data frame to predict and extrapolate species occurrence across the region, using the model-averaged parameters. We standardised this data, by the mean and standard deviation, and used this information to extrapolate our predictions and to create occurrence maps for each species for the region using *raster* (Hijmans, 2012), *rgdal* (Bivand et al., 2015), *sp* (Pebesma and Bivand, 2005), and *tmap* R package (Tennekes, 2018).

Results

We detected bat-passes in 8,111 (8.15%) out of 99,526 recordings. We recognised the occurrence of at least 23 taxa in the studied area, and we were able to identify 11 species of the Molossidae and the Vespertilionidae families. Four species were categorised as open-space foragers – *Molossus* cf.

TABLE 2 Total number of bat passes in each of the five sampled areas, and information on species, family, and foraging guild, regarding bat acoustic sampling during spring and summer 2019 and 2020 in the Brazilian Pampa.

Family	Species	Foraging guild	TA	CP	MA	PU	CJ	Total
Molossidae	<i>Molossus cf. currentium</i>	Open-space	0	3	13	184	312	512
	<i>Molossus molossus</i>	Open-space	0	0	1	11	69	81
	<i>Molossus rufus</i>	Open-space	2	10	48	347	75	482
	<i>Promops centralis</i>	Open-space	2	17	124	126	156	425
	<i>Molossops temminckii</i>	Edge-space	8	29	139	39	203	418
Vespertilionidae	<i>Eptesicus brasiliensis</i>	Edge-Space	0	2	4	36	175	217
	<i>Eptesicus furinalis</i>	Edge-Space	0	22	12	291	1234	1559
	<i>Histiotus cf. velatus</i>	Edge-Space	2	9	11	148	478	648
	<i>Lasiurus blossevillii</i>	Edge-Space	1	0	3	5	15	24
	<i>Myotis albescens</i>	Edge-Space	2	1	42	8	30	83
	<i>Myotis ruber</i>	Edge-Space	0	1	0	0	8	9
				17	94	397	1.195	2.755

Area's abbreviations: TA (Tápera), CP (Cerro dos Porongos), MA (Maronna), PU (Posto do Umbu), and CJ (Cerro do Jarau).

currentium, *Molossus*, *Molossus rufus*, and *Promops centralis*. Seven species were categorised as edge-space foragers, including one molossid – *Molossops temminckii* – and six vespertilionids – *Eptesicus brasiliensis*, *Eptesicus furinalis*, *Lasiurus blossevillii*, *Myotis albescens*, *Myotis ruber*, and *Histiotus cf. velatus* (Table 2).

Site occupancy models

Lasiurus blossevillii and *Myotis ruber* were excluded from occupancy modelling because they accounted for less than 1% of the total bat passes. Of the nine bat species included in the occupancy modelling, *E. furinalis* presented the highest finite-sample occupancy ($\psi_{FS} = 55.97$), followed by *M. cf. currentium* ($\psi_{FS} = 55.81$), *H. cf. velatus* ($\psi_{FS} = 54.47$), *P. centralis* ($\psi_{FS} = 51.83$), *M. temminckii* ($\psi_{FS} = 47.98$), *E. brasiliensis* ($\psi_{FS} = 44.78$), *M. rufus* ($\psi_{FS} = 44.69$), *M. albescens* ($\psi_{FS} = 36.33$) and, finally, *M. molossus* ($\psi_{FS} = 34.33$). Most species were registered in over half the sites; however, the highest number of bat passes does not necessarily reflect occurrence in more sites (Table 2 and Figure 2).

The models of occupancy converged and showed good fits for the nine species, with discrepancy values ranging from 0.01 to 0.93 and \hat{c} ranging from 0.55 to 2.88. Detection estimates ranged from 0.10 to 0.55, while occupancy estimates ranged from 0.51 to 0.99 (Figure 3).

