



Vulnerability of Cerrado threatened mammals: an integrative landscape and climate modeling approach

Paulo De Marco Jr.¹ · Sara Villén¹ · Poliana Mendes¹ · Caroline Nóbrega^{1,2} · Lara Cortes³ · Tiago Castro³ · Rodrigo Souza⁴

Received: 11 October 2017 / Revised: 18 July 2018 / Accepted: 21 August 2018
© Springer Nature B.V. 2018

Abstract

Species vulnerability is defined based on their exposition, sensitivity and adaptive capacity to a given impact. Considering limitations to estimate the sensitivity component, we developed a framework integrating the knowledge on ecological niche models and extinction thresholds, generating species sensitivity scenarios at the landscape scale. Our aim was to assess species and landscape vulnerability for threatened mammal species from the Brazilian Cerrado by considering seven types of human-impacts and climatic suitability. We assumed that climatic-suitable landscapes with less than 50% of remaining natural vegetation are not suitable for species, while in landscapes with 50–60% of remaining natural vegetation, populations are highly vulnerable. We found a spatial match between climatic-suitable areas and highly-impacted landscape (<50% of remaining vegetation), specifically in southern Cerrado. We attribute this result to two main reasons: (1) similar characteristics affecting both suitability for species and human activities; and (2) highly impacted landscapes are likely to shelter threatened species. Vulnerable cells, with 50–60% of remaining vegetation, were distributed throughout Cerrado, meaning that there is no spatial bias within their distribution. Range-restricted species exhibited higher variability in vulnerability compared to widely-distributed species, what could be explained by human occupation being spatially clumped. Agriculture is the major impact affecting highly-impacted landscapes (<50% of remaining vegetation), transport infra-structure has higher impact on vulnerable landscapes. We believe that our approach can be easily applied for assessing species and landscape vulnerability in many ecological domains by adapting extinction thresholds according to the focus taxon.

Keywords Species vulnerability · Habitat loss · Extinction threshold theory · Threatened species · Land use changes

Communicated by Guarino Rinaldi Colli.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10531-018-1615-x>) contains supplementary material, which is available to authorized users.

✉ Paulo De Marco Jr
pdemarcojr@gmail.com

Extended author information available on the last page of the article

Introduction

Species vulnerability is defined as the overlap among their exposition, sensitivity and adaptability to human-induced changes within their distribution (Dawson et al. 2011; Foden et al. 2013). Species distributions are the result of spatial colonization-extinction processes constrained by species eco-physiological adaptations during an evolutionary history, which determine their perception of large scale climatic suitability (Soberón 2007; De Marco et al. 2008). Moreover, species dispersal history also highlights how spatial processes shape species distributions (Barve et al. 2011). Species vulnerability can be considered as a spatial problem. This spatial nature of vulnerability assessment is recognized in current species vulnerability frameworks (Dawson et al. 2011; Foden et al. 2013) that identify exposition a spatial overlap between threats and species distributions— as a primary analytical step. Unfortunately, the lack of better ecological and natural history information on threatened species precluded the advance to the next steps of the vulnerability assessment; the sensitivity and adaptive capacity assessment. Sensitivity is assumed to be the ability of species to respond to environmental changes and persist in altered areas. Adaptive capacity relates to the possibility of evolutionary and behavioral changes or other adjustments that alter both exposition and sensitivity. The evaluation of exposition is important to establish which species are most threatened and where land-use changes are causing the most important effects, but the development of tools to deal with sensitivity to those changes is an urgent call for conservation research. Here, we propose an integrative approach to assess species and landscape vulnerability by using (1) climate-based environmental niche modelling to predict species distribution; (2) human impact data to predict species exposition to land-use changes, and (3) extinction thresholds to predict sensitivity to human-induced changes.

