Diversity and Distributions WILEY

Where are the bats? An environmental complementarity analysis in a megadiverse country

Ludmilla M. S. Aguiar[1] [iD] | **Maria João R. Pereira**[2,3] [iD] | **Marlon Zortéa**[4] [iD] | **Ricardo B. Machado**[1] [iD]

[1]Department of Zoology, Universidade de Brasilia, Brasília, Brazil

[2]PPGBAN and PPG Ecologia, Department of Zoology, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

[3]Centro de Estudos do Ambiente e do Mar, Universidade de Aveiro, Aveiro, Portugal

[4]Universidade Federal de Goiás, Jataí, Brazil

Correspondence
Ludmilla M. S. Aguiar, Department of Zoology, Universidade de Brasilia, 70910-900 Brasilia, DF, Brazil.
Email: ludmillaaguiar@unb.br

Funding information
Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq)

Editor: Orly Razgour

Abstract

Aim: Field surveys are necessary to overcome Wallacean shortfalls. The task is even more important when human pressure on tropical—megadiverse—ecosystems is considered. However, due to financial constraints, spatial and temporal prioritization is required. Here, we used the concept of environmental complementarity to identify non-surveyed regions for bats that are environmentally different from other already surveyed regions. We highlighted regions in Brazil where field inventories could be conducted to locate new occurrences or even new bat species.

Location: Brazil.

Methods: We based our analysis on environmental characterization aiming to identify dissimilar regions to those already sampled for bats in Brazil. We used 21 environmental variables to characterize 1,531 unique localities where bats occur. Then, we applied the parameters of a generalized linear model (GLM) to extrapolate the expected values of the environmental variables for the entire country. We compared the predicted values of localities with newly described bat species occurrence against the values for other bat species.

Results: We found that sites from which recently discovered species were described are environmentally distinct from the sites where previously described species occur. Therefore, new occurrences and even new species could be found in regions that are environmentally dissimilar from those already surveyed. By crossing the model with a human footprint map, we defined temporal priorities for field inventories. Regions such as the Northern Cerrado and Western Caatinga should be surveyed first. Similar approaches could be undertaken for other biological groups or regions, allowing the identification of spatial congruence and the development of a comprehensive national programme for biological field inventories.

Main conclusion: Newly described species occurred in environments dissimilar to those previously identified, showing that environmental complementarity analysis is a valid approach to define priority regions for new bat inventories.

1 | INTRODUCTION

Knowledge concerning the spatial distribution of organisms on Earth is the cornerstone for understanding biogeographic patterns, historical speciation events, formation of centres of endemism, and how local and regional biodiversity might respond to increasing human pressure. The difference between what we know and what we should know about species distribution is called the "Wallacean shortfall" (Lomolino, 2004; Whittaker et al., 2005); this difference imposes immense constraints on the implementation of effective management and conservation actions (Cardoso, Erwin, Borges, & New, 2011). The search for data on species distributions started with the first biogeographers at least two centuries ago; nonetheless that challenge persists, as primary biodiversity data for several terrestrial and marine areas are still incomplete or even completely missing (Funk, Richardson, & Ferrier, 2005; Lobo et al., 2018; Lomolino, 2004; Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000; Olson & Dinerstein, 1998).

Field expeditions in remote or unsampled areas are one way to obtain data on species occurrence, but this activity is time-consuming, and costs may vary enormously depending on the region (Balmford & Gaston, 1999). Therefore, funding for this task should be allocated strategically and several approaches have been proposed on how to do it: rapid assessments (Herzog, Kessler, & Cahill, 2002; Higgins & Ruokolainen, 2004; Kerr, Sugar, & Packer, 2000; Oliver & Beattie, 1996), indirect assessments (Sueur, Pavoine, Hamerlynck, & Duvail, 2008) and passive techniques (Steenweg et al., 2014). Nevertheless, these techniques try to solve the problem of how to do the surveys, but not where to do them, which remains a key question when time and money are major constraints. There have been some reports in the literature addressing the question of where to conduct additional biodiversity field surveys. Using a multicriteria modelling technique (the overlay of different standardized information, such as biodiversity, climate, terrain, and others, to map poorly surveyed areas), Chapman and McCaw (2017) analysed the environmental characteristics of 420 surveyed points in south-western Australia. They divided their study region into several land conservation units, each one with different environmental attributes and identified regions where additional surveys should be made. In Denmark, Brunbjerg et al. (2019) used the ecospace framework to select sites for conducting field inventories. This framework is based on the principle that low-dimensional environmental hyperspace can predict variations among multi-taxa species richness. After analysing the environmental gradient along the study region, Brunbjerg et al. (2019) selected 130 sites for field inventories. Their findings included 142 new species and 143 new occurrences for Denmark.

The use of spatial units for the identification of priority areas for biodiversity surveys is a common aspect between the studies of Chapman and McCaw (2017) and Brunbjerg et al. (2019). The first study defined "land conservation units" and the second "ecospaces." The definition of spatial units adds some potential subjectivity to the analysis because the parameters for its definition may vary between researchers. Other authors have suggested other strategies. In the survey gap analysis proposed by Funk et al. (2005), there is no need to a-priori divide a region into spatial or environmental units. However, there is a need for defining weights for each environmental variable in the linear regression model. According to these authors, a researcher with enough expertise may define "the relative importance of each variable in driving biological variation."

Here we propose a novel method, aiming to diminish, as much as possible, the influence of the researcher on the definition of priority areas for biological inventories. Our method is based on the identification of non-surveyed sites that are environmentally dissimilar to those sites where biodiversity surveys have already been carried out. Thus, additional occurrences for taxa already described, but also unknown taxa, would be expected to occur as a result of surveying such distinct areas. We also combined the gradient of environmental similarity with a human pressure map to identify both spatial and temporal priorities and incorporate existing trends in the threats to the native ecosystems.

We used Brazilian bats as a model system; there are several reasons for this. First, Brazil is one of the most diverse countries for Chiroptera, harbouring at least 182 species (Nogueira et al., 2018); however, information on Brazilian bat diversity and distribution is still scarce. In fact, 60% of the 8.5 million km^2 constituting the continental Brazilian territory has never been surveyed for bats, and none of the six terrestrial Brazilian biomes—Amazonia, Cerrado, Caatinga, Atlantic Forest, Pantanal, and Pampas—is adequately surveyed (Bernard, Aguiar, & Machado, 2011). Second, human pressure on natural areas in Brazil is huge, and increasing alarmingly every day, with the constant loosening of biodiversity conservation policies. According to the Food and Agriculture Organization (FAO), over the last 15 years Brazil lost more forest area than any other tropical country (FAO, 2015). Several authors have demonstrated that although the responses of bats to human pressure are often species-specific, the prevailing trend is negative (see Voigt & Kingston, 2016 for details) which can cause decreases in populations and even local extinction of bat species (Aguiar, Brito, & Machado, 2010; Epstein et al., 2009). Thus, we used the human footprint index or map (Sanderson et al., 2002) as a surrogate for anthropogenic pressures. The human footprint index or map can be used to indicate regions where bats may be most affected by environment alterations. Consequently, it will be possible to define spatial and temporal priorities to conduct field surveys in Brazil. Third, because bats respond subtly to changes in land use, management intensities and extreme weather events (Sherwin, Montgomery, &

Lundy, 2013), they are considered good bioindicators (Jones, Jacobs, Kunz, Willig, & Racey, 2009), which favours their use in analysis where anthropic pressures and gap knowledge are combined.

Recent reports have shown that increases in bat species richness across time are not stabilizing (Nogueira et al., 2018), meaning that the probability of finding new species is high if additional surveys are made in appropriately targeted regions. A synthesis of possible situations when and where to find new species is shown in Figure 1. The niche conservatism hypothesis states that closely related species tend to occupy similar niches (Peterson, Soberón, & Sánchez-Cordero, 1999; Wiens & Graham, 2005), suggesting that regions with environmental conditions similar to those more recently surveyed and where new species have been described could harbour undescribed—potentially cryptic—species. Indeed, over the past decade, 13 new bat species have been described in Brazil, of which 12 belong to an existing genus (Nogueira et al., 2018). Based on the niche conservatism hypothesis, new species could be found in regions environmentally similar to those of newly described species, regardless of whether the area is poorly or well-surveyed, that is, in regions C and D (Figure 1). Alternatively, finding new species would be feasible if different environments are explored, preferable away from the already surveyed areas (regions A and B in Figure 1). It is well known that the similarity between species communities

decreases as distance between the communities increases; this is a consequence of environmental or climate gradients or a consequence of the organisms' dispersal limitations (Condit et al., 2002; Nekola & White, 1999).