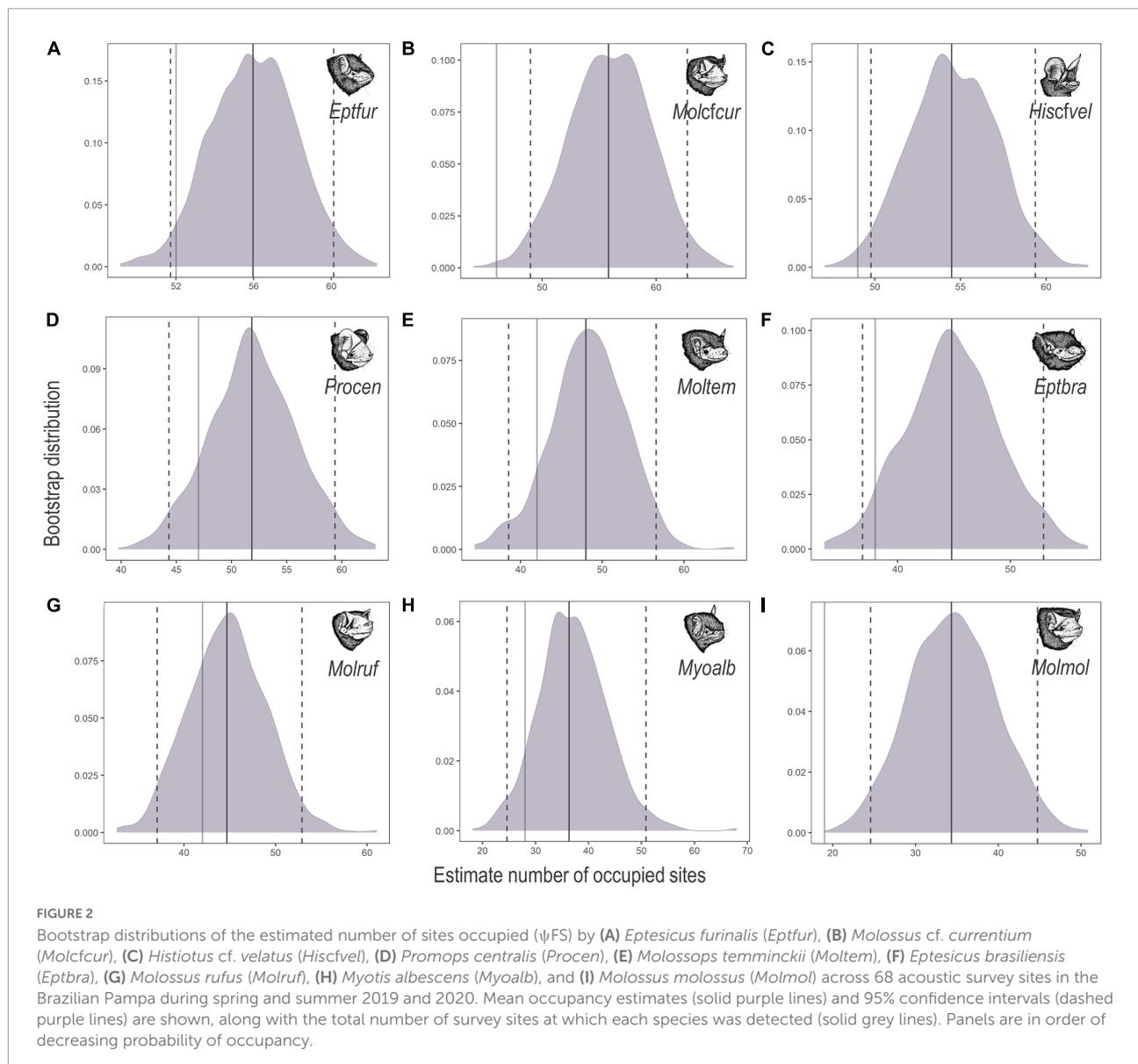
Effect of microclimate on bat detection probability

Among the sampled sites, the mean temperature ranged from 8.03 to 31.99°C while the mean relative humidity varied

from 37.1 to 99.88%. Best supported models ($\Delta AIC_c < 2$ and β p -value < 0.05) for the probability of detection varied by species, guild, and scale. Considering the highest weighted models, mean temperature and mean relative humidity positively affected the detection probability of the edge-space forager *E. brasiliensis* and the open-space forager *M. cf. currentium* at the 500 m scale and of the edge-space forager *H. cf. velatus* at the 5.0 km scale (Table 3). The detection probability of the edge-space forager *M. temminckii* increased with mean temperature at the 500 m scale, the open-space forager *M. molossus* responded positively to the temperature at the intermediate scale of 3.0 km, and the edge-space forager *E. furinalis* and the open-space forager *M. rufus* had a similar response, but at the larger scale of 5.0 km. The detection of *M. albescens* and *P. centralis* did not respond to any of the microclimatic variables.