Climate can mediate several constraints in mammals' eco-physiological characteristics, such as torpor, hibernation, behavior, and reproductive parameters, altering the length of a breeding season for example (Humphries et al. 2002; Isaac et al. 2009). For this reason, macroclimate is expected to play an important role determining mammal distribution (Martinez-Meyer et al. 2004; Isaac 2009). Thus, ecological models based on climate are expected to predict broad-scale species suitability (Illoldi-Rangel et al. 2004; Elith et al. 2006). Ecological niche models (ENM) have been also proposed as an estimator of species ranges or extent of occurrence (EOO) and area of occupancy (AOO) of a species for conservation purposes (Marcer et al. 2013; Pena et al. 2014), despite some possible interpretative limitations (Attorre et al. 2013). Since common EOO estimation procedures (International Union for Conservation of Nature [IUCN] 2012; Syfert et al. 2014) may lack discrimination among areas with different climatic suitability within its limits, we consider that the ENM at least provide more informative data for vulnerability assessments by considering that suitable climate is an *a priori* condition for species survival.

Land-use changes affect biodiversity by modifying natural ecosystems, what may cause habitat loss for several mammal species, consequently reducing species persistence due to reduction of required resources (Pardini et al. 2010; Thornton et al. 2011; Melo et al. 2017). However, the effects of habitat depletion on biodiversity may be not linear, as biodiversity changes when habitat loss in landscapes reach a certain threshold (Huggett 2005; Toms and Villard 2015), what may be caused by many reasons including Allee effects or time lags (Swift and Hannon 2010). Below this threshold, populations tend to decrease at a higher rate than above this threshold. Considering a vulnerability framework, this threshold clearly serves as an operational definition for sensitivity at the landscape scale and can vary highly among

species (Fahrig 2001). Otherwise, empirical studies have suggested threshold values between 30 and 50% of habitat amount in a landscape (Andr n 1994; Rueda et al. 2013; Muylaert et al. 2016). The existence of this threshold is an attractive tool for conservation management, since it allows to differentiate priority landscapes for conservation actions, despite mechanisms related to species responses to land-use changes still need more clarification (van der Hoek et al. 2015). We propose the use of a threshold of natural vegetation amount as the minimal necessary to guarantee species persistence in a given landscape as a feasible strategy to conduct a vulnerability assessment.

Land-use changes result from a complex balance of economic forces (hopefully) under governance restrictions related to conservation issues. This balance creates a political conflict between forces that aim to increase productive areas and those that aim to reduce threats to wildlife populations. The Brazilian Cerrado is one of those areas where these forces are shaping landscapes and probably deciding the future of its biodiversity. Half of this savanna region has already been converted to human-altered landscapes and future scenarios do not change these general ongoing land-use changes that will define the future of the Cerrado biodiversity (Strassburg et al. 2017). Moreover, among the world biodiversity hotspots, the Cerrado is predicted to have one of the highest future expansion of pasturelands (Bellard et al. 2014). Despite of its importance in terms of the number of endemic and threatened species, the Cerrado has been neglected in conservation policies compared to forest ecosystems surrounding it (Overbeck et al. 2015). One challenge in developing such conservation policies is taking biodiversity distribution and sensitivity into account while considering the impacts caused by human activities in ecosystems.

Asserting that land conversion affects approximately half of Cerrado does not imply that all species are being affected by this same proportion. Oppositely, species vulnerability to land-use changes may vary widely. Regions under a stronger human impact are more likely to have endangered species just because human impacts are major drivers of extinction risk. We hypothesize that human-impacted areas within Cerrado will have more threatened species than other regions, meaning that loss of suitable areas for narrow-distributed species will be proportionally higher than if they were distributed through all Cerrado. Cerrado mammals may be either endemic, widely distributed in other biomes of Brazil, or marginally occurring in Cerrado (Paglia et al. 2012). We also hypothesize that among restricted species we will find more variation in vulnerability than among widespread species, because they may be restricted to areas with either high or low impacts.

Our objective is to answer three pivotal questions related to the current conservation status of threatened mammals in Brazilian Cerrado biome: (1) Which areas are priorities for conservation considering climate suitability for threatened mammal species and human activities? (2) Which species are more vulnerable considering the proportion of original suitable area impacted? and (3) Which human activities have a higher impact on climatically suitable areas for those species? We use the extinction thresholds to define unsuitable landscapes for species due to high habitat loss and vulnerable landscapes that may become unsuitable for species in the near future. Unsuitable landscapes due to high habitat loss demand reactive conservation strategies for species. Vulnerable landscapes demand proactive conservation strategies, since local extinction can still be avoided if habitat conversion ceases.