Divergent natural selection then leads to distinct adaptations, evolutionary divergence and, eventually, to new species following a pattern of adaptive radiation into new environments (Schluter, 1996; Simpson, 1953). Adaptive radiation is likely to occur after the invasion of a new environment by one or a few lineages, or through the evolution of "key-innovations" opening new adaptive zones that may subsequently be partitioned ecologically (Simpson, 1953). So, speciation (and radiation) events may be occurring in regions A or B, which are environmentally different from regions C and D (Figure 1). Furthermore, if the environmental characteristics of undersampled areas such as regions A and D are different from the regions already studied (i.e., regions B and C), then we should expect to find more new species in the regions that have been undersampled and that have a low similarity to the already surveyed regions (region A).

Thus, in this study, we test two hypotheses: (1) considering that the existing pattern of surveys in Brazil is very concentrated in the southeastern region, areas not surveyed in Brazil (regions A and D, Figure 1) will be environmentally different from those already surveyed (regions B and C, Figure 1); and (2) newly described bat species (in or after 2010) will tend to occur in areas that are environmentally distinct from those of the species described before 2010 (regions A and B, Figure 1).
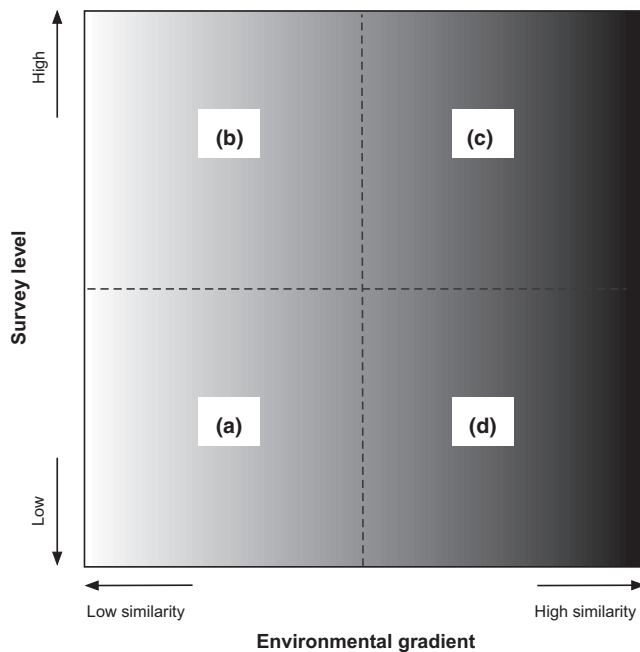
2 | METHODS

2.1 | Bat species occurrence points

We compiled a list of all bat species known to occur in Brazil, considering the list of 182 species by Nogueira et al. (2018) and its update found on the site of the Brazilian Bat Research Society—SBEQ (https://www.sbeq.net/lista-de-especies), plus four additional species recently described: *Eumops chimaera* Gregorin, Moras, Acosta, Vasconcellos, Poma, Santos & Paca 2016, *Histiotus diaphanopterus* Feijó, Rocha & Althoff 2015, *Lonchophylla inexpectata* Moratelli & Dias 2015, and *Pteronotus alitonus* Pavan, Bobrowieck & Percequillo 2018 (Table S1). We used a database organized by L.M.S. Aguiar over three decades by searching for distribution records in specialized literature, museums, and complementing this with records from online databases (e.g., Global Information Facility—GBIF). From the database of over 44,000 records for South America, we selected 17,055 records for bats occurring in Brazil. Recently obtained and other unpublished records from the personal collections of M.J.R. Pereira and M. Zortea were also added to this data set. We considered as a unique location any locality with one or more bats within a radius of 10 km. We used the package *rangeBuilder* (Rabosky et al., 2016) in R (R Core Team, 2019) to apply a spatial filter to eliminate all duplicated coordinates and keeping just one-point location (see details in R script—Supporting Information). Thus, we obtained a total of

FIGURE 1 Hypothetical situations where new bat species could be found in Brazil. The abscissa represents an environmental gradient related to the similarity between points. The ordinate represents a variation on the level of biological surveys in a region. The two lines represent the mean value of each axis. The contrast of the quadrants A + B versus C + D represents the hypothesis of the expected environmental difference between areas where newly described bat species occur in Brazil (after 2010) and areas where earlier described species occur. The contrast of the quadrants A + D versus B + C represents the hypothesis of the expected difference between regions with and without bat records in Brazil

8,110 records from 1,531 unique localities (considering a minimum distance of 10 km between localities). We categorized occurrence records of 13 bat species that were described in the last decade (after 2010) as recently described location records (Table 1). They represent the species described in a short period during the last decade, considering the cumulative curve of described species over time (Figure S1).

2.2 | Environmental variables

We selected 21 environmental variables, 19 bioclimatic (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), a continuous vegetation field (CVF) image (see below) and a digital elevation model (DEM). The CVF (DiMiceli et al., 2010) is composed of images created with the Moderate Resolution Imaging Spectroradiometer sensor (MODIS), carried by the Terra and Aqua satellites. The images contain estimates of vegetation cover, which are represented at a scale of 0 (no vegetation) to 1 (100% vegetation coverage) at a spatial resolution of 250 m (product MOD44B v006). We obtained 17 tiles to produce a single image covering the Brazilian territory and used the MODIS Reprojection Tool (actually renamed HEG—available at https://wiki.earthdata.nasa.gov/) to mosaic and project them to geographical degrees with the WGS84 datum. Then, we used the *raster* package

(Hijmans, 2017) to resample the map to the same spatial resolution as the bioclimatic variables (2.5 arc minutes or approximately 5×5 km per pixel). Additionally, we used a DEM derived from the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) available at https://www.usgs.gov/land-resources/eros/coastal-changes-and-impacts/gmted2010. The GMTED2010 is a topographic data set covering all regions of the globe. We downloaded the file corresponding to the maximum elevation found in each cell at 30 arc second of spatial resolution. Then, we clipped the file to the boundaries of Brazil and followed the same procedures described above to resample the DEM image, downscaling to 2.5 arc minutes.

2.3 | Spatial analysis

We used a generalized linear model (GLM) to create a map of the environmental characteristics of the Brazilian territory comparing the localities with and localities without bat records. First, we used the packages *sf* (Pebesma, 2018) and *raster* (Hijmans, 2017) to create a 50-km buffer around each one of the 1,531 localities where bats had been recorded, using the buffer as a mask (Figure S2). Then, we used the function *kfold* from package *dismo* (Hijmans, Phillips, Leathwick, & Elith, 2017) to randomly generate a set of 1,531 points outside the mask. Hence, we created a balanced database with 50% of the points with bat occurrences

TABLE 1 List of bat species recently described (since 2010) that occurs in Brazil

Species	Year	Author(s)	English name	Type locality	Coordinates
Chiroderma vizottoi	2010	Taddei and Lim	Vizotto's Big-eyed Bat	Teresina, Piauí, Brazil	5°02′S–42°45′W
Peropteryx pallidoptera	2010	Lim, Engstrom, Reid, Simmons, Voss and Fleck	Pale-winged Dog-like Bat	Orellana, Ecuador	0°48′S–76°24′W
Platyrrhinus angustirostris	2010	Velazco, Gardner and Patterson	Slender Broad-nosed Bat	Bongará, Peru	5°58′S–77°55′W
Platyrrhinus fusciventris	2010	Velazco, Gardner and Patterson	Brown-bellied Broad-nosed Bat	Cerro Neblina, Venezuela	0°49′S–66°09′W
Myotis lavali	2011	Moratelli, Peracchi, Dias and de Oliveira	LaVal's Myotis	Exu, Pernambuco, Brazil	7°30′S–39°43′W
Myotis izecksohni	2011	Moratelli, Peracchi, Dias and de Oliveira	Izecksohn's Myotis	Balsa Nova, Paraná, Brazil	25°34′S–49°37′W
Dryadonycteris capixaba	2012	Nogueira, Lima, Peracchi and Simmons		Linhares, Espírito Santo, Brazil	19°22′S–40°04′W
Lonchophylla peracchii	2013	Dias, Esberard and Moratelli	Peracchi's Nectar Bat	Rio de Janeiro, Brazil	22°50′S–43°15′W
Thyroptera wynneae	2014	Velazco, Gregorin, Voss and Simmons	Patricia's Disk-winged Bat	Loreto, Peru	45°05′S–73°40′W
Histiotus diaphanopterus	2015	Feijó, Rocha and Althoff	Transparent-winged Big-eared Bat	Sento Sé, Bahia, Brazil	9°52′S–41°04′W
Lonchophylla inexpectata	2015	Moratelli and Dias		Barra, Bahia, Brazil	12°42′S–41°33′W
Eumops chimaera	2016	Gregorin, Moras, Acosta, Vasconcellos, Poma, Santos and Paca	Chimeraís Bonneted Bat	Marliéria, Minas Gerais, Brazil	19°44′S–42°38′W
Pteronotus alitonus	2018	Pavan, Bobrowieck and Percequillo		Manaus, Amazonas, Brazil	2°20′S–60°06′W