Effect of landscape structure on bat site-occupancy probability

Considering the highest weighted models, connectivity is increased, that is, the closer the fragments of favourable habitat are, the greater the chances of occupancy by *E. brasiliensis* and *M. cf. currentium* at the 500 m scale. The open-space forager *M. molossus* was the only species whose probability of occupancy responded to landscape heterogeneity, and negatively, at the 3.0 km scale. The probability of occupancy of the edge-space foragers *E. furinalis* and *H. cf. velatus* was negatively affected by connectivity at the 5.0 km scale, while the open-space forager *P. centralis* responded positively to landscape heterogeneity at the same scale. *M. rufus* responded negatively to native vegetation cover and positively to landscape heterogeneity at the 5.0 km scale. Meanwhile, the occupancy of the



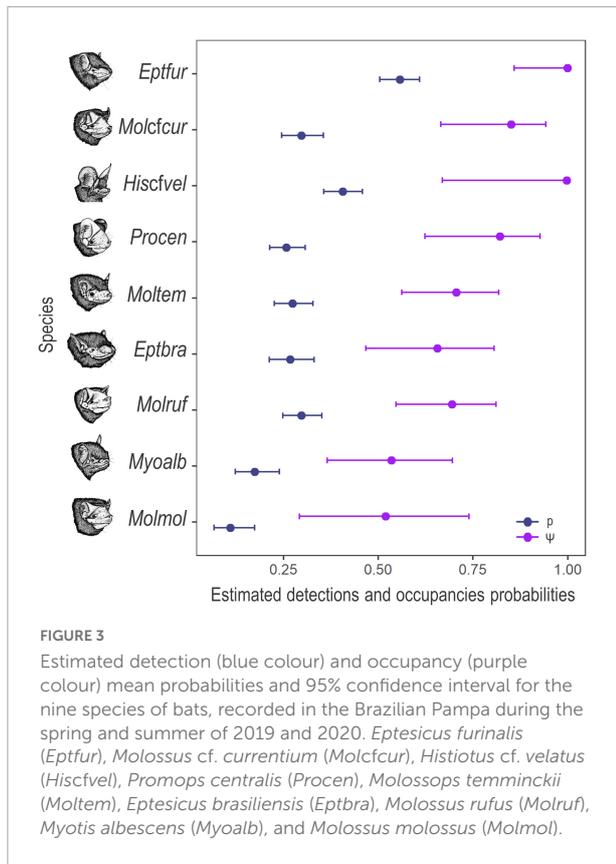
edge-space foragers *M. albescens* and *M. temminckii* did not significantly respond to any of the evaluated landscape metrics (Table 3).

Spatial extrapolation of the species' occupancy

Species showing the highest estimated occupancy probabilities (values ranging from $\beta\psi$ 0.55 to 1.00) in the two main phytophysionomies – shallow soil fields and mixed stands of andropogon grass – present in the Brazilian and Uruguayan portion of the Uruguayan Savanna were *E. furinalis* and *H. cf. velatus*. Those were followed by *M. rufus* and *P. centralis* (values ranging from $\beta\psi$ 0.34 to 0.99), and finally,

E. brasiliensis, *M. cf. currentium*, and *M. molossus* with moderate occupancy probabilities (values ranging from $\beta\psi$ 0.04 to 0.89; Figure 4).

The projected occupancy of the edge-space foragers, *H. cf. velatus*, *E. brasiliensis*, *E. furinalis*, and the open-space forager, *M. cf. currentium*, was higher in areas characterised by native forests including the *espinilho* tree, riparian forests, and water bodies, but was still moderate in areas characterised by monoculture plantations of fast-growing exotic trees and agriculture. On the other hand, the projected occupancy of the open-space forager *M. molossus* was higher in large open areas of native grasslands, with patches of native forest formations and small and medium water bodies, with considerable restriction of potential occurrence in environments with an excess of silviculture and



agriculture. On the other hand, the projected occupancy of *M. rufus* and *P. centralis* was more related to heterogeneous elements of the landscape, floodplains, and large bodies of water, but still moderate in matrices of silviculture and agriculture.

