Environmental Conservation (2018) **45** (1): 67–74 © Foundation for Environmental Conservation 2017 doi:10.1017/S0376892917000194

Bat species vulnerability in Cerrado: integrating climatic suitability with sensitivity to land-use changes

POLIANA MENDES AND PAULO DE MARCO*

Theoretical, Metacommunities and Landscape Ecology laboratory, Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Campus II, Goiânia, Goiás, 74690-000, Brazil

Date submitted: 15 June 2016; Date accepted: 22 February 2017; First published online 30 March 2017

SUMMARY

Climate variables are commonly used to predict suitability for species occurrence, but local processes, such as landscape changes, may affect habitat suitability. We identified levels of exposure to deforestation of suitable climatic areas for eight bat species in the Brazilian Cerrado and explored how sensitivity to land-use changes could reduce their persistence. We created scenarios of sensitivity to land-use changes using theoretical species persistence thresholds to natural vegetation loss in landscapes (70%, 50% and 30% of loss). We also assessed sensitivity to land-use changes using empirical data. Species are under higher exposure to land-use changes in the southern Cerrado, a region more affected by humans due to its proximity to major urban areas. Changes in land use in the Cerrado mostly affect *Myotis nigricans*, *Artibeus cinereus* and *Platyrrhinus lineatus*. Empirically derived scenarios encountered significant thresholds at 50% of natural vegetation loss in landscapes for *Artibeus lituratus* and *P. lineatus*. Deforestation has already affected a half of the Cerrado area, but in terms of possibly vulnerable suitable areas, a larger proportion has been lost, amounting to up to 80% of the suitable area. We propose that information on species-specific sensitivity thresholds to habitat loss and on the exposure of suitable landscapes to land-use changes can be useful to assessing species vulnerability.

Keywords: Chiroptera, critical thresholds, habitat loss, landscape scale, Mammalia, species distribution modelling

INTRODUCTION

The concept of the ecological niche is that real populations will persist in a set of conditions defined by a hypervolume of environmental variable space, which can be projected into the geographic space and express a set of biotopes (i.e. localities with environmental characteristics suitable for species occurrence; Colwell *et al.* 2009). Current understanding of the processes that determine observed species distributions (Soberón & Nakamura 2009) suggests that, at large scales, climate variables such as temperature and humidity can directly affect species ranges (Thomas 2010), and they have been extensively used as predictors of local suitability within an ecological niche modelling (ENM) framework (Soberón 2007). However, the recent and frequent use of ENM for conservation issues has been challenged by some important scale issues (Carvalho *et al.* 2010; Wiens *et al.* 2010). ENMs are usually developed at a regional scale, comprising large areas within a geographic distribution. However, threats to species persistence are mostly related to smaller-scale processes, such as land-use changes (Foley *et al.* 2005; Haddad *et al.* 2015). Several species, including bats (Jones *et al.* 2009), are exposed to a range of human-induced environmental changes in terms of climate, land use, biological invasions, pollution and water contamination (Dirzo *et al.* 2014; Murphy & Romanuk 2014). Despite the recognized effects of climate variables on bat diversity (Estrada-Villegas *et al.* 2012; Stevens 2013), landscape variables may have an even stronger predictive power (Mehr *et al.* 2011; López-González *et al.* 2014), and so it is reasonable to consider changes at the landscape scale when exploring bat vulnerability.

Vulnerability is a term that denotes how threatened a species is in relation to both natural and anthropogenic environmental changes with regards to the exposure to those environmental changes, the intrinsic sensitivity of the species and the adaptability of the species to a new set of conditions (Dawson *et al.* 2011; Foden *et al.* 2013). Habitat loss and fragmentation are among the most impacting environmental changes affecting biodiversity in the world (Haddad *et al.* 2015). This means that while an area may have suitable conditions for species persistence, such as conditions related to climate, it might not guarantee species survival due to exposure to land-use pressures in the area. Still, some species could be more affected by this exposure than others (Betts *et al.* 2014). Differences in sensitivity (i.e. the likelihood of a species being affected by exposure to stressor agents) are probably related to the particular ecological traits of each species, which may be difficult to predict (Henle *et al.* 2004; Cardillo *et al.* 2006). Both the level of exposure and the degree of sensitivity of a particular species may determine

---

*Correspondence: Prof Paulo De Marco Jr e-mail: pdemarco@gmail.com

Supplementary material can be found online at https://doi.org/10.1017/S0376892917000194 what conservation actions are required to mitigate any current threats to survival.

The Cerrado biome, a Brazilian savanna, has been highly impacted by land-use changes; 50% of this biome has already been converted into pasturelands, urban areas or croplands (Klink & Machado 2005; Sano *et al.* 2010). The bat fauna of Cerrado comprise more than 100 species, with a variety of food habits, such as frugivory, nectarivory, insectivory, carnivory and haematophagy. However, this biome is still relatively unknown when compared to other biomes in Brazil, with only 6% of the biome having been minimally surveyed until 2009 (Bernard *et al.* 2011). In Brazil, seven bat species are currently at risk of extinction, with five of them inhabiting this biome and two of them being endemic.