Variable	Variance Inflation Factor (VIF)			GLM output		
	Full model	Selected?	Initial model	Final model	Estimate	z value	p Value
Bioclim 1	469.263		–	–	–	–	–
Bioclim 2	90.565		2.241	2.290	−0.466	−10.766	<.001
Bioclim 3	50.725		3.503	2.873	−0.091	−11.116	<.001
Bioclim 4	590.018		–	–	–	–	–
Bioclim 5	1.91×10^{14}		–	–	–	–	–
Bioclim 6	8.87×10^{14}		–	–	–	–	–
Bioclim 7	6.18×10^{14}		–	–	–	–	–
Bioclim 8	12.990		3.591	1.944	0.052	1.593	.085
Bioclim 9	29.297		–	–	–	–	–
Bioclim 10	416.139		–	–	–	–	–
Bioclim 11	2,467.380		–	–	–	–	–
Bioclim 12	64.292		–	–	–	–	–
Bioclim 13	51.396		1.834	–	–	–	–
Bioclim 14	177.222		2.749	2.416	−0.009	−0.075	<.001
Bioclim 15	15.746		–	–	–	–	–
Bioclim 16	100.530		–	–	–	–	–
Bioclim 17	196.950		–	–	–	–	–
Bioclim 18	4.067		1.897	1.626	0.001	3.773	<.001
Bioclim 19	5.324		–	–	–	–	–
DEM	7.283		3.217	–	–	–	–
CVF	2.447		2.419	2.362	−0.003	−6.521	<.001

Note: The column "Full model" shows the VIF values when all variables were considered. The column "Initial model" shows the VIF values after excluding variables with values greater than 5. The column "Final model" shows the VIF value after the stepwise GLM analysis. Variables in boldface are those used to the GLM analysis.

Observation: Bioclim 1 = Annual Mean Temperature, Bioclim 2 = Mean Diurnal Range (Mean of monthly (max temp–min temp)), Bioclim 3 = Isothermality (Bioclim 2/Bioclim 7) (* 100), Bioclim 4 = Temperature Seasonality (standard deviation *100), Bioclim 5 = Max Temperature of Warmest Month, Bioclim 6 = Min Temperature of Coldest Month, Bioclim 7 = Temperature Annual Range (Bioclim 5–Bioclim 6), Bioclim 8 = Mean Temperature of Wettest Quarter, Bioclim 9 = Mean Temperature of Driest Quarter, Bioclim 10 = Mean Temperature of Warmest Quarter, Bioclim 11 = Mean Temperature of Coldest Quarter, Bioclim 12 = Annual Precipitation, Bioclim 13 = Precipitation of Wettest Month, Bioclim 14 = Precipitation of Driest Month, Bioclim 15 = Precipitation Seasonality (Coefficient of Variation), Bioclim 16 = Precipitation of Wettest Quarter, Bioclim 17 = Precipitation of Driest Quarter, Bioclim 18 = Precipitation of Warmest Quarter, Bioclim 19 = Precipitation of Coldest Quarter.

Abbreviations: CVF, Continuous Vegetation Fields; DEM, Digital Elevation Model.

and other 50% with no bat occurrence. Then, we used the package *sf* (Pebesma, 2018) to build a buffer with a 10-km radius around each set of the 3,062 points (1,531 inside the mask and 1,531 outside the mask), and, by using the package *velox* (Philipp, 2017), we extracted the mean value of all the 21 environmental variables in each buffer. We also used the function *kfold* from the *dismo* package (Hijmans et al., 2017) to split

the data set into two groups: 80% ($N = 2,449$) were used as training points in the GLM analysis, and the other 20% ($N = 613$) were used as testing points to calculate the accuracy of the model (see below).

2.4 | Environmental variables selection and model accuracy

We used the package *MASS* (Venables & Ripley, 2002) for model selection based on a stepwise process (ran in both directions, i.e. forward and backward) with Akaike information criterion calculation and an analysis of variance (ANOVA) for the selected predictors. Considering that bioclimatic variables can be highly correlated, we used the function *vif* (variance inflation factor—VIF) from the package *car* (Fox & Weisberg, 2019) to eliminate all correlated explanatory variables of the full model, that is the initial model with all 21 environmental variables. The variance inflation occurs when explanatory variables present some level of collinearity, which causes the inflation of the standard errors of the parameters with the square root of $1/(1 − R^2_j)$ (Zuur, Ieno, & Elphick, 2010). We analysed the VIF value for all variables and eliminated those that presented VIF above 3 (Zuur et al., 2010) following the decreasing order from high to low values. After the VIF analysis, our initial model included eight environmental variables (Table 2). After running the stepwise analysis on the GLM, we ended up with six environmental variables, all presenting a VIF value below 3 (Table 2).

Considering that our main goal was to predict regions in Brazil where field inventories should be carried out to maximize the chance of finding new occurrences, or even new species, we evaluated how well the obtained model is performing with respect to predicting values from an independent set of data. Basically, the approach was to apply the parameters of the fitted model (predictors and their weight) using an independent set of testing data (the above mentioned 20% of testing data) to validate the predicted values.

We used the functions *prediction* and *performance* from the *ROCR* package (Sing, Sander, & Beerenwinkel, 2005) to test the model's accuracy. The function *prediction* standardizes the values from the GLM model, and the function *performance* tests different and increasing cut-off values (resulting from the *prediction* function) to identify the peak of the model's accuracy. The "peak" is the value where most of the testing points, which are classified as 0 (localities with no bat records) and 1 (localities with bat records), are correctly classified.

To test our first hypothesis (areas with no bat records are environmentally different from the areas with bat records), we extracted the model's predicted values for 1,531 localities with bat records and 1,531 random localities with no bat records. Considering that the model values do not follow a normal distribution (Shapiro test, $W = 0.9486$, $p < .001$), we used the Wilcoxon nonparametric test to identify whether the training data and the testing data had statistically similar distribution. We used the same procedures to extract values from the prediction model for localities where bat species had been reported before 2010, and for the newly described bat species.

The model values for earlier described (<2010) and newly described (≥2010) species also do not follow a normal distribution (Shapiro test, $W = 0.9486$, $p < .001$ for newly described species, and $W = 0.96541$, $p < .01$ for older species). Therefore, we also used the Wilcoxon test for this case. Considering the unbalanced sample size for earlier described species ($N = 8,110$) and newly described species ($N = 110$), we created a routine in R to randomly select 110 records from the earlier described species data set and test the difference by using the Wilcoxon nonparametric test. We repeated this routine 1,000 times to obtain the mean values for W and p for the performed tests.

2.5 | Spatial prioritization

We applied the function *predict* from the R *raster* package (Hijmans, 2017) to the resulting GLM to create a map for the entire country, to estimate the relative similarities or dissimilarities of the environmental predictors at any region to the conditions at the localities of known bat occurrences. The procedure is similar, but not identical, to an ecological niche modelling, where regions with occurrences of a species under analysis are environmentally characterized (e.g., ranges of temperature, precipitation or topography) and extrapolated to other regions that might have the same parameters (Peterson, 2001; Soberón & Peterson, 2005).