Discussion

Different bats perceive the landscape differently

We predicted that species occupancy should be influenced by landscape structure, with structural connectivity as the most important factor affecting the occupancy of edge-space foraging bats. This prediction assumed that, in altered landscapes, well-connected woodland patches should provide increased availability of roosts, temporary perches, and foraging resources, determining the occupancy of edge-space aerial insectivorous bats. Indeed, the occupancy of three of the five edge-space foragers detected, *E. brasiliensis*, *E. furinalis*, and *H. cf. velatus* responded to the structural landscape connectivity, although the first positively and the two latter negatively. Also, the occupancy of the open-space

forager *M. cf. currentium* was positively affected by this landscape trait.

Molossus cf. currentium and *Eptesicus brasiliensis* are seldom captured by mist nets and, therefore, we do not have basic information about these species in the Brazilian-Uruguayan savanna ecoregion (Reis et al., 2017; Barquez and Díaz, 2020). Our results indicate that these bats prefer well-connected natural landscape elements rather than extensive open areas or anthropogenic elements at local scales. Similar results were found for aerial insectivorous bat assemblages in modified landscapes of the Brazilian Atlantic Forest, where bat activity and composition responded to landscape structure at small scales (Falcão et al., 2021). Landscape elements, particularly trees, especially in open areas, may provide roosting and foraging sites with potentially greater insect availability and protection from wind (Russ et al., 2003). Open-space foragers, despite their general increased dispersal ability, may also avoid flying in completely open areas to minimise predation risks (Jones and Rydell, 1994) or because they use linear elements of the landscape, such as forest patches, perhaps for increased spatial orientation (Verboom and Huiteima, 1997).