Methods

Study species and occurrence data

We focused on threatened mammal species from the Cerrado according to the most recent evaluation organized by the Chico Mendes Institute for Biodiversity Conservation—ICMBio (Brasil 2014). We followed the literature to find which species inhabit the Cerrado (Paglia et al. 2012). We selected the study species based on the conservative criteria of the existence of validated occurrence points with a higher percentage of their total range in the Cerrado biome. We considered only species with more than 5% of their predicted range within Cerrado (see *Modeling procedures* for range estimation) to avoid those species occurring only at the biome boundaries, but more associated with other biomes were included. From a total of 110 threatened and 24 near-threatened mammal species at the national level, we selected 39 species under these criteria, distributed in eight mammal orders (Table 1). Also, we selected only species with more than ten occurrences at different locations due to restrictions related to species distribution modeling, totaling 32 species analyzed.

Human activities and land-use change

We obtained all information on human activities from official databases. Despite it, we found some inconsistencies, such as distinct geographic information for the same human activity from different official agencies. To deal with this sort of problem, we decided to use always the data with visually more complete information. We also looked for other sources of inconsistencies, for example, some roads data presented geographic inconsistencies when verified against satellite images. This was not a common problem, but when verifying this kind of inconsistency, we manually corrected the maps. The geographic extension of large hydroelectric dams was also verified. However, verifying the consistency most of infrastructure maps was not possible. Thus, we assumed the official data as correct regarding the information we could not check. In all cases, human activities were scaled to a 50 m cell resolution for the analysis.

Impacts of infrastructure projects are generally not restricted to their area; instead, they directly and indirectly affect surrounding areas. Influence zones of those impacts were delimited during a specialist meeting promoted by ICMBio according with the expected impact of specific human activities in local biodiversity (Table 2). We separated human activities in the following classes: agriculture, energy, transport, oil, mining, settlements and urban. Agriculture maps were separated into croplands and pasturelands. Cropland maps were obtained from the Brazilian Institute of Geography and Statistics—IBGE (<http://www.ibge.gov.br/>), the governmental agency responsible for geosciences and social, demographic and economic statistics. Pastureland maps were obtained from the Laboratory of Geoprocessing and Image Processing—LAPIG (Federal University of Goiás—<http://maps.lapig.iesa.ufg.br/sae>), being the only non-official data, but used due its high quality.

We obtained energy data from the National Agency of Electric Energy—ANEEL. Based on their account, influence zones of wind energy facilities were defined according to the number of wind turbines and available power. Most studies determine buffers of 150 m radius around each aerogenerator (Roscioni et al. 2014); however, the location of each aerogenerator was not available in our data. ICMBio defined the following buffer

Table 1 Threatened and near-threatened mammal species selected for evaluation of vulnerability in Cerrado

Mammal order	Number of species	Threat category	Species
Artiodactyla	3	VU	<i>Blastocerus dichotomus</i> , <i>Ozotoceros bezoarticus</i> , <i>Tayassu pecari</i>
Carnivora	1	NT	<i>Lontra longicaudis</i>
	9	VU	<i>Chrysocyon brachyurus</i> , <i>Leopardus braccatus</i> , <i>Leopardus wiedii</i> , <i>Lycalopex vetulus</i> , <i>Panthera onca</i> , <i>Pteronura brasiliensis</i> , <i>Puma concolor</i> , <i>Puma yaguarondi</i> , <i>Speothos venaticus</i>
Chiroptera	1	EN	<i>Leopardus tigrinus</i>
	1	NT	<i>Lonchophylla bokermanni</i> *
	3	VU	<i>Furipterus horrens</i> , <i>Glyphoncyteris behnii</i> , <i>Lonchorrina aurita</i>
Didelphimorphia	1	EN	<i>Lonchophylla dekeyseri</i>
	1	NT	<i>Marmosops ocellatus</i>
	1	VU	<i>Thylamys velutinus</i>
Perissodactyla	1	EN	<i>Thylamys macrurus</i>
	1	VU	<i>Tapirus terrestres</i>
Pilosa	2	VU	<i>Myrmecophaga tridactyla</i> , <i>Priodontes maximus</i>
	1	EN	<i>Tolypeutes tricinctus</i>
Primates	3	NT	<i>Alouatta caraya</i> , <i>Mico melanurus</i> , <i>Sapajus libidinosus</i>
	1	VU	<i>Sapajus cay</i>
	1	EN	<i>Alouatta ululata</i>
Rodentia	2	VU	<i>Kerodon acrobata</i> *, <i>Thalpomys cerradensis</i> *
	5	EN	<i>Euryoryzomys lamia</i> *, <i>Gyldenstolpia fronto</i> , <i>Microakodontomys transitorius</i> *, <i>Phyllomys brasiliensis</i> , <i>Thalpomys lasiotis</i> *
	1	CR	<i>Juscelinomys candango</i> *