Relationships between population persistence and habitat loss are not commonly linear, instead following an abrupt change at some threshold of habitat loss at which population persistence approximates zero (Huggett 2005; Swift & Hannon 2010). This nonlinear relationship may have many causes, including landscape configuration effects under low habitat cover, Alee effects or time lag effects (Swift & Hannon 2010). The relationship between bat species richness and forest loss in the Cerrado has a critical threshold at approximately 50% (Muylaert *et al.* 2016). Considering that some bat species are more sensitive to land-use conversion than others (Duchamp & Swihart 2008; García-Morales *et al.* 2013; Farneda *et al.* 2015), it is expected that habitat loss thresholds may be different among bat species.

We assess current vulnerability in human-dominated ecosystems by exploring how suitable climatic areas for eight bat species are under pressure due to land-use changes, creating scenarios in which species would be sensitive to different thresholds of habitat loss (Fig. 1). In this sense, we are combining regional and landscape scales to gain a more accurate perception of species exposure to environmental changes. We consider that accessing suitable climatic areas for bat species is a feasible way to predict where they can reach maximum abundance (Weber *et al.* 2016). We looked for landscapes with suitable climates for bat species where species are more or less vulnerable due to land-use changes according to different scenarios of sensitivity. We created scenarios in which eight bat species would disappear in a landscape when 70%, 50% or 30% was deforested. This theoretical threshold represents the value of habitat loss in which population survival probability turns negative (Fahrig 2001; Rueda *et al.* 2013). We also obtained empirically derived critical thresholds. The main aim of this study is to use the best information available about species-specific critical thresholds of habitat area to find regions with high climate suitability, but impoverished landscape structure conditions for a species. Overall, the objectives were to: (1) determine where suitable climatic areas are subject to natural vegetation loss and fragmentation; (2) determine where species would disappear first if they were sensitive to a particular threshold of habitat loss; and (3) propose the use of empirical thresholds of habitat loss in the evaluation of species' vulnerabilities.

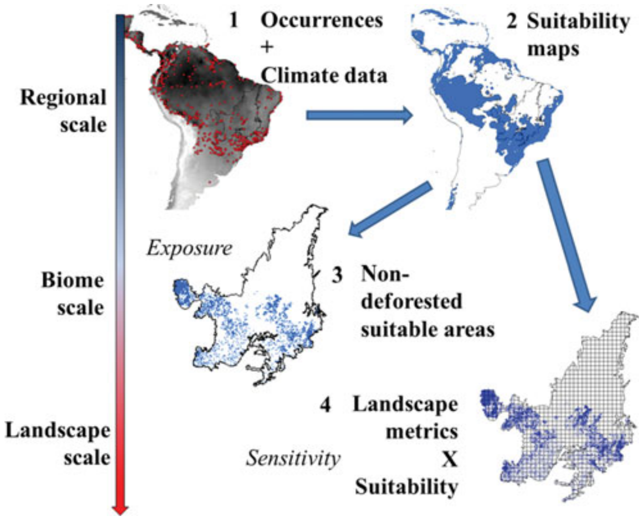

Figure 1 A conceptual model for relating species vulnerability to land-use changes using ecological niche modelling. Changes in scale are represented by an arrow on the left-hand side. At the continental scale, (1) species occurrence data and bioclimatic data were used to build ecological niche models (2) representing the suitable areas for that species. At the regional scale, (3) these suitable areas can be overlapped with deforested areas to evaluate species exposure to deforestation. At the landscape scale, (4) the biome was subdivided into landscapes and landscape metrics were calculated for each grid cell.

METHODS

Step 1: ENM

Previous studies have shown that climate variables may affect bat distribution, abundance and species richness (Estrada-Villegas *et al.* 2012; Stevens 2013), suggesting that the use of climate variables as predictors of suitable sites for bats is coherent. We selected eight bat species occurring on the Cerrado biome: *Artibeus cinereus*, *Artibeus lituratus*, *Desmodus rotundus*, *Glossophaga soricina*, *Myotis nigricans*, *Platyrrhinus incarum*, *Platyrrhinus lineatus* and *Sturnira lilium* (Table S1) (available online). We obtained geographic coordinates from occurrence data from a diversity of sources (Appendix S1). Whenever no geographical coordinates were obtained, we looked for an identifiable landmark related to that occurrence, such as the name of a conservation unit. Then, we looked for the coordinates of that landmark.

We developed ecological niche models using data from climate variables provided by WorldClim (available at http://www.worldclim.org/) at a resolution of 9.24 × 9.24 km grid cells for the entire Neotropical region (Fig. S1). We opted to use the Neotropical region because bat species have large geographic ranges there (Barve *et al.* 2011). A total of 19 bioclimatic variables were used, derived from monthly temperature and rainfall data. The strong collinearity among variables may have been a problem in modelling procedures (Jiménez-Valverde *et al.* 2011); therefore, we ran a principal component analysis and used the principal component axis explaining 95% of the variability in order to perform species distribution modelling (Table S2). Only one occurrence per cell (9.24 × 9.24 km) was considered for species distribution modelling in order to prevent the results being affected by sampling bias. We built ecological niche models using four algorithms: maximum entropy (MaxEnt), support vector machine (SVM), random forest (RF) and generalized linear model (GLM). All methods use presence background data, and 10,000 random background units were considered in the model in order to improve suitability estimation. Suitability varies from zero to one, and we converted suitability maps into binary maps using the maximum sensitivity and specificity (Pearce & Ferrier 2000). We chose the best model by comparing the true skill statistics, using a random division in training and test samples (70% and 30%) (Allouche *et al.* 2006; Liu *et al.* 2011). Only the best corresponding model was carried forward in the following steps.