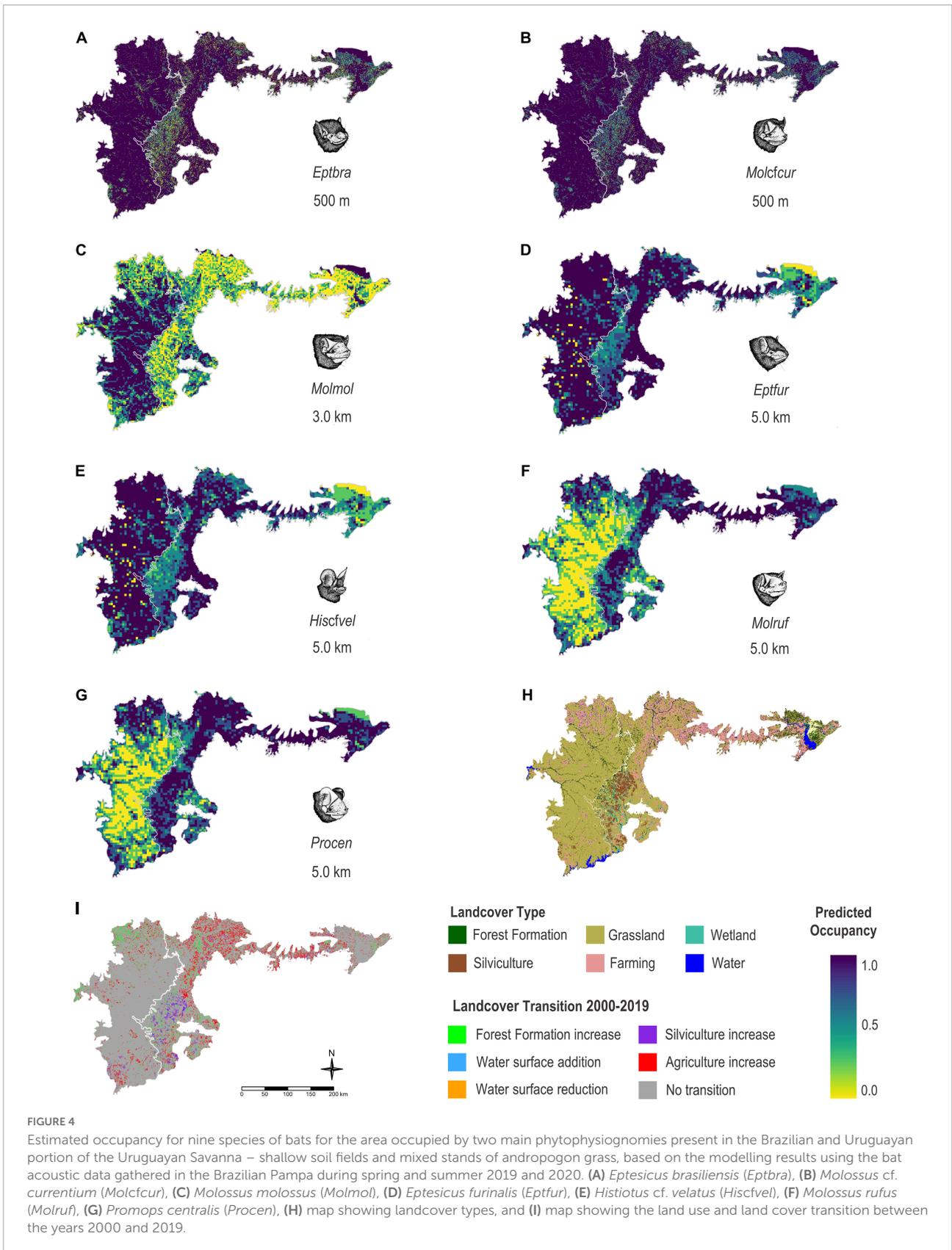
The occupancy of *E. furinalis* and *H. cf. velatus* was negatively affected by structural landscape connectivity at a larger scale. Previous studies have shown that the connectivity between forest patches is directly related to the quality and permeability of the surrounding matrix (Kupfer et al., 2006; Watling et al., 2011). In modified landscapes, the matrix can positively influence the occurrence and persistence of many species, for example, by providing greater diversity of prey, corridors, and stepping stones, or negatively, for instance, acting as a dispersal barrier (Ricketts, 2001; Bernard and Fenton, 2007; Watling et al., 2011; Brändel et al., 2020; Farneda et al., 2020; Mendes and Srbeek-Araujo, 2021). *E. furinalis* and *H. cf. velatus* seem to avoid areas composed of large extensions of exotic trees and monocultures. Possibly, such a matrix reduces the possibility of acquiring resources, such as food, protection, and roosts even for bats able to fly long distances, making it difficult for them to move between the favourable neighbouring fragments of native vegetation. Occupancy should thus be higher in areas showing small patches of native or riparian vegetation, or even other isolated elements in the landscape, such as scattered trees. Our results are consistent with those found for aerial insectivorous bats in rural landscapes in southeastern Australia (Lumsden and Bennett, 2005) and for fruit bats in the northernmost portion of Mexico (Galindo-González and Sosa, 2008), where in both cases, trees dispersed in rural land mosaics showed high value as foraging or roosting habitat for bats.

We also predicted that landscape heterogeneity would positively affect the occupancy of open-space bats. Still, only the occupancy probabilities of *P. centralis* increased with

TABLE 3 Summary of the best-fit models and the significant variables for detection (p) and occupancy (Ψ) for nine species of bats recorded in the Brazilian Pampa during spring and summer 2019 and 2020.