Threat category: *NT* near threatened, *VU* vulnerable, *EN* endangered and *CR* critically endangered. * Species with less than ten occurrences at different locations excluded from analyses due to modelling restrictions

classes: below 7 wind generators, the buffer zone had 1 km of radius; from 8 to 12 wind generators, 1.8 km; from 13 to 20 wind turbines, 3 km; above 21 wind generators, 4.5 km. Maps of transmission lines, nuclear, and thermoelectric energy facilities were obtained from ANEEL. ICMBio defined buffer zones of 500 m surrounding transmission lines, 5 km from nuclear energy, and 2 km from thermoelectric facilities. Hydroelectric station locations were obtained from ANEEL, but reservoir data were delimited to each hydroelectric dam. Locations of airports, railways, and harbors were downloaded from the Transport Ministry website (<http://www.transportes.gov.br>), and buffer zones were 5 km, 1 km and 1.5 km from each infrastructure, respectively. A road map was obtained from the National Department of Transport Infrastructure—DNIT (<http://www.dnit.gov.br>) and comprises all the official roads, including paved and unpaved roads. ICMBio delimited as buffer zones 2 km from each road. Rural settlement data was obtained from the National Institute of Colonization and Agrarian Reform—INCRA (www.incra.gov.br). Urban area data were obtained from IBGE, containing villages and cities. Mining locations were obtained from

Table 2 Summary of human activities data. *Sources* ANEEL—Brazilian Agency of Electric Energy, ANP—Brazilian Agency of Petroleum, ANTT—Brazilian Agency of Terrestrial Transportation, DNIT—Brazilian Agency of Infrastructure to Transports, DNPM—Brazilian Agency of Mineral Production, IBGE—Brazilian Agency of Statistics and Geography, INCRA—Brazilian Agency of Colonization and Agrarian Reform, LAPIG/UFG Laboratory of Image Processing of Federal University of Goiás, and MT Brazilian Ministry of Transport

Thematic axe	Human activity	Buffer	Source
Agriculture	Cropland	–	IBGE
	Pasture	–	Lapig/UFG
Energy	Wind energy	150 m–4.5 km	ANEEL
	Transmission line	500 m	ANEEL
	Nuclear energy	5 km	ANEEL
	Thermoelectric energy	2 km	ANEEL
	Reservoir	–	ANEEL
Mining	Mining processes		DNPM
Oil	Blocks of oil and gas exploration		ANP
	Airports	5 km	MT
	Railways	1 km	MT e ANTT
	Harbors	1.5 km	MT
	Roads	2 km	DNIT
Settlement	Settlement projects	–	INCRA
Urban	Urban area	–	IBGE

We delimited influence zones for some human activities according with recommendations from ICMBio specialists

the National Department of Mineral Production—DNPM (www.dnpm.gov.br), while oil extraction locations data were obtained from the National Agency of Petroleum, Natural Gas, and Biofuels—ANP (<http://www.anp.gov.br>).

We validated the data on habitat loss derived from human activities with actual natural remnants mapped by the TerraClass Cerrado project, a consortium with INPE (National Institute of Space Research), UFG, UFU (Federal University form Uberlândia) IBAMA, EMBRAPA (Brazilian Agriculture Research Company). This project used segmentation of 121 images from LANDSAT-8 satellite (with a 30×30 m spatial resolution) to 2013, in a scale of 1:250,000, to determine land-use and vegetation cover for the entire Cerrado (Brasil 2015). Supplementary Material 1 shows the general distribution of human activities in Cerrado and Supplementary Material 2 shows the high spatial congruence between expected habitat loss derived from human activities and TerraClass Cerrado data.