Step 2: landscape structure

We used two sources of land cover data: one from the year 2010 from the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) (http://siscom.ibama.gov.br/monitorabiomas/cerrado/index.htm) and another from 2011–2014 from the Image Processing and Geoprocessing Laboratory (LAPIG) (http://siscom.ibama.gov.br/). IBAMA used a previous land-use dataset from the Projeto de Conservação e Utilização Sustentável da Diversidade Biológica Brasileira (PROBIO) project, dated 2002, and added deforestation data collected using the Land Remote Sensing Satellite (LANDSAT) from 2002 until 2010. LAPIG used data from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite (MOD13Q1), and validated these data by using data from the LANDSAT and China–Brazil Earth Resources Satellite (CBERS) satellites to monitor deforestation yearly. We transformed deforestation data into a grid 100-times smaller than the suitability data (0.0925 × 0.0925 km grid cells).

We calculated natural vegetation loss and the landscape shape index (LSI) for each of the 9.24 × 9.24 km cells defined in the modelling procedures (Table S3). This cell size is compatible with maximum daily movements for bats in the Neotropical region (Trevelin *et al.* 2013; Aguiar *et al.* 2014), so we believe that it is also a good landscape size for predicting bat responses to changes in landscape structure. Natural vegetation loss was the sum of non-forested pixels. LSI was calculated as the total edge perimeter divided by the edge perimeter if all natural vegetation in a landscape was within a single circle. Total edge was calculated as the sum of the sizes of pixel edges adjacent to a non-forested pixel or a border of the landscape.

Step 3: critical thresholds

We are aware that thresholds of habitat loss may be species specific (Rueda *et al.* 2013). They can also result from a number of processes, such as time lag in species responses or relationships between landscape configurations and compositions (Swift & Hannon 2010). Differences in reproductive rates and dispersal capacities are related to those thresholds, which can vary from 1% to 99% of habitat amount in a landscape (Fahrig 2001). In the south of the Brazilian Cerrado, for example, a critical threshold of 50% of forest loss has been estimated for bat species richness (Muylaert *et al.* 2016). We used theoretical scenarios of 30%, 50% or 70% of natural vegetation loss, above which species would disappear in a landscape.

Table 1 Environmental niche modelling performance compared among four algorithms: maximum entropy (MaxEnt), support vector machine (SVM), random forest (RF) and generalized linear model (GLM). Area under curve values are shown for each species and algorithm. In order to test these statistics, data were separated by train (70% of data) and test (30%).

Species	*MaxEnt*	*SVM*	*RF*	*GLM*
Artibeus cinereus	0.853	0.890	0.883	0.829
Artibeus lituratus	0.731	0.830	0.865	0.718
Desmodus rotundus	0.726	0.809	0.839	0.695
Glossophaga soricina	0.758	0.825	0.864	0.738
Myotis nigricans	0.725	0.803	0.820	0.708
Platyrrhinus incarum	0.852	0.862	0.835	0.798
Platyrrhinus lineatus	0.861	0.906	0.909	0.809
Sturnira lilium	0.746	0.816	0.853	0.717

We also tested the existence of empirically derived thresholds. We used data from standardized field sampling in the Cerrado of Brazil (Appendix S1; Mendes *et al.* 2017). To obtain empirical thresholds, we looked for a sharp threshold using a piecewise regression between habitat loss and abundance. Piecewise regressions search for a sharp change in slope in certain breakpoints that can be found via the least squares estimations (Toms & Villard 2015). We performed a linear regression of abundance on natural vegetation loss and then tested the significance of the insertion of a breakpoint in that relationship using the Davies' test, which shows whether there is a change in the slope of a relationship after a breakpoint (Muggeo 2016). Piecewise regressions were performed using a segmented package in R (Muggeo 2016). Each night was considered as one sampling unit. In accordance with the theoretical expectations (Swift & Hannon 2010), after a certain breakpoint in habitat loss, the slope of the relationship with biodiversity will decrease towards a negative relationship. We checked whether the slopes of the piecewise regression were compatible with this prediction.

RESULTS

The algorithm with the best performance in modelling the climate niche of *A. cinereus*, *P. incarum* and *P. lineatus* was the SVM, while for *A. lituratus*, *D. rotundus*, *G. soricina*, *M. nigricans* and *S. lilium*, it was the RF model, although for some species both algorithms resulted in similar performance (Table 1). The first axis from the principal components

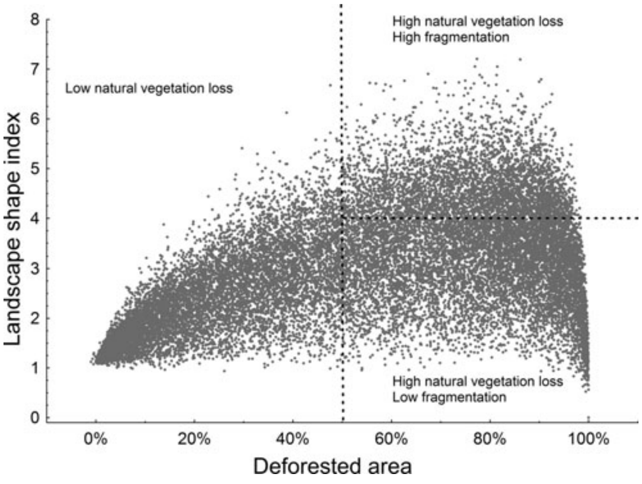

Figure 2 Distribution of natural vegetation loss and fragmentation in the Cerrado biome. The vertical line represents one possible scenario for a critical threshold of habitat loss (50% of loss). Landscapes with high natural vegetation loss could be found with high or low fragmentation, measured with the landscape shape index. The median of the variation in landscape shape index (horizontal line) was used to categorize landscapes into highly or lowly fragmented. Each unit is a landscape measuring 9.24 × 9.24 km.