Species	Scale	Model	Intercept	Detection	Intercept	Occupancy	AIC	Δ AIC	AICwt
			(β p; SE)	(β p; SE)	(β Ψ ; SE)	(β Ψ ; SE)			
<i>Eptesicus furinalis</i>	5.0 km	p(temp) Ψ (enn_mn)	(0.23; 0.11)	(1.21; 0.14)	(7.58; 3.95)	(8.34; 3.25)	551.31	0.00	1.00
<i>Molossus cf. currentium</i>	500 m	p(temp + humi) Ψ (enn_mn)	(−0.86; 0.13)	(0.98; 0.15) + (0.23; 0.11)	(1.74; 0.54)	(−1.12; 0.54)	570.57	0.00	0.44
	5.0 km	p(temp + humi) Ψ (pland_nvc)	(−0.83; 0.14)	(0.94; 0.16) + (0.22; 0.11)	(1.78; 0.57)	(−1.43; 0.70)	570.93	0.44	0.36
	4.0 km	p(temp + humi) Ψ (shei)	(−0.88; 0.13)	(0.97; 0.16) + (0.23; 0.11)	(2.05; 0.70)	(1.45; 0.70)	572.11	1.54	0.20
<i>Histiotus cf. velatus</i>	5.0 km	p(temp + humi) Ψ (enn_mn)	(−0.38; 0.11)	(0.64; 0.13) + (0.36; 0.11)	(5.83; 2.62)	(6.75; 2.90)	621.04	0.00	1.00
<i>Promops centralis</i>	5.0 km	p(null) Ψ (shei)	(−1.06; 0.13)		(1.52; 0.52)	(1.33; 0.49)	536.13	0.00	0.70
	5.0 km	p(null) Ψ (15000 m. pland_nvc)	(−1.04; 0.13)		(1.46; 0.47)	(−1.24; 0.50)	537.84	1.71	0.30
<i>Molossops temminckii</i>	Null	p(temp) Ψ (null)	(−0.97; 0.13)	(0.60; 0.13)	(0.87; 0.32)		508.65	0.00	0.63
<i>Eptesicus brasiliensis</i>	500 m	p(temp + humi) Ψ (enn_mn)	(−1.01; 0.15)	(0.70; 0.17) + (0.27; 0.12)	(0.64; 0.40)	(−1.59; 0.58)	496.31	0.00	1.00
<i>Molossus rufus</i>	5.0 km	p(temp) Ψ (pland_nvc)	(−0.86; 0.13)	(0.38; 0.13)	(0.82; 0.32)	(−1.07; 0.41)	516.38	0.00	0.31
	5.0 km	p(temp) Ψ (shei)	(−0.86; 0.13)	(0.39; 0.13)	(0.75; 0.31)	(0.95; 0.35)	516.70	0.32	0.26
	4.0 km	p(temp) Ψ (pland_nvc)	(−0.86; 0.13)	(0.39; 0.13)	(0.82; 0.32)	(−0.96; 0.38)	517.03	0.65	0.22
<i>Myotis albescens</i>	Null	p(null) Ψ (null)	(−1.56; 0.21)		(0.14; 0.35)		328.91	0.00	1.00
<i>Molossus molossus</i>	3.0 km	p(temp) Ψ (shei)	(−2.10; 0.27)	(1.27; 0.28)	(0.07; 0.49)	(−1.43; 0.64)	242.27	0.00	0.64
	2.0 km	p(temp) Ψ (shei)	(−2.08; 0.28)	(1.24; 0.29)	(−0.06; 0.45)	(−1.11; 0.52)	243.94	1.66	0.28

temp (temperature), humi (relative humidity), enn_mn (Connectivity), shei (Heterogeneity), and pland_nvc (Native vegetation).



landscape heterogeneity at the largest scale. The occupancy by *P. centralis* seems to be favoured by the combination of suitable habitat patches immersed in a complex mosaic of other land use cover types in the surrounding matrix. Positive relationships between heterogeneous habitats and bat species diversity are well-documented at local and regional scales (Ramos Pereira et al., 2009; Frey-Ehrenbold et al., 2013; Mendes et al., 2017; Monck-Whipp et al., 2018). Artificial elements dispersed in the landscape, such as artificial ponds, created for irrigation in agricultural landscapes, perhaps provide greater variability and availability of foraging resources and drinking opportunities for bats (Korine et al., 2015; Ancillotto et al., 2019). The presence of ponds and even artificial lighting can change the dynamics of competitive exclusion by food disputes between bats with different sensitivities (Arlettaz et al., 2000; Russo and Ancillotto, 2015), promoting more diverse and abundant prey assemblages at different times of the night. Like most molossids, *P. centralis* presents great plasticity in its echolocation calls, probably allowing individuals of this species to explore a wide range of habitats, including urban areas (Hintze et al., 2020).