Environmental variables

We used 19 bioclimatic variables from WorldClim (<http://www.worldclim.org>), derived from monthly temperature and rainfall values (Hijmans et al. 2005). Those variables are largely used to estimate climatic suitability in ecological studies (Peterson and Nakazawa 2008; Dupin et al. 2011). The extension of the dataset was the entire Neotropical region with a spatial resolution of approximately 9.25×9.25 km cell size. Considering that we evaluated the effects of environmental information at two different scales, regional and landscape, hereafter we refer to grid cells as a landscape cells.

Bioclimatic variables are highly correlated, which is an undesirable property in modeling procedures (Dormann et al. 2008; Rodda et al. 2011). Hence, we used a principal component analysis (PCA) based on the correlation matrix of the environmental variables to derive new, uncorrelated variables for the study, according to standard procedures (Manly 1994). Original variables for the same geographical extension present high collinearity, with nearly 85% of the variation in the overall dataset retained in first two PCA axis (Silva et al. 2013). We used the fixed cumulative eigenvalue criterion (Peres-Neto et al. 2005) of retaining 95% of total variance, which selected the first six axes (Silva et al. 2014). PCA scores of these axes for each cell were re-projected in geographic space as *ASCII* files for further analyses (dataset available from the corresponding author).

Ecological niche modeling

Overall strategy

The choice of modeling procedures is a major source of uncertainty in predicting species distributions (Syphard and Franklin 2009; Diniz-Filho et al. 2009; Aguirre-Gutierrez et al. 2013). Different modeling techniques may differ on a variety of their intrinsic properties (e.g., degree of overfitting or shape of response function related to environmental variables), which directly affect the resulting spatial prediction. Given those differences, one approach is to use different modeling strategies and apply an ensemble procedure of the overall results (Araujo and New 2006; Marmion et al. 2009). We followed this strategy but we also recognize problems derived from biased sampling of the species environmental space, which is a common problem considering the origin of occurrence points (Kramer-Schadt et al. 2013). Those biases may affect the balance between omission and commission rates, which are also an intrinsic aspect of every ecological niche model exercise. Autocorrelated occurrence points may increase model overfitting and omission errors. Sampling points in areas where a species was observed, but where it could not maintain persistent populations (sink sites), may contribute to high commission errors. As we target conservation issues, which are highly debatable with different conflicting views among possible societal forces, it is sensible to produce spatial predictions that minimize commission errors. Predicted areas where species are not present may impact both the efficiency and credibility of the model to be used in real conservation actions. Thus, we consider that minimizing commission errors has the desirable consequence of selecting areas with the highest mean probability of species presence, even at the cost of increased omission of areas without known occurrence points. To achieve this conservative approach, we apply here the protocol of Allouche et al. (Allouche et al. 2008), described below.

Modeling procedures

We used three different procedures which are commonly used and considered as highly effective (Elith et al. 2006; Meynard and Quinn 2007; Oppel et al. 2012): Maximum Entropy (Maxent), Random Forest (RF) and Support Vector Machine (SVM). Maxent is a machine-learning method conceptually based on the principle of maximum entropy (Phillips et al. 2004, 2006), which tries to minimize the relative entropy between the probability density estimated from the occurrence points and the probability density estimated from the environmental variables (Elith et al. 2011). To control for the known overfitting