analysis of suitability maps explained between 75% (for *P. lineatus*) and 84% (for *A. cinereus*) of the variation in environmental suitability, meaning that the algorithms had high congruence among them. Total suitable area (i.e. cells with suitability above the balanced threshold) ranged from 5,700,000 km^2 for *P. incarum* to 2,800,000 km^2 for *D. rotundus* (Fig. S2). Within the Cerrado, *A. lituratus* had the largest area with high suitability (1,600,000 km^2). For almost all of the species, high-suitability areas were located in the southern Cerrado (Fig. S2).

Natural vegetation loss in Cerrado landscapes ranged from 0% to 100%, while the LSI varied from 1 to 7; higher values were obtained in more fragmented landscapes (Fig. 2). Three scenarios of critical thresholds of habitat loss were tested (Fig. S3), and *M. nigricans*, *A. cinereus* and *P. lineatus* were expected to lose a larger percentage of suitable areas if they responded to natural vegetation loss in any of the three scenarios (critical thresholds of 30%, 50% or 70%; Table 2). *D. rotundus* and *A. lituratus*, in turn, were predicted to be less affected. Even considering the less conservative critical threshold, in which 70% of a landscape had to be deforested for a reduction in population persistence, up to 68% of the highly suitable landscapes were above this threshold (Table 2). Species with suitable areas in the southern Cerrado were even more affected by landscape changes than species with suitable areas in the northern Cerrado (Figs 3 and S4).

Empirical thresholds in the relationships between abundance and natural vegetation loss were found for *A. lituratus* and *P. lineatus*, both at 50% of natural vegetation loss (Table 3). *P. incarum* abundance showed a negative linear relationship with natural vegetation loss; however, no critical threshold was encountered. *A. lituratus* abundance was negatively related to natural vegetation loss until a breakpoint of 50%, and then the predicted abundance remained constant (Fig. 4). *P. lineatus* abundance, on the other hand, was negatively related to natural vegetation loss until a breakpoint of 50%, and it was positively related to natural vegetation loss after this breakpoint.

DISCUSSION

Exposure of climatically suitable areas to natural vegetation loss

Among the analysed species, *M. nigricans*, *A. cinereus* and *P. lineatus* were the most exposed to deforestation in suitable areas of the Cerrado. Such results may not seem to be relevant, since such species are widely distributed across a range of vegetation types (Zortéa & Alho 2008; Oprea *et al.* 2009; Talamoni *et al.* 2013). However, we noted that the Cerrado biome is close to marginal areas for the distributions of *P. lineatus* and *A. cinereus* (Gardner 2007). While the northwest Cerrado is marginal to the distribution of *P. lineatus*, *A. cinereus* does not occur in the west of the Cerrado, except for a few occurrences in Bolivia (Gardner 2007). Habitat in marginal areas of a species distribution is usually less suitable, with smaller and more fluctuating populations (Brown 1984; Cuervo & Møller 2013). Additionally, for *A. cinereus*, *M. nigricans* and *P. lineatus*, highly suitable areas were located in the southern Cerrado, which were most affected by deforestation in this biome (Klink & Machado 2005; Sano *et al.* 2010). Patterns of exposure to land-use changes among those species may be explained by the marginality of the Cerrado in terms of species distribution and the greater suitability of areas that are under human pressure.

Southern areas of the Cerrado are the most impacted by pastures and croplands due to the occupation history of this biome that began in the south, closer to major urban areas (Klink & Machado 2005; Sano *et al.* 2010). Croplands, the major driver of fragmentation, are more concentrated in southern areas of the Cerrado, whereas pasturelands are distributed throughout the biome (Carvalho *et al.* 2009). Southern Cerrado areas also have greater species richness (Blamires *et al.* 2008; Diniz-Filho *et al.* 2008), although, for bats, the lower species richness of northern areas may also be related to disproportionately fewer bat surveys having been performed (Bernard *et al.* 2011). In situations in which a species has a large suitable area, exposure to impacts in one part of its geographic range would buffer the effects of that impact (Dawson *et al.* 2011). Therefore, species that are climatically likely to occur throughout the Cerrado, such as *D. rotundus* and *G. soricina*, would be less affected by an impact that varies with latitude.

Scenarios of critical thresholds to land-use changes

Simulation of different critical thresholds of natural vegetation loss is one possible approach for integrating climate suitability at a regional scale to species responses at the landscape scale.