We superimposed the environmental model with the Human Footprint (HFP) map version 2—1995–2004 (Wildlife Conservation Society—WCS & Centre for International Earth Science Information Network—CIESIN—Columbia University, 2005), here used as an indicator of temporal priorities. The HFP map is a combination of layers representing the Human Influence Index normalized by biome and realm. It uses different layers such as population pressure (population density), human land use and infrastructure (built-up areas, night-time lights, land use/land cover) and human access (coastlines, roads, railroads, navigable rivers) to represent a map of anthropogenic impact on nature. Thus, we used the HFP values to indicate the urgency of surveys, with higher values suggesting a temporal priority over lower values. To combine both maps (GLM prediction and the HFP), we reclassified the GLM prediction map values into a 0–100 scale, which is the same range of values of the HFP map. Then, we summed both maps and extracted the mean value. Thus, low values in the final map represent areas with low environmental similarity and low pressure, while high values represent areas with high environmental similarity and high pressure. All data processing and statistical analysis were done in R v.3.5.3 (R Core Team, 2019), and maps were done with the packages *sf* (Pebesma, 2018), *raster* (Hijmans, 2017), and *tmap* (Tennekes, 2018).

3 | RESULTS

Our GLM model included the variables Mean Diurnal Range (Bioclim 2), Isothermality (Bioclim 3), Mean Temperature of Wettest Quarter

(Bioclim 8), Precipitation of Driest Month (Bioclim 14), Precipitation of Warmest Quarter (Bioclim 18) and the Continuous Vegetation Fields (CVF) as the main predictors (Table 1) and model accuracy of 0.7812 with a cut-off of 0.5598 (Figure S3). The model extrapolation map (Figure 2) shows two contrasting regions, represented by the levels of red (low similarity) and levels of green (high similarity). Areas located in the Amazon, Northern Cerrado and Western Caatinga are environmentally different from areas located in the Central-South Cerrado, Eastern Caatinga, Pantanal, and most of the Atlantic Forest.

Localities with bat records are environmentally different from the localities with no bat records (Figure 3a). The GLM values from localities with bat records tend to have positive values (mean 0.7873, $N = 1531$), while regions with no bat records tend to have negative values (mean $= -0.8085$, $N = 1531$). Therefore, we corroborated our first working hypothesis that areas with and without bat records would be environmentally different.
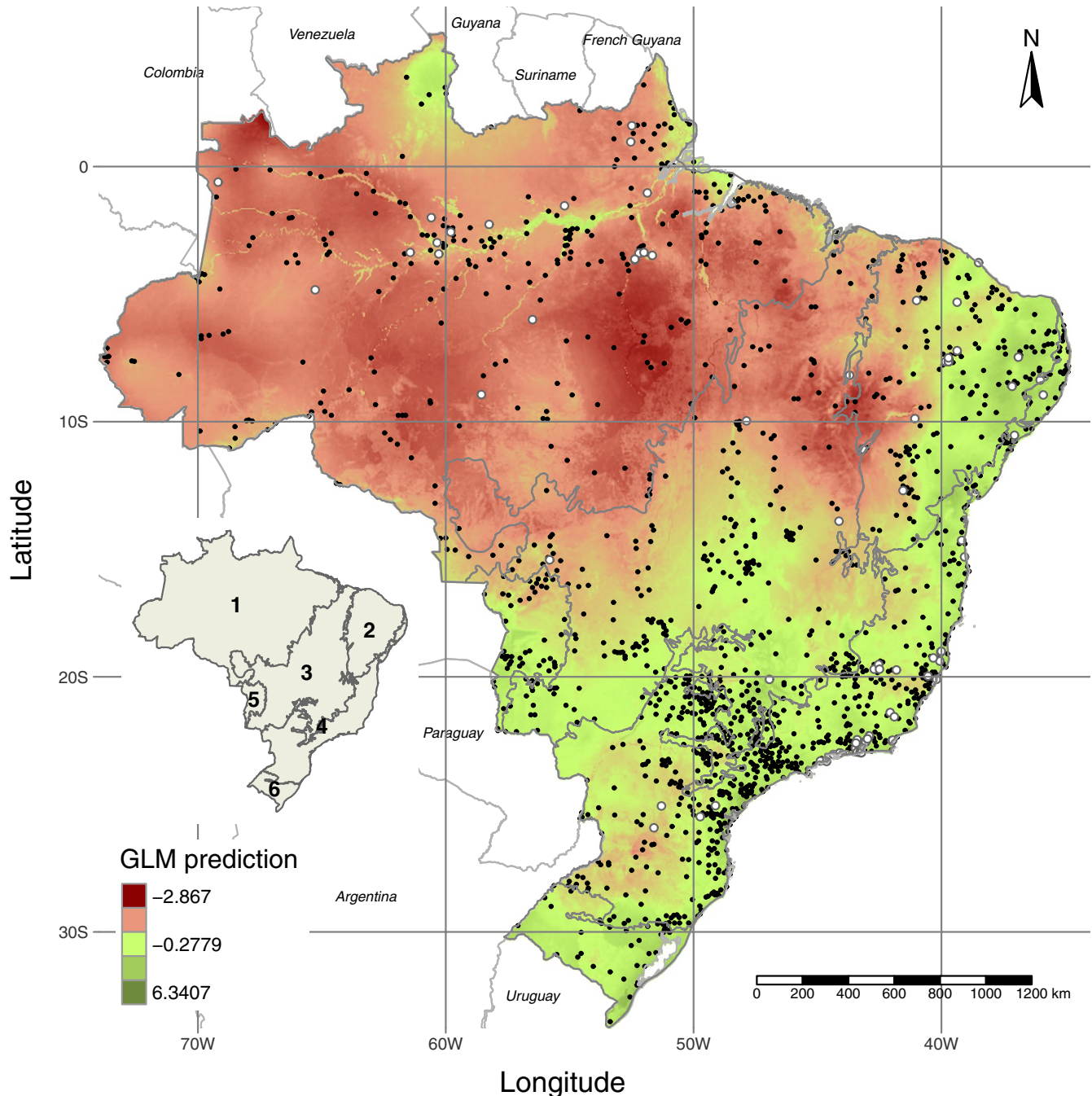

FIGURE 2 Extrapolation of predicted values of the GLM model for the Brazilian territory. Values represent a combination of bioclimatic variables (2, 3, 8, 14 and 18), and the continuous vegetation field. Regions with positive values (green colours) are environmentally similar to each other, but environmentally different from those regions with negative values (red colours). The black points represent the localities with bat records in Brazil, and the white points represent the localities with bats described after 2010. Divisions on the smaller map represent the biomes: 1—Amazonia, 2—Caatinga, 3—Cerrado, 4—Atlantic Forest, 5—Pantanal, 6—Pampas

FIGURE 3 Comparison of the GLM predicted values for regions with (w/) and without (w/o) bat records in Brazil (a), and for localities with bat species described prior and after 2010 (b). In both figures, the white square points represent the mean values, and the horizontal lines represent the median for each category
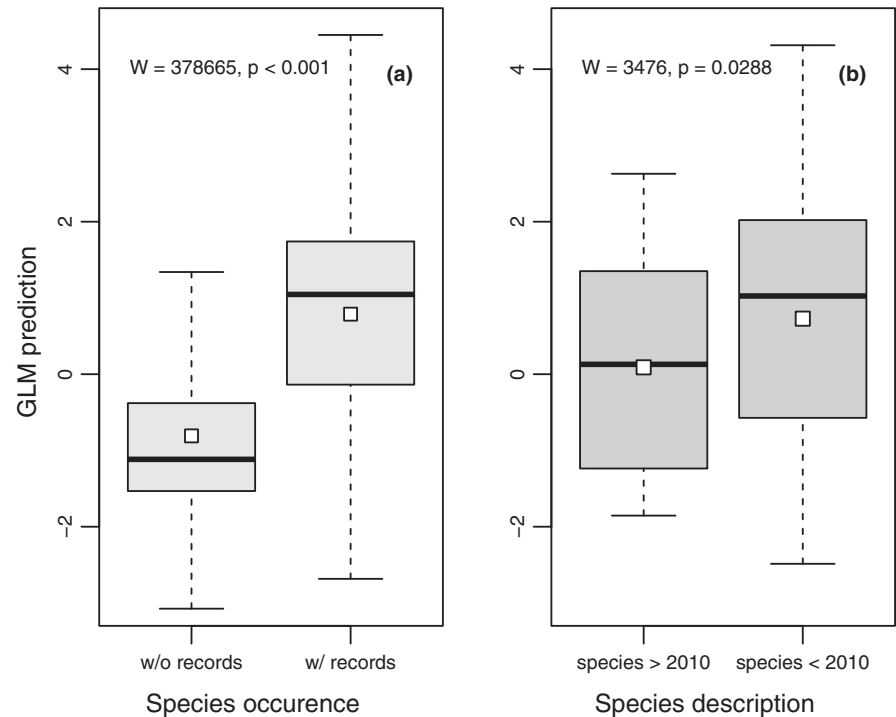
We found a total of 110 records in Brazil belonging to 13 bat species described after 2010 (Figure 3b, Table 2). Values predicted by the multivariate GLM stepwise analysis, which reflects the environmental characteristics, indicated that areas where newly described bat species were found differed statistically from those areas where species had been described earlier in 89.8% of the 1,000 runs (mean values for $W = 3,476$, and for $p = .028$) (Figure 3b). Therefore, we also corroborate our second working hypothesis.