problems (Anderson and Gonzalez 2011), we used only the linear and quadratic features (de Souza and De Marco 2014) with default regularization values, logistic output format. SVM uses linear models to find a non-linear decision hyperplane that split samples in different classes (Kamath 2009; Salcedo-Sanz et al. 2014). The optimal hyperplane maximizes the buffer between the boundary and the data (Kuhn and Johnson 2013). These models were built based on probability classes, performed with a radial basis kernel (RBF) and with a constant cost value ($C = 1$). RF comprises a family of algorithms that perform classification- and regression-tree analyses, which build a model based on the average of a large collection of de-correlated trees (Hastie et al. 2009). A random sample of predictors is chosen as candidates from the full set of predictors at each tree node, tuned to determine the optimal number of predictors randomly sampled at each split. RF was parameterized as 500 trees at the tuning step, with default values of the step factor and the improvement in out-of-bag (OOB) error parameter. For all models we use 1000 background points randomly chosen within the cells of the Neotropics. All algorithms were implemented using the R packages “dismo” (Hijmans et al. 2017), “kernlab” (Karatzoglou et al. 2004) and “randomForest” (Liaw and Wiener 2002).

Spatial constraints

The ecological niche modeling approach recognizes the importance of spatial restrictions in determining actual species distribution (Soberón 2007; Barve et al. 2011). Dispersal limitations and geographic barriers, as well as simply distance from source areas, constrain the distribution of accessible areas for species with suitable abiotic and biotic niche parameters (Allouche et al. 2008; Barve et al. 2011). To properly use ecological niche modeling in a conservation discussion, we need to reduce commission errors that result in the prediction of inaccessible areas for species as suitable for them. We used a method developed by Allouche et al. (2008) to alter model predictions based on restrictions empirically derived from known occurrence records. We produced a restriction layer for each species with the sum of the distances from each pixel to the known occurrence records, standardized by the maximum observed value. This layer is different for each species and reflects specific spatial constraints. This procedure will use known occurrence points to constrain predicted species distributions under the premise that predicted areas near known occurrence points have higher probability of maintaining populations of the species simply by the colonization-extinction process that is the ultimate motor of species distributions. This layer was included as an input of modeling procedures as another environmental variable.

Evaluation procedures

Evaluation of model predictions is crucial to provide an objective view of the quality of models and their intrinsic uncertainties (Liu et al. 2011). A good evaluation protocol needs to provide independent data for model evaluation. The more common protocol produces “independent” data by splitting the data into train (used to fit the models) and test partitions (used for evaluation). Nevertheless, this scheme may not assure that those points are statistically independent due to the high level of spatial autocorrelation observed in the basic environmental data and, consequently, in the model results. To produce a better evaluation scheme we follow other studies that produce spatially partitions in the geographic space increasing independence among training/test partitions (Wenger and Olden 2012; Verbruggen et al. 2013). Here we use latitudinal strips to create these partitions. We fitted

models in odd strips and use even strips as training. The number of strips was optimized for each species based on the spatial distribution of occurrence data in a process designed to maximize environmental similarity among training and test partitions.

We use the true-skill statistic (TSS) as a synthetic measure of model quality. This measure assumes values in the interval $(-1, 1)$ and is considered less dependent on species prevalence (Allouche et al. 2006), a common problem in other metrics frequently used (Lobo et al. 2008). TSS is used here both as a general appraisal about model efficiency as to make comparisons among different modeling procedures. All results of model evaluation under the transferability perspective are presented in Supplementary Material 3.

Ensemble models

ENM predictions are exposed to a variety of different sources of uncertainty, being the choice of the procedures as one of the great relevance (Diniz-Filho et al. 2009). Different procedures may produce different predictions due to their intrinsic properties, such as what is the expected relation between occurrence and environmental variation. Ensemble modeling is advised as both a technique to produce more robust model predictions as to provide a measure for the degree of similarity among different model results. The simpler, and probably most efficient, ensemble method produces a principal component analysis (PCA) of model predictions based on a correlation matrix. The first axis of this PCA will reflect the most important correlations among the models for each species. To this established methodology we add an important restriction. Usually, concordance among different procedures are evaluated in both areas with higher suitability and lower suitability. Nevertheless, concordance in the low suitability portion does not contribute to estimate best models and small non-linear effects may bias the final ensemble model.

To assure that only areas with higher suitability will contribute to derive the correlations for the procedure, we assign the value zero to all cells with predicted value lower than the threshold derived from the receiver operation curve (ROC) for each procedure. The ROC-derived threshold represent a balance between omission and commission rates (Liu et al. 2011). All loadings of the three procedures in the PCA are presented in Supplementary Material 4. For many species, the total variance retained in the first axis was higher than 0.8, indicating a high degree of concordance amount the modeling procedures. All values of variance retained were higher than 0.66, suggesting at least a good agreement considering that this PCA had three axes.