Table 2 Scenarios of possible population loss thresholds of 70%, 50% and 30% in landscapes with high climatic suitability. The threshold is the percentage of habitat loss below which populations will no longer persist in that landscape. Shown values are the climatic suitable areas where species would not persist according to that scenario. Landscapes were divided into high or low fragmentation based on the landscape shape index (see 'Methods' section). The mean of the landscape shape index over all landscapes was used as a threshold for this subdivision. Percentages in the parentheses represent the amounts climatically suitable areas in the Cerrado that would be lost if species were sensitive to 70%, 50% or 30% habitat deforestation in a landscape.

Species		*Highly suitable and deforested landscapes (km^2)*			
	Highly suitable landscapes (km^2)	*Sensitivity to habitat loss at 70%*	*Sensitivity to habitat loss at 50%*	*Sensitivity to habitat loss at 30%*	*Highly suitable and fragmented landscapes (km^2)*
Artibeus cinereus	573,310	337,412 (59%)	410,068 (72%)	463,515 (81%)	191,928 (33%)
Artibeus lituratus	1,595,365	750,896 (47%)	1,018,469 (64%)	1,018,469 (64%)	273,806 (17%)
Desmodus rotundus	541,379	234,959 (43%)	320,763 (59%)	401,104 (74%)	135,238 (25%)
Glossophaga soricina	1,508,963	701,120 (46%)	956,997 (63%)	1,149,353 (76%)	436,791 (29%)
Myotis nigricans	393,505	268,171 (68%)	313,591 (80%)	342,961 (87%)	118,845 (30%)
Platyrrhinus incarum	725,453	339,888 (47%)	474,272 (65%)	562,296 (77%)	333,143 (46%)
Platyrrhinus lineatus	1,328,219	691,217 (52%)	905,173 (68%)	1,053,986 (79%)	407,763 (31%)
Sturnira lilium	451,135	222,408 (49%)	292,076 (65%)	354,829 (79%)	125,761 (28%)

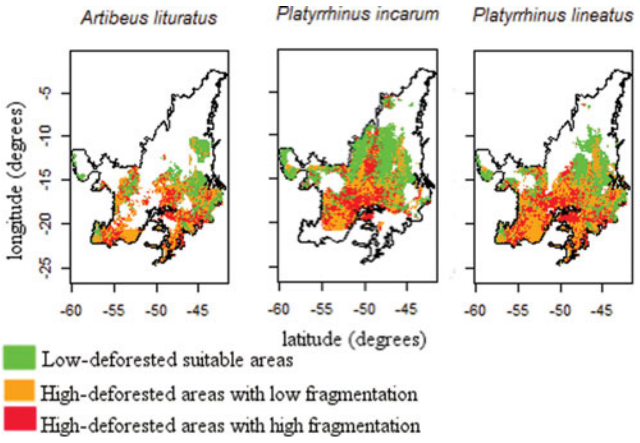

Figure 3 Spatial distribution of suitable cells and effects of land-use changes on three bat species in the Cerrado that showed empirical relationships with natural vegetation loss, considering the most realistic scenario of critical thresholds.

Table 3 Results of Davies' tests showing whether there is a difference in slope in piecewise regression; the test is significant if there is a breakpoint. Regression coefficients from linear models and *p*-values are also shown for comparison. Bold values represent significant breakpoints and *p*-values ($p \leq 0.05$).

Species	*Breakpoint (Davies' test)*	*p-value*	*Linear regression coefficient*	*p-value*
Artibeus cinereus	0.735	0.566	0.261	0.199
Artibeus lituratus	**0.494**	**<0.001**	**–5.358**	**<0.001**
Desmodus rotundus	0.735	0.169	1.020	0.222
Glossophaga soricina	0.735	0.067	–0.245	0.761
Myotis nigricans	0.494	0.965	0.119	0.824
Platyrrhinus incarum	0.494	0.804	**–0.714**	**0.011**
Platyrrhinus lineatus	**0.494**	**0.029**	**–4.566**	**<0.001**
Sturnira lilium	0.735	0.677	–0.167	0.476

We considered those theoretical thresholds as an equivalent to a certain value of natural vegetation loss in which the persistence probability of a population would be negative, although we were not attributing a cause to the existence of this threshold (see Swift & Hannon 2010), such as the effect of fragmentation in landscapes with high habitat loss (Andrén 1994). One caveat in these scenarios is the lack of specific thresholds for different foraging guilds or according to species' body attributes. Habitat loss thresholds for population persistence are, in general, species specific (Rueda *et al.* 2013), and vary with a number of parameters, such as matrix quality (Fahrig 2001).

Some empirical species-specific thresholds are available for some taxonomic groups, such as birds (e.g. Rueda *et al.* 2013). Most such thresholds occur when at least 50% of the habitat remains in the landscape, despite varying from 1% to 99% of the remaining habitat (Swift & Hannon 2010). Such results have reinforced the idea that critical thresholds of habitat loss are taxon specific (Swift & Hannon 2010); therefore, generalizing is difficult. Scenarios are useful tools for assessing biological patterns or processes whenever realistic datasets are not available (Peterson *et al.* 2003), but their interpretation requires caution, since they may well depart from reality. Regarding the scenarios created above, some species may not be sensitive to land-use changes because they are resilient to these changes, being able to find resources such as food and to roost in highly modified landscapes (García-Morales *et al.* 2013). Bat species are also sensitive to other environmental factors not explored here, such as pesticide use, climate