The combination of environmental similarity and HFP maps reveals a gradient of prioritization of areas for new field surveys (Figure 4). As a general pattern, large areas with low environmental similarity and high human pressure are located in a diagonal that crosses Brazil from the Northeast to the Southwest, with some sparse areas along the coast. Areas with low environmental similarity and low human pressure are located mostly in the Amazon, Northern Cerrado and Western Caatinga biomes. Areas with high similarity and high human pressure are located in the Eastern Caatinga, most of the Atlantic Forest, Southern Cerrado and parts of the Pampas.

4 | DISCUSSION

The distribution of bat species is shaped by environmental variables, such as temperature, precipitation seasonality and vegetation coverage. Even just considering presence-only data, we were able to distinguish regions with and without bat records based on their environmental similarity. Our findings indicate a huge contrast between different regions in Brazil, especially for the Brazilian coast (from the Northeastern to Southern regions, including the biomes of the Caatinga, Atlantic Forest and Pampas) in comparison with the Northern Cerrado and the Amazon, where there are few bat

records. There are several possible explanations for the lack of field inventory for bats, which is also true for other groups. Due to its natural characteristics, access in the Amazonian region is primarily by river; roads are not only scarce, but also precarious. According to the 2018 Yearbook on Transport in Brazil prepared by the National Confederation on Transport—CNT (CNT, 2018), the roads in the states making up Amazonia represent only 8.7% (150,000 km) of the Brazilian roads (1.72 million km). From those roads, only 38% were classified as "fine" or "good" for use, which imposes an enormous restriction on access to the region. While this inaccessibility has meant that these areas have maintained their value with respect to conservation, access to non-surveyed regions is a primary condition to promote biodiversity inventories.

The conduction of systematic inventories in Brazil, not only for bats but for all biodiversity components, is a demand of the Brazilian Decree 4339 that establishes the National Policy for Biodiversity (Brasil, 2002). However, since its publication, no consistent or long-term programmes aiming to cover poorly studied regions have been implemented in the country. It has been estimated that if we keep the same pace in conducting inventories without a systematic and targeted programme for biodiversity surveys, we will take around 200 years to survey the whole country for bats (Bernard et al., 2011). Our results suggest that a survey gap analysis based on an environmental complementarity approach highlights not only regions where new distribution records can be registered but also those regions where there is a higher chance of finding new species.

Contrary to the hypothesis of niche conservatism (Peterson et al., 1999; Wiens & Graham, 2005), we found that newly described bat species in Brazil are located in regions environmentally different from those regions where earlier described species had been reported. The importance of niche conservatism in the
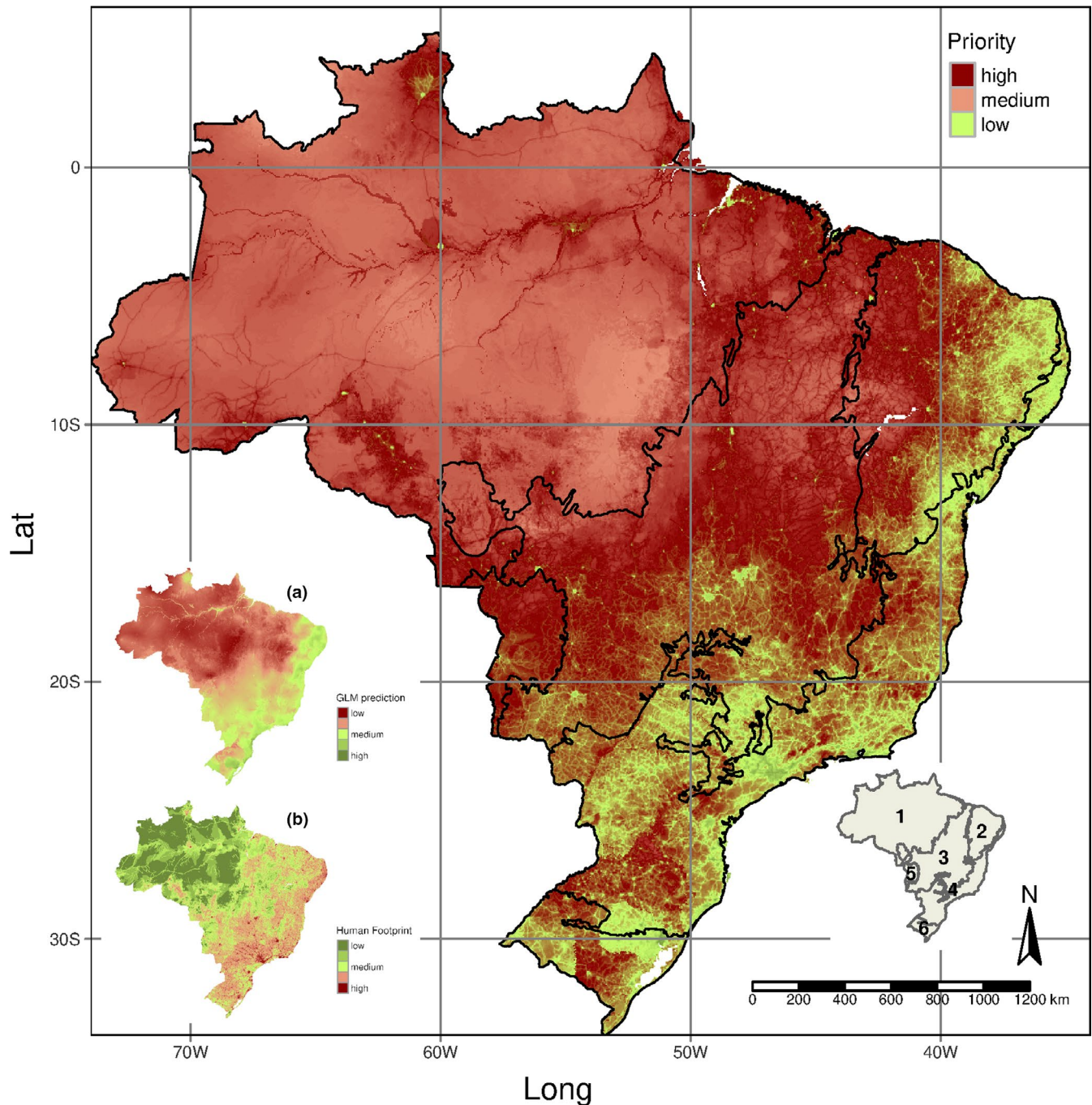
FIGURE 4 Priority areas for bat inventories in Brazil resulting from the combination of environmental characteristics of the localities with and without bat occurrences (small map 'a'), and the Human Footprint Index (small map 'b'). Dark red areas represent the top priority for conduction new inventories (low environmental similarity plus high human pressure). Light red areas are those with low environmental similarity plus high human pressure (medium priority). Green areas are those with high environmental similarity and high human pressure (low priority). Divisions on the smaller map (right side) represent the biomes: 1—Amazonia, 2—Caatinga, 3—Cerrado, 4—Atlantic Forest, 5—Pantanal, 6—Pampas

evolutionary process can change from group to group, and possibly from region to region, as suggested by the tropical niche conservatism hypothesis (Wiens & Donoghue, 2004). While a conservative evolution of niche characteristics was found for sister species of butterflies, birds and mammals in Mexico (Peterson et al., 1999), a more dynamic change in niche evolution was observed for ovenbirds (*Geosita* genus, composed by 11 species)

(Ribeiro, Peterson, Werneck, & Machado, 2017) and bats (Peixoto, Villalobos, & Cianciaruso, 2017; Ramos Pereira & Palmeirim, 2013; Stevens, 2011; Villalobos, Lira-Noriega, Soberón, & Arita, 2014) in South America. For ovenbirds, it was suggested that the rapid environment changes along the Andes caused by orogenic events during the Miocene resulted in pronounced niche evolution for the birds (Ribeiro et al., 2017).