Contrary to our expectations, the occurrence of *M. molossus* seems to follow an opposite trend – this species preferred less heterogeneous habitats at medium scales (2.0 – 3.0 km). *M. molossus* is considered relatively common in urban areas and usually uses artificial roosts (Pacheco et al., 2010). Despite this, our models suggest that this species avoids areas with excess silviculture, preferring homogeneous areas in large open landscapes characterised by native grasslands and scattered native trees. *M. molossus* seems to take advantage of linear landscape elements, which is in line with previous findings, where linear elements in agricultural landscapes appear to be more attractive for some aerial insectivorous bats (Verboom and Huitema, 1997; Boughey et al., 2011; Toffoli, 2016; Rodríguez-San Pedro et al., 2018; Finch et al., 2020), probably because they are used as orientation landmarks and reference points during flight (Schnitzler et al., 2003; Schaub and Schnitzler, 2007), creating corridors for daily commute routes or occasional regional dispersal (Gelling et al., 2007).

Increased native vegetation cover does not favour the probability of occupancy of the black mastiff bat, *M. rufus*, contradicting our hypothesis that this landscape feature would favour the occupation of all species, especially the edge-space foragers. *M. rufus* is the largest species of this genus in the Brazilian territory and presents gregarious and synanthropic habits (Barquez et al., 1999; Esbérard et al., 1999). Our results suggest that, as for *P. centralis*, *M. rufus* presents higher occupancy in areas with greater heterogeneity and environmental complexity. This is especially concerning as areas, where the occupancy of the two species is maximum, are being rapidly converted by

humans, through intensive livestock production in natural grasslands, and silviculture and agriculture in otherwise converted fields.

Finally, edge-space foragers *M. temminckii* and *M. albescens* did not respond to any landscape metrics at the different scales evaluated. *M. temminckii* is the only species of the Molossidae capable of exploring background-cluttered environments while remaining able to exploit clearings and overall open environments, by changing from short downward frequency-modulated calls with short pulse intervals in cluttered environments to long upward frequency-modulated calls with longer intervals and shorter bandwidth in uncluttered sites (Oliveira et al., 2018). *M. albescens* is one of the most widely distributed species of its genus, occurring from southern Mexico to Brazil (Braun et al., 2009), this may be mirrored by a wide dietary plasticity, favoured by the changes in the activity of different species of prey at different thermal niches during the night. *M. albescens* is known for its trawler-style foraging and is therefore often captured in wetlands, using its high-frequency echolocation calls to detect its prey and capture it with its feet (Fenton and Bogdanowicz, 2002). Perhaps the phenotypic plasticity of *M. temminckii* and the foraging style of *M. albescens* make them less sensitive to connectivity, heterogeneity, or the amount of native vegetation cover in open grasslands at the analysed scales or they perceive the landscape at even larger scales. Due to the high specificity of bat responses to landscape configuration, the multiple-scale approach proved to be crucial to understand how bats respond to different changes in the composition and configuration of the landscape, considering the matrix and its quality (Meyer and Kalko, 2008; Martins, 2016).

Microclimate and bat detection: Finding species optimum detection interval

Temperature and relative humidity had, overall, positive effects on the detection of most bat species. However, nightly temperatures probably did not get high enough (maximum temperature recorded 33°C, but in 95% of the nights below 20°C) to test the prediction that, above a given limit, bats would decrease their activity in response to the increased cost of overheating. However, our data suggest that the optimum temperature range is between 19°C and 24°C, the interval within which we recorded most bat passes (Supplementary Figure 1). Generally, the feeding activity of aerial insectivores tends to increase on warmer nights due to the greater activity of their prey, flying arthropods (Racey and Swift, 1985; Aldridge and Rautenbach, 1987; Schowalter, 2006). Thus, we can assume that if bats are more active, they will soon be more detected, as has been effectively

observed in temperate environments (Kaiser and O'Keefe, 2015; Blakey et al., 2019). Still, above certain temperatures, the cost of endothermy, specifically cooling may become too high for animals with such increased metabolism. Indeed, despite the advantages and efficiency of air transport, the flight is a metabolically expensive mode of locomotion: the metabolic rates of flying bats can be as high as 3 to 5 times those of terrestrial mammals of the same size, with heart rates going over 1,000 beats per minute (Thomas and Suthers, 1972; Maina, 2000). Bats have several metabolic adaptations and perhaps they also show behavioural adaptations, avoiding too high temperatures even if their preys are still available, particularly if the gain by ingestion does not compensate for the physiological risk of overheating. However, nightly temperatures above 25°C seem to be rare even in the Pampean summer, so a scenario where bats trade-off hunting for inactivity because of potential overheating seems unlikely.