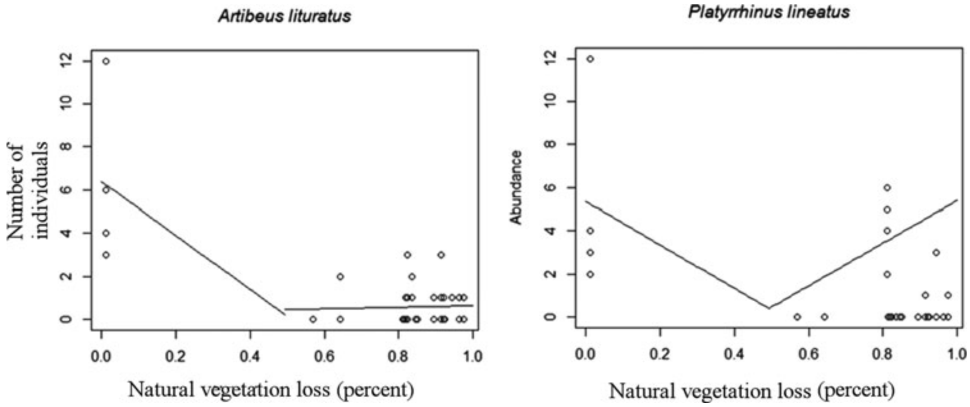

Figure 4 Predicted values from piecewise regressions with significant breakpoints calculated using the Davies' test.

change, wind turbines or lighting (Jones *et al.* 2009). The most realistic approach to assessing species sensitivity to land-use changes is relating species persistence, incidence or abundance to those changes, thereby making it possible to find a land-use threshold for this relationship.

Empirically derived sensitivity

Piecewise regression is a common and well-stablished method in empirical evaluations of sharp habitat loss critical thresholds (e.g. Rompré *et al.* 2009; Toms & Villard 2015; Muylaert *et al.* 2016). Categorical thresholds can be tested using regression trees and smooth thresholds can be tested using non-linear relationships (Huggett 2005; Swift & Hannon 2010). Any of these methods could be adequate in the proposed approach for predicting which climatically suitable landscape populations are more vulnerable to land-use changes. We opted for the most commonly used method.

Relationships between bat abundance and vegetation cover are highly variable among species. *S. lilium* abundance has been identified as being positively related to forest cover and negatively related to edge density, *M. nigricans* is fragmentation sensitive and *A. lituratus* is positively related to edge density (Gorresen *et al.* 2005; Klingbeil & Willig 2010; Avila-Cabadilla *et al.* 2012). We found evidence of empirical thresholds for two of the eight analysed species: *A. lituratus* and *P. lineatus*. Empirical thresholds were similar to the 50% theoretical scenario and congruent with the empirical threshold found for bat species richness in the same biome (Muylaert *et al.* 2016). However, absence of a critical threshold does not mean that a species is not sensitive to natural vegetation loss. A linear relationship with natural vegetation cover, for example, indicates that a species is sensitive to those changes, but no critical threshold could be found, such as for *P. incarum*. Those specific cases would benefit from a gradient approach, in which a continuum of vulnerability might be explored further.

CONCLUSION

Comparing scenarios with empirical data is useful whenever it is possible. Our empirically derived sensitivities were compatible with scenarios; however, just two species showed a critical threshold in the empirical test. Even with those differences, we argue that scenarios of sensitivity may be useful for predicting impacts on potentially sensitive species whenever empirical data are unavailable. Our scenarios were precautionary since they assumed that all species could be potentially sensitive. Impacts on species at the landscape scale might integrate with those at a regional scale; an example of this approach would be using fragmentation and climate change data (Kerr *et al.* 2007; Faleiro *et al.* 2013; Haddad *et al.* 2015). We have taken a small step in this direction; our findings improve understanding of how suitable climatic areas are likely to be affected by landscape changes in the Cerrado. Overall, our results showed that small, suitable areas in the Cerrado were determinants for predicting species vulnerability to land-use changes. Therefore, a threatened species in the Cerrado is not necessarily also threatened in other biomes. While a wider approach considering the landscape of the entire country or the continent would provide a more complete picture of bat species vulnerability, we believe that regional approaches are also important for improving understanding of vulnerability (Ferrier 2002) on a more feasible scale for conservation management.

ACKNOWLEDGEMENTS

We are grateful to M. Oprea and T.B. Vieira for providing occurrence data. P. Mendes received a CNPq scholarship. P. De Marco Jr was funded by a continuous productivity CNPq grant. The work was funded by International Foundation for Science (D/5288-1) and CNPq (486057/2012-7). Empirical data were obtained with partial financial help from Anglo American Brasil, CAPES and the PELD-UFG project. We thank P.H. Coelho Ramos for providing occurrence data of bat species, A. Andrade for helping with the evaluation of ecological niche modelling and developing a script for running environmental niche models, S. Villen for commenting on our analysis and figures, C.H.G. Cezare for helping with land-use data and L.M.O. Laureto, P.H.P. Braga and C.E.A. Soares for helpful comments on the text. We also thank A.P. Paglia, D.C.S. Brito, M.C. Ribeiro and R.D. Loyola for review and helpful comments, and B.J.C. Unwin for reviewing the

English syntax. We thank S. de Jesus, P.V.S. Bernardo, L.M. Camargos, P.H.P. Braga, B.C. Gomes, C. Sobral, P. Coelho and A. Bispo for help with the sampling design and fieldwork; landowners, National Forest of Silvânia and Emas National Park for site access; and ICMBio for providing the necessary permits to sample the bats.