For bats, the importance of niche conservative can vary among families (Peixoto et al., 2017; Ramos Pereira & Palmeirim, 2013). For example, the Phyllostomidae seems to be firmly attached to the tropical niche conservatism theory, since the species are concentrated in their region of geographical origin (the tropics). However, the diversity of the Vespertilionidae, presumably of temperate origin, was not associated with the niche conservatism theory (Ramos Pereira & Palmeirim, 2013). Considering that half of the newly described species in Brazil belong to the Phyllostomidae (six of 13 newly described species), our results are consistent with the tropical niche conservatism theory, and the regions with the occurrence of new species should be similar to the regions with old species occurrence. The number of newly described Vespertilionidae is also significant (four of 13 species), suggesting that the lower richness of vespertilionids in South America, when compared to North America, and which Ramos Pereira and Palmeirim (2013) theorized as resulting from historical contingency (i.e., competition from the diverse bat fauna already present in South America before the arrival of vespertilionids would have limited their richness in the region), is probably also the result of: (a) data deficiencies, (b) a higher trend for crypticity, as suggested by recent descriptions in Neotropical and Afrotropical areas (e.g., Koubínová, Irwin, Hulva, Koubek, & Zima, 2013; Moratelli & Wilson, 2014; Moratelli, Wilson, Gardner, Fisher, & Gutiérrez, 2016) or (c) a more recent history of diversification of the family in this region, an explanation supported by the recent arrival in South America—only 7–10 million years ago—of the genus with the most species in the Vespertilionidae, *Myotis* (Stadelmann, Lin, Kunz, & Ruedi, 2007). These are, in fact, three highly interconnected explanations.

One possible explanation for our result is the lack of data. As indicated previously, bats have been little studied in Brazil (Bernard et al., 2011), and most of the country is undersampled. We were able to find only 110 points of occurrences for the 13 newly described species (an average of 8.4 points per species). Unfortunately, this is the current level of understanding about bat species occurrence in Brazil, and it is the exact point where our study can contribute the most.

We were able to show the existence of differences in the environmental characteristics between regions where earlier described and newly described bat species were found, supporting our second working hypothesis. Regions with higher chances of harbouring new bat species are located mostly in the Eastern Caatinga, Northern Cerrado, most of the Amazonia biome, and some areas situated in the Eastern and Southeastern regions (Atlantic Forest, and Pampas). A search for newly described species in Brazil on 'Web of Science' and 'Scopus' using the search terms "Brazil" and "new species" and "Mammal*") revealed that at least 18 new species of mammals have been found since 2010. This includes a new species of tapir (Cozzuol et al., 2013), a new species of river dolphin (Hrbek et al., 2014), and a new species of primate (Dalponte, Silva, & de Silva Júnior, 2014), and potentially seven new species of silky anteater (Miranda, Casali, Perini, Machado, & Santos, 2018); many of these were found in the

same priority areas we identified for bats, such as the Cerrado–Amazonia transition.

It is worth noting that new species can be found in any place, similar or not to those places already surveyed. Raxworthy et al. (2003) mapped the potential distribution of chameleon species in Madagascar and found three non-surveyed regions with potential occurrence of new species. It turned out that two new species were found in the regions indicated by their model, corroborating the need to conduct surveys in undersampled areas. The results of our analysis of environmental complementarity point out huge areas in Brazil that need to be surveyed. Regions with no bat records represented around 61% of the Brazilian territory, or nearly 5.2 million km^2 (equivalent to about half the area of Europe). Because the area is huge, the addition of a surrogate for human pressure as a second dimension enabled us to better define the priority regions for future field surveys. The combination of these two dimensions (spatial and temporal variables) is a common approach in the definition of, for instance, conservation priorities. Different institutions and non-governmental organizations have proposed such prioritization scheme (for a revision see Brooks et al., 2006), which is based on the selection of some measurement of biodiversity (number of endemic species or irreplaceable sites for instance) and some measurement of the vulnerability of native areas (percentage or remaining native coverage). In terms of temporal prioritization, it is clear that the creation of roads, human settlements, agribusiness activities and extensive infrastructure are the most critical drivers of habitat destruction in most of Brazil (Diniz-Filho et al., 2009; Fearnside, 2014; Klink & Machado, 2005; Oliveira Filho & Metzger, 2006; Strassburg et al., 2017). Thus, temporal priorities are essentially concentrated in two significant regions in Brazil: (a) the Eastern region (high pressure) and (b) the Western region (low pressure).

Considering human pressure on the environment, some regions should receive urgent attention as there is a risk of the loss of biodiversity occurring before the species are even described by science. Previous studies have indicated that it will take at least 200 years to minimally survey the Brazilian territory for bats if we maintain the same effort as in the past decades of study (Bernard et al., 2011). Obviously, we cannot wait that long. Although Brazil is one of the countries with highest rates of deforestation in the world (FAO, 2015), we still have a huge knowledge gap concerning how that is impacting the country's biodiversity. Although Brazil was the first signatory to the Convention on Biological Diversity (CBD) in 1992, there is no official or comprehensive programme for biodiversity inventory in the country. According to the First National Report to the CBD—Brazil (Brasil, 2015), only a few taxonomic groups (e.g., plants) have specific programmes for field inventories, and most actions are concentrated on gathering information to contribute to databases. In summary, the identification of regions for conducting optimized field inventories is just the first step to fill gaps in species distributions—the so-called "Wallacean shortfall," sensu Lomolino (2004), Whittaker et al. (2005); however, a large-scale and long-term inventory programme is the key subsequent action.

4.1 | The application of our approach in other regions

The method that we developed can be applied in any region and at any geographical scale if an appropriate data set is available. With respect to climate data, we consider that for any regional of subcontinental analysis (as we did for Brazil), the Worldclim data set is adequate. However, analysis at a smaller scale will demand the preparation of environmental maps with a finer resolution. For such cases, perhaps the use of satellite images would be the best starting point. Images generated by Landsat (Operational Land Imager—OLI) or Aqua/Terra MODIS satellites can be used to represent the environmental characteristics of any region in the world. MODIS images have the advantage of offering specific products (e.g., surface temperature, primary productivity, vegetation indices) for free and ready to be used at 250-m, 500-m and 1-km spatial resolutions (https://lpdaac.usgs.gov/). If local data on temperature and precipitation are available, maps similar to the bioclimatic variables can be produced by interpolation techniques (Sluiter, 2009). Once the geographical database is set, the method applied in this study can be easily replicated.

5 | CONCLUSIONS

Environmental complementarity analysis proved to be useful in identifying important regions for future bat surveys in Brazil. The combination of our statistical model and a map of the human footprint provided an indication of priority areas in which to conduct bat field surveys. Areas with high human pressure, such as the Northern Cerrado (woodland savanna) and Western Caatinga (seasonal tropical dry forest), are gaps in bat knowledge. In such areas, our statistical model predicts that unknown bat species could well be found. We also recommend that similar analyses are conducted with other taxonomic groups to identify spatial congruences and, therefore, to build a comprehensive national programme for field inventories.