Reducing the Wallacean shortfall through acoustic monitoring

Here, we present the first comprehensive study of aerial insectivorous bats in the Brazilian Pampa using acoustic monitoring. Previous records resulted almost exclusively from mist-net sampling and roost searches (but see Barros, 2012), and represented less than 20% of the species occurring in Brazil (Garbino et al., 2020, 2022). With acoustic monitoring we added to the Pampa biome, records for two new species – *P. centralis* and *M. cf. currentium* – and records for at least six species from the genera *Cynomops*, *Eumops*, *Nyctinomops*, *Eptesicus*, *Histiotus*, and *Molossus* were to be identified in the future, when we can unambiguously identify the species of those complexes through their echolocation calls. Therefore, we estimate that the bat fauna of the Brazilian Pampa may easily exceed 40 species. Through acoustic monitoring, it is evident that the bat fauna of the Pampa is far more diverse than previously thought, deserving more attention, both from researchers and government agencies.

Most detected species are categorised as least concern, although *E. brasiliensis* and *P. centralis* are also still lacking basic ecological information, including distribution ranges, population sizes, and regional threats to their conservation, which is certainly preventing an adequate assessment of their conservation status; *M. cf. currentium* is classified as data deficient in Brazil (ICMBio, 2018). Indeed, it was recently shown that the distribution of *P. centralis* is much broader in South America than previously predicted, adding over 3.8 million km² to its former known area (Hintze et al., 2020). Our work has shown that the distribution

of this species goes even further south in the Neotropic and that its occupancy is far from low in the Pampean landscapes. Also, if confirmed, the detection of *M. cf. currentium* would represent the southernmost record of the species in Brazil, and the first for the Brazilian portion of the Uruguayan Savanna; this species also shows a high probability of occupancy in the region, potentially suggesting that this is not its distribution limit and that, perhaps, it has a much wider distribution range than previously thought.

The occupancy estimates projected for the regions neighbouring those sampled suggest that the landscape is reasonably favourable for the overall assemblage of aerial insectivorous bats, particularly the areas with native elements including the *espinilho* tree, *Vachellia caven*, wetlands, water, and riparian forests. This remains to be validated by further field data and for the remaining regions of the Uruguayan Savanna, but sites with those landscape elements are potentially the ones with higher probabilities of detection of aerial insectivore bats. Our results significantly add to the knowledge of Pampean bats and are alarming: environments characterised by native vegetation, highly suitable for the occupancy of a wide range of diversity of aerial insectivorous bat species, are rapidly disappearing by intense anthropogenic activities. In the last two decades, silviculture and agriculture have increased their areas by 34 and 44%, respectively, replacing native grasslands, particularly in mixed stands of the native andropogon grass. In shallow soil fields, intensive agriculture is almost impracticable and is here replaced by intensive livestock production. Such economic activities, when carried out inappropriately and at such excessive levels, often cause direct contamination of water resources by the release of pesticides and herbicides, leading to soil depletion and unproductivity, while facilitating the establishment of invasive plant species that generate not only loss of biodiversity, but also the de-characterisation of the gaucho cultural identity.

For all these reasons, future acoustic monitoring is paramount in areas of the Brazilian Pampa undergoing more intense anthropogenic changes, where acoustic monitoring will be key to increasing the knowledge of the distribution and occupancy of aerial insectivores, and how the ecosystem services provided by these bats, particularly in the context of the traditional agricultural systems, are being affected.

Data availability statement

The original contributions presented in this study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author/s.

Author contributions

CC and MR contributed equally to the article and approved the submitted version.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.937139/full#supplementary-material>

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