Supplementary material

To view supplementary material for this article, please visit http://doi.org/10.1017/S0376892917000194

References

Aguiar, L.M.S., Bernard, E. & Machado, R.B. (2014) Habitat use and movements of *Glossophaga soricina* and *Lonchophylla dekeyseri* (Chiroptera: Phyllostomidae) in a Neotropical savannah. *Zoologia* **31**: 223–229.

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* **43**: 1223–1232.

Andrén, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**: 355–366.

Avila-Cabadilla, L.D., Sanchez-Azofeifa, G.A., Stoner, K.E., Alvarez-Añorve, M.Y., Quesada, M. & Portillo-Quintero, C.A. (2012) Local and landscape factors determining occurrence of phyllostomid bats in tropical secondary forests. *PLoS ONE* **7**: e335228.

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P, Peterson, A.T., Soberón, J. & Villalobos, F. (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modeling* **222**: 1810–1819.

Bernard, E., Aguiar, L.M. & Machado, R.B. (2011) Discovering the Brazilian bat fauna: a task for two centuries? *Mammal Review* **41**: 23–39.

Betts, M.G., Fahrig, L., Hadley, A.S., Halstead, K.E., Bowman, J., Robinson, W.D., Wiens, J.A. & Lindenmayer, D.B. (2014) A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. *Ecography* **37**: 517–527.

Blamires, D., Oliveira, G., Barreto, B.S. & Diniz-Filho, J.A.F. (2008) Habitat use and deconstruction of richness patterns in Cerrado birds. *Acta Oecologica* **33**: 97–104.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *The American Naturalist* **124**: 255–279.

Cardillo, M., Mace, G.M., Gittleman, J.L. & Purvis, A. (2006) Latent extinction risk and the future battlegrounds of mammal conservation. *Proceedings of the National Academy of Sciences of the United States of America* **103**: 4157–4161.

Carvalho, F.M.V., De Marco, P. & Ferreira, L.G. (2009) The Cerrado into-pieces: habitat fragmentation as a function of landscape use in the savannas of central Brazil. *Biological Conservation* **142**: 1392–1403.

Carvalho, S.B., Brito, J.C., Pressey, R.L., Crespo, E. & Possingham, H.P. (2010) Simulating the effects of using different types of species distribution data in reserve selection. *Biological Conservation* **143**: 426–438.

Colwell, R.K., Rangel, T.F., Grinnell, J. & Elton, C. (2009) Hutchinson's duality: the once and future niche. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 19651–19658.

Cuervo, J.J. & Møller, A.P. (2013) Temporal variation in population size of European bird species: effects of latitude and marginality of distribution. *PLoS ONE* **8**: e77654.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science* **332**: 53–58.

Diniz-Filho, J.A.F., Bini, L.M., Vieira, C.M., Blamires, D., Terribile, L.C., Bastos, R.P., Oliveira, G. & Souza, B. (2008) Spatial patterns of terrestrial vertebrate species richness in the Brazilian Cerrado. *Zoological Studies* **47**: 146–157.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014) Defaunation in the Anthropocene. *Science* **345**: 401–406.

Duchamp, J.E. & Swihart, R.K. (2008) Shifts in bat community structure related to evolved traits and features of human-altered landscapes. *Landscape Ecology* **23**: 849–860.

Estrada-Villegas, S., McGill, B.J. & Kalko, E.K.V. (2012) Climate, habitat, and species interactions at different scales determine the structure of a Neotropical bat community. *Ecology* **93**: 1183–1193.

Fahrig, L. (2001) How much habitat is enough? *Biological Conservation* **100**: 65–74.

Faleiro, F.V., Machado, R.B. & Loyola, R.D. (2013) Defining spatial conservation priorities in the face of land-use and climate change. *Biological Conservation* **158**: 248–257.

Farneda, F.Z., Rocha, R., Lopez-Baucells, A., Groenenbert, M., Silva, I., Palmeirim, J.M., Bobrowiec, P.E.D. & Meyer, C.F.J. (2015) Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology* **52**: 1381–1391.

Ferrier, S. (2002) Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? *Systematic Biology* **51**: 331–363.

Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vié, J.C., Akçakaya, H.R., Angulo, A., De Vantier, L.M., Gutsche, A., Turak, E., Cao, L., Donner, S.D., Katariya, V., Bernard, R., Holland, R.A., Hughes, A.F., O'Hanlon, S.E., Garnett, S.T., Şekercioğlu, Ç.H. & Mace, G.M. (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE* **8**: e65427.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A, Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science* **309**: 570–574.

García-Morales, R., Badano, E.I. & Moreno, C.E. (2013) Response of Neotropical bat assemblages to human land use. *Conservation Biology* **27**: 1096–1106.

Gardner, A.L. (2007) *Mammals of South America, Volume* **1***: Marsupials, Xenarthrans, Shrews, and Bats*. New York, NY: Chicago Press.

Gorresen, P.M., Willig, M.R. & Strauss, R.E. (2005) Multivariate analysis of scale-dependent associations between bats and landscape structure. *Ecological Applications* **15**: 2126–2136.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X. & Townshend, J.R. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* **1**: e1500052.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiveristy and Conservation* **13**: 207–251.