ORCID

Ludmilla M. S. Aguiar https://orcid.org/0000-0002-9180-5052

Maria João R. Pereira https://orcid.org/0000-0002-9365-5166
Marlon Zortéa https://orcid.org/0000-0002-0827-7704
Ricardo B. Machado https://orcid.org/0000-0002-6508-9005

REFERENCES

Aguiar, L. M. S., Brito, D. C., & Machado, R. B. (2010). Do current vampire bat (*Desmodus rotundus*) population control practices pose a threat to Dekeyser's Nectar Bat's (*Lonchophylla dekeyseri*) long-term persistence in the Cerrado? *Acta Chiropterologica*, *12*(2), 275–282. https://doi.org/10.3161/150811010X537855

Balmford, A., & Gaston, K. J. (1999). Why biodiversity surveys are good value. *Nature*, *398*, 204–205. https://doi.org/10.1038/18339

Bernard, E., Aguiar, L. M. S., & Machado, R. B. (2011). Discovering the Brazilian bat fauna: A task for two centuries? *Mammal Review*, *41*(1), 23–39. https://doi.org/10.1111/j.1365-2907.2010.00164.x

Brasil (2002). *Decree 4339 from August, 22, 2002 - National Policy for Biodiversity*. Retrieved from http://www.planalto.gov.br/ccivil_03/decreto/2002/D4339.htm

Brasil (2015). *First National Report to the Convention on Biological Diversity – Brazil* (p. 231). Retrieved from https://www.cbd.int/doc/world/br/br-nr-05-en.pdf

Brooks, T. M., Mittermeier, R. A., da Fonseca, G. A. B., Gerlach, J., Hoffmann, M., Lamoreux, J. F., … Rodrigues, A. S. L. (2006). Global biodiversity conservation priorities. *Science*, *313*, 58–61. https://doi.org/10.1126/science.1127609

Brunbjerg, A. K., Bruun, H. H., Brøndum, L., Classen, A. T., Dalby, L., Fog, K., … Ejrnæs, R. (2019). A systematic survey of regional multi-taxon biodiversity: Evaluating strategies and coverage. *BMC Ecology*, *19*(1), https://doi.org/10.1186/s12898-019-0260-x

Cardoso, P., Erwin, T. L., Borges, P. A. V., & New, T. R. (2011). The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, *144*(11), 2647–2655. https://doi.org/10.1016/j.biocon.2011.07.024

Chapman, T. F., & McCaw, W. L. (2017). Where to survey? Spatial biodiversity survey gap analysis: A multicriteria approach. *Pacific Conservation Biology*, *23*(2), 189. https://doi.org/10.1071/PC16030

CNT (2018). *2018 CNT Yearbook on Transports – Consolidated Statistics*. National Confederation on Transports – CNT. Retrieved from http://anuariodotransporte.cnt.org.br/2018/Inicial

Condit, R., Pitman, N., Leigh, E. G. Jr, Chave, J., Terborgh, J., Foster, R. B., … Hubbell, S. P. (2002). Beta-diversity in tropical forest trees. *Science*, *295*(5555), 666–669. https://doi.org/10.1126/science.1066854

Cozzuol, M. A., Clozato, C. L., Holanda, E. C., Rodrigues, F. H. G., Nienow, S., de Thoisy, B., … Santos, F. R. (2013). A new species of tapir from the Amazon. *Journal of Mammalogy*, *94*(6), 1331–1345. https://doi.org/10.1644/12-MAMM-A-169.1

Dalponte, J. C., Silva, F. E., & de Silva Júnior, J. S. (2014). New species of titi monkey, genus *Callicebus* Thomas, 1903 (Primates, Pitheciidae), from Southern Amazonia, Brazil. *Papéis Avulsos de Zoologia (São Paulo)*, *54*(32), 457–472. https://doi.org/10.1590/0031-1049.2014.54.32

DiMiceli, C. M., Carroll, M. L., Sohlberg, R. A., Huang, C., Hansen, M. C., & Townshend, J. R. G. (2010). *Annual global automated MODIS Vegetation Continuous Fields (MOD44B) at 250 spatial resolution for data years beginning day 65, 2000–2010, Collection 5 - Percent Tree Cover*. Retrieved from http://glcf.umd.edu/data/vcf/

Diniz-Filho, J. A. F., Oliveira, G., Lobo, F., Ferreira, L. G., Bini, L. M., & Rangel, T. F. L. V. B. (2009). Agriculture, habitat loss and spatial patterns of human occupation in a biodiversity hotspot. *Scientia Agricola*, *66*(6), 764–771. https://doi.org/10.1590/S0103-90162009000600007

Epstein, J. H., Olival, K. J., Pulliam, J. R. C., Smith, C., Westrum, J., Hughes, T., … Daszak, P. (2009). *Pteropus vampyrus*, a hunted migratory species with a multinational home-range and a need for regional

management. *Journal of Applied Ecology*, *46*(5), 991–1002. https://doi.org/10.1111/j.1365-2664.2009.01699.x

FAO (2015). *The Global Forest Resources Assessment 2015: How are the world's forests changing?* (2nd ed., p. 46). Retrieved from http://www.fao.org/3/a-i4793e.pdf

Fearnside, P. M. (2014). Impacts of Brazil's Madeira River Dams: Unlearned lessons for hydroelectric development in Amazonia. *Environmental Science and Policy*, *38*(3), 164–172. https://doi.org/10.1016/j.envsci.2013.11.004

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.) Thousand Oaks, CA: Sage. Retrieved from https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Funk, V. A., Richardson, K. S., & Ferrier, S. (2005). Survey-gap analysis in expeditionary research: Where do we go from here? *Biological Journal of the Linnean Society*, *85*, 549–567. https://doi.org/10.1111/j.1095-8312.2005.00520.x

Herzog, S. K., Kessler, M., & Cahill, T. M. (2002). Estimating species richness of tropical bird communities from rapid assessment data. *The Auk*, *119*(3), 749–769. https://doi.org/10.1642/0004-8038(2002)119[0749:ESROTB]2.0.CO;2

Higgins, M. A., & Ruokolainen, K. (2004). Rapid tropical forest inventory: A comparison of techniques based on inventory data from western Amazonia. *Conservation Biology*, *18*(3), 799–811. https://doi.org/10.1111/j.1523-1739.2004.00235.x

Hijmans, R. J. (2017). *Raster v2.3: Geographic data analysis and modeling.* Retrieved from https://cran.r-project.org/package=raster

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high-resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978. https://doi.org/10.1002/joc.1276

Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2017). *dismo: Species Distribution Modeling.* R package version 1.1-4. Retrieved from https://CRAN.R-project.org/package=dismo

Hrbek, T., da Silva, V. M., Dutra, N., Gravena, W., Martin, A. R., & Farias, I. P. (2014). A new species of River Dolphin from Brazil or: How little do we know our biodiversity. *PLoS One*, *9*(1), e83623. https://doi.org/10.1371/journal.pone.0083623

Jones, G., Jacobs, D., Kunz, T., Willig, M., & Racey, P. (2009). *Carpe noctem*: The importance of bats as bioindicators. *Endangered Species Research*, *8*, 93–115. https://doi.org/10.3354/esr00182

Kerr, J. T., Sugar, A., & Packer, L. (2000). Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. *Conservation Biology*, *14*(6), 1726–1734. https://doi.org/10.1111/j.1523-1739.2000.99275.x

Klink, C. A., & Machado, R. B. (2005). Conservation of the Brazilian Cerrado. *Conservation Biology*, *19*(3), 707–713. https://doi.org/10.1111/j.1523-1739.2005.00702.x

Koubínová, D., Irwin, N., Hulva, P., Koubek, P., & Zima, J. (2013). Hidden diversity in Senegalese bats and associated findings in the systematics of the family Vespertilionidae. *Frontiers in Zoology*, *10*, 48. https://doi.org/10.1186/1742-9994-10-48

Lobo, J. M., Hortal, J., Yela, J. L., Millán, A., Sánchez-Fernández, D., García-Roselló, E., … Guisande, C. (2018). KnowBR: An application to map the geographical variation of survey effort and identify well-surveyed areas from biodiversity databases. *Ecological Indicators*, *91*, 241–248. https://doi.org/10.1016/j.ecolind.2018.03.077

Lomolino, M. V. (2004). Conservation biogeography. In M. A. Lomolino, & L. R. Heaney (Eds.), *Frontiers of biogeography – new directions in the geography of nature.* Sunderland, MA: Sinauer Associates Inc. Publishers.