Huggett, A.J. (2005) The concept and utility of ecological thresholds in biodiversity conservation. *Biological Conservation* **124**: 301–310.

Jiménez-Valverde, A., Peterson, A., Soberón, J., Overton, J.M., Aragón, P. & Lobo, J.M. (2011) Use of niche models in invasive species risk assessments. *Biological Invasions* **13**: 2785–2797.

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.

Kerr, J.T., Kharouba, H.M. & Currie, D.J. (2007) The macroecological contribution to global change solutions. *Science* **316**: 1581–1584.

Klingbeil, B.T. & Willig, M.R. (2010) Seasonal differences in population-, ensemble- and community-level responses of bats to landscape structure in Amazonia. *Oikos* **119**: 1654–1664.

Klink, C.A. & Machado, R.B. (2005) Conservation of the Brazilian Cerrado. *Conservation Biology* **19**: 707–713.

Liu, C., White, M. & Newell, G. (2011) Measuring and comparing the accuracy of species distribution models with presence–absence data. *Ecography* **34**: 232–243.

López-González, C., Presley, S.J., Lozano, A., Stevens, R.D. & Higgins, C.L. (2014) Ecological biogeography of Mexican bats: the relative contributions of habitat heterogeneity, beta diversity, and environmental gradients to species richness and composition patterns. *Ecography* **38**: 261–272.

Mehr, M., Brandl, R., Hothorn, T., Dziock, F., Förster, B. & Müller, J. (2011) Land use is more important than climate for species richness and composition of bat assemblages on a regional scale. *Mammalian Biology* **76**: 451–460.

Mendes, P., With, K.A., Signorelli, L. & De Marco Jr, P. (2017) The relative importance of local versus landscape variables on site occupancy in bats of the Brazilian Cerrado. *Landscape Ecology* doi:10.1007/s10980-016-0483-6.

Muggeo, V.M.R. (2016) Segmented: an R package to fit regression models with broken-line relationships segmented. *R News* **8**: 20–25.

Murphy, G.E.P. & Romanuk, T.N. (2014) A meta-analysis of declines in local species richness from human disturbances. *Ecology and Evolution* **4**: 91–103.

Muylaert, R.L., Stevens, R.D. & Ribeiro, M.C. (2016) Threshold effect of habitat loss on bat richness in Cerrado-forest landscapes. *Ecological Applications* **26**: 1854–1867.

Oprea, M., Mendes, P., Vieira, T.B. & Ditchfield, A.D. (2009) Do wooded streets provide connectivity for bats in an urban landscape? *Biodiversity and Conservation* **18**: 2361–2371.

Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* **133**: 225–245.

Peterson, G.D., Cumming, G.S. & Carpenter, S.R. (2003) Scenario planning: a tool for conservation in an uncertain world. *Conservation Biology* **17**: 358–366.

Rompré, G., Robinson, W.D., Desrochers, A. & Angehr, G. (2009) Predicting declines in avian species richness under nonrandom patterns of habitat loss in a Neotropical landscape. *Ecological Applications*;**19**: 1614–1627.

Rueda, M., Hawkins, B.A., Morales-Castilla, I., Vidanes, R.M., Ferrero, M. & Rodríguez, M.Á. (2013) Does fragmentation increase extinction thresholds? A European-wide test with seven forest birds. *Global Ecology and Biogeography* **22:** 1282–1292.

Sano, E.E., Rosa, R., Brito, J.L.S. & Ferreira, L.G. (2010) Land cover mapping of the tropical savanna region in Brazil. *Environment Monitoring Assessment* **166**: 113–124.

Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* **10**: 1115–1123.

Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 19644–19650.

Stevens, R.D. (2013) Gradients of bat diversity in Atlantic Forest of South America: environmental seasonality, sampling effort and spatial autocorrelation. *Biotropica* **45:** 764–770.

Swift, T.L. & Hannon, S.J. (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. *Biological Reviews* **85**: 35–53.

Talamoni, S., Coelho, D., Dias-Silva, L. & Amaral, A. (2013) Bat assemblages in conservation areas of a metropolitan region in Southeastern Brazil. *Brazilian Journal of Biology* **73**: 309–319.

Thomas, C.D. (2010) Climate, climate change and range boundaries. *Diversity and Distributions* **16**: 488–495.

Toms, J.D. & Villard, M. (2015) Threshold detection: matching statistical methodology to ecological. *Avian Conservation and Ecology* **10**: 2.

Trevelin, L.C., Silveira, M., Port-Carvalho, M., Homem, D.H. & Cruz-Neto, A.P. (2013) Use of space by frugivorous bats (Chiroptera: Phyllostomidae) in a restored Atlantic forest fragment in Brazil. *Forest Ecology and Management* **291**: 136–143.

Wiens, J.J., Ackerly, D.D., Allen, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, T.J., Grytnes, J.-A., Harrison, S.P., Hawkins, B.A., Holt, R.D., Mccain, C.M. & Stephens, P.R. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13**: 1310–1324.

Weber, M.M., Stevens, R., Diniz-Filho, J.A.F. & Grelle, C.E.V. (2016) Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. *Ecography* **39**: 1–12.

Zortéa, M. & Alho, C.J.R. (2008) Bat diversity of a Cerrado habitat in central Brazil. *Biodiversity and Conservation* **17**: 791–805.