Miranda, F. R., Casali, D. M., Perini, F. A., Machado, F. A., & Santos, F. R. (2018). Taxonomic review of the genus *Cyclope*s Gray, 1821 (Xenarthra: Pilosa), with the revalidation and description of new

species. *Zoological Journal of the Linnean Society*, *183*, 687–721. https://doi.org/10.1093/zoolinnean/zlx079

Moratelli, R., & Wilson, D. E. (2014). A new species of *Myotis* (Chiroptera, Vespertilionidae) from Bolivia. *Journal of Mammalogy*, *95*(4), 17–25. https://doi.org/10.1644/14-MAMM-149

Moratelli, R., Wilson, D. E., Gardner, A., Fisher, R. D., & Gutiérrez, E. E. (2016). A new species of *Myotis* (Chiroptera: Vespertilionidae) from Suriname. *Special Publications of the Museum of Texas Tech University*, *65*, 49–66.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*, 853–858. https://doi.org/10.1038/35002501

Nekola, J. C. C., & White, P. S. S. (1999). The distance decay of similarity in biogeography and Ecology. *Journal of Biogeography*, *26*(4), 867–878. https://doi.org/10.2307/2656184

Nogueira, M. R., Lima, I. P., Garbino, G. S. T., Moratelli, R., Tavares, V. C., Gregorin, R., & Peracchi, A. L. (2018). *Updated checklist of Brazilian bats: version 2018. Comitê da Lista de Morcegos do Brasil—CLMB. Sociedade Brasileira para o Estudo de Quirópteros (Sbeq).* Retrieved from https://www.sbeq.net/lista-de-especies

Oliveira Filho, B., & Metzger, J. P. (2006). Thresholds in landscape structure for three common deforestation patterns in the Brazilian Amazon. *Landscape Ecology*, *21*, 1061–1073. https://doi.org/10.1007/s10980-006-6913-0

Oliver, I., & Beattie, A. J. (1996). Designing a cost-effective invertebrate survey: A test of methods for rapid assessment of biodiversity. *Ecological Applications*, *6*(2), 594–607. https://doi.org/10.2307/2269394

Olson, D. M., & Dinerstein, E. (1998). The Global 200: A representation approach to conserving the Earth's most biologically valuable ecoregions. *Conservation Biology*, *12*(3), 502–515. https://doi.org/10.1046/j.1523-1739.1998.012003502.x

Pebesma, E. (2018). Simple features for R: Standardized support for spatial vector data. *The R Journal*, *10*(1). https://doi.org/10.32614/RJ-2018-009

Peixoto, F. P., Villalobos, F., & Cianciaruso, M. V. (2017). Phylogenetic conservatism of climatic niche in bats. *Global Ecology and Biogeography*, *26*(9), 1055–1065. https://doi.org/10.1111/geb.12618

Peterson, A. T. (2001). Predicting species' geographic distributions based on ecological niche modeling. *The Condor*, *103*, 599–605. https://doi.org/10.1093/condor/103.3.599

Peterson, A. T., Soberón, J., & Sánchez-Cordero, V. (1999). Conservatism of ecological niches in evolutionary time. *Science*, *285*(5431), 1265–1267. https://doi.org/10.1126/science.285.5431.1265

Philipp, H. (2017). *velox: fast raster manipulation and extraction.* R package version 0.2.0. Retrieved from https://CRAN.R-project.org/package=velox

R Core Team (2019). *R: A language and environment for statistical computing.* Retrieved from https://www.r-project.org/.

Rabosky, A. R. D., Cox, C. L., Rabosky, D. L., Title, P. O., Holmes, I. A., Feldman, A., & McGuire, J. A. (2016). Coral snakes predict the evolution of mimicry across New World snakes. *Nature Communications*, *7*, 1–9. https://doi.org/10.1038/ncomms11484

Ramos Pereira, M. J., & Palmeirim, J. M. (2013). Latitudinal diversity gradients in new world bats: Are they a consequence of niche conservatism? *PLoS One*, *8*(7), e69245. https://doi.org/10.1371/journal.pone.0069245

Raxworthy, C. J., Martinez-Meyer, E., Horning, N., Nussbaum, R. A., Schneider, G. E., Ortega-Huerta, M. A., & Peterson, A. T. (2003). Predicting distributions of known and unknown reptile species in Madagascar. *Nature*, *426*(6968), 837–841. https://doi.org/10.1038/nature02205

Ribeiro, V., Peterson, A. T., Werneck, F. P., & Machado, R. B. (2017). Ecological and historical views of the diversification of *Geositta*

miners (Aves: Furnariidae: Sclerurinae). *Journal of Ornithology*, *158*(1), 15–23. https://doi.org/10.1007/s10336-016-1398-3

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., & Woolmer, G. (2002). The human footprint and the last of the wild. *BioScience*, *52*(10), 891–904. https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2

Schluter, D. (1996). Ecological causes of adaptive radiation. *The American Naturalist*, *148*, S40–S64.

Sherwin, H. A., Montgomery, W. I., & Lundy, M. G. (2013). The impact and implications of climate change for bats. *Mammal Review*, *43*(3), 171–182. https://doi.org/10.1111/j.1365-2907.2012.00214.x

Simpson, G. G. (1953). *The major features of evolution*. New York, NY: Columbia University Press.

Sing, T., Sander, O., Beerenwinkel, N., & Lengauer, T. (2005). ROCR: Visualizing classifier performance in R. *Bioinformatics*, *21*(20), 7881. https://doi.org/10.1093/bioinformatics/bti623

Sluiter, R. (2009). *Interpolation methods for climate data – Literature review*. Royal Netherlands Meteorological Institute – KNMI intern rapport (2009–04). Retrieved from https://www.knmi.nl/over-het-knmi/about

Soberón, J., & Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, *2*, 1–10. https://doi.org/10.17161/bi.v2i0.4

Stadelmann, B., Lin, L.-K., Kunz, T. H., & Ruedi, M. (2007). Molecular phylogeny of New World *Myotis* (Chiroptera, Vespertilionidae) inferred from mitochondrial and nuclear DNA genes. *Molecular Phylogenetics and Evolution*, *43*, 32–48. https://doi.org/10.1016/j.ympev.2006.06.019

Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J. T., Burton, C., & Rich, L. N. (2014). Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. *Frontiers in Ecology and the Environment*, *15*(1), 26–34. https://doi.org/10.1002/fee.1448

Stevens, R. D. (2011). Relative effects of time for speciation and tropical niche conservatism on the latitudinal diversity gradient of phyllostomid bats. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1717), 2528–2536.

Strassburg, B. B. N., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., ... Balmford, A. (2017). Moment of truth for the Cerrado hotspot. *Nature Ecology and Evolution*, *1*(4), 1–3. https://doi.org/10.1038/s41559-017-0099

Sueur, J., Pavoine, S., Hamerlynck, O., & Duvall, S. (2008). Rapid acoustic survey for biodiversity appraisal. *PLoS One*, *3*(2), e4065. https://doi.org/10.1371/journal.pone.0004065

Tennekes, M. (2018). tmap: Thematic Maps in R. *Journal of Statistical Software*, *84*(6), 1–39. https://doi.org/10.18637/jss.v084.i06

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). New York, NY: Springer.

Villalobos, F., Lira-Noriega, A., Soberón, J., & Arita, H. T. (2014). Co-diversity and co-distribution in phyllostomid bats: Evaluating the relative roles of climate and niche conservatism. *Basic and Applied Ecology*, *15*(1), 85–91. https://doi.org/10.1016/j.baae.2013.11.001

Voigt, C. C., & Kingston, T. (Eds.) (2016). *Bats in the Anthropocene: Conservation of bats in a changing world* (pp. 1–606). Cham, Switzerland: Springer International Publishing. https://doi.org/10.1007/978-3-319-25220-9

Whittaker, R. J., Araújo, M. B., Jepson, P., Ladle, R. J., Watson, J. E. M., Willis, K. J., ... Willis, K. J. (2005). Conservation Biogeography: Assessment and prospect. *Diversity and Distributions*, *11*, 3–23. https://doi.org/10.1111/j.1366-9516.2005.00143.x

Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, *19*(12), 639–644. https://doi.org/10.1016/j.tree.2004.09.011

Wiens, J. J., & Graham, C. H. (2005). Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecological and Evolution Systematic*, *36*(1), 519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431

Wildlife Conservation Society – WCS, & Center for International Earth Science Information Network – CIESIN – Columbia University (2005). *Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Footprint Dataset (Geographic)*. Retrieved from https://doi.org/10.7927/H4M61H5F

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

BIOSKETCH

Ludmilla M. S. Aguiar, Maria João R. Pereira and Marlon Zortea have been working with bats in all biomes in Brazil over the past three decades. Ricardo B. Machado has been working with conservation planning over the last decades. Although the authors are associated with different universities, their common interest is on the diversity, distribution and conservation of bats. Additional research lines include plant-bat interactions, conservation biology, biogeography, bioacoustics and taxonomy of bats.

Author contributions: L.M.S.A. and R.B.M. conceived the paper. R.B.M. performed GIS analysis. L.M.S.A., M.J.R.P. and R.B.M. did statistical analyses. Bat species data were organized and reviewed by L.M.S.A., M.J.R.P. and M.Z.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.