Analytical procedures

Our approach is based on an integration of (i) suitability estimated at a low-resolution grid and reflecting large scale climatic variables with (ii) a high-resolution land-use map reflecting human activities. This integration is based on the Extinction Threshold Theory that predicts that species may be loss in landscapes with total habitat amount lower than a specific threshold (Bascompte and Sole 1996; Boukal wz and í Bereczw 2002; Ovaskainen et al. 2002). Simulation studies suggest that percolation in random landscapes is lost at 41% of remaining habitat (Bascompte and Sole 1996) but it could occur with nearly 60% of remaining habitat, depending on how dispersal is modeled (Plotnick and Gardner 2002). Field tests for this theory found that most values are near the 10–30% remaining habitat proposed by Andrén (1994) but many studies also found higher values between the 40–50% prediction (Swift and Hannon 2010). Nevertheless, it is reasonable to expect that different

species may have specific threshold values according to their own sensitivity to both small habitat amount and connectivity. Recently, our general approach was successfully applied to bats in Cerrado areas (Mendes and De Marco 2017), using empirically derived values for this threshold. Most threatened species have little information on both their natural history and their sensitivity to low habitat amounts. Thus, we safely use a general value of 50% as the expected threshold to identify which landscapes may not maintain persistent population of those species. This value is a conservative choice compared to original Andr  n (1994) predictions.

Our procedure was simply to calculate the amount of remaining natural vegetation in climatic suitable landscapes of 9.25×9.25 km. Climatic unsuitable landscapes were excluded. The overlap of all activities in each cell allows deriving the total remaining habitat in each cell. Cells with total remaining habitat lower than 50% are considered lost. Cells with remaining habitat between 50 and 60% are considered vulnerable, as additional activities may turn them into lost cells. Here, the distribution of lost cells is directly interpreted as changes in Area of Occupancy (AOO). AOO is defined as the area within extent of occurrence that is occupied by a taxon (IUCN Standards and Petitions Subcommittee 2014). We consider that habitat loss will directly reduce the AOO by reducing available suitable patches within the landscape. Otherwise, AOO has been used in similar studies that use SDM as descriptors of species ranges for conservation prioritization (Marger et al. 2013; Guillera-Aroita et al. 2015). Nevertheless, we use the relations between all historical distribution of species predicted by SDM (as an estimation of EOO) in relation to the amount of remaining habitat constrained by a landscape threshold (an estimation of AOO) to describe the relative vulnerability among species.

Results

All TSS for individual models (Maxent, SVM and RF) were positive with at least one individual model higher than 0.4 for most of the species (Supplementary Material, Table S1.3). As TSS and other evaluation metrics are sensitive to prevalence, species with larger distribution presented usually lower TSS. Otherwise, the three individual models showed higher concordance, with first principal component representing more than 74% of the model's variation for all species.

Only 41.07% of Cerrado landscape cells have more than half of their area covered by remaining natural vegetation. Habitat loss in the Cerrado is higher in areas of distribution of threatened species (Fig. 1). Human impacts increase towards the southern Cerrado, where many landscapes are expected to have been completely lost (see white cells in Fig. 1a). At the same time, highly-preserved landscapes are mostly found in the northern half of the biome (see black cells in Fig. 1a). Species richness of threatened mammals in the Cerrado shows higher levels in southern parts of the biome (Fig. 1b). Thus, landscapes with high richness of threatened species are broadly lost, while more preserved landscapes host a lower number of threatened species (Fig. 1c). In fact, there is a strong relationship between the two distributions (Fig. 2, $R^2 = 0.906$, $p < 0.001$), with threatened species richness decreasing at a rate of 0.5 species by each 10% of habitat remaining increase (Fig. 2). Consequently, average AOO of species (34.2%) is lower than the average habitat remaining in the Cerrado (41.07%; compare black and green lines in Fig. 3).

We identified 983 vulnerable landscape cells with remaining habitat values between 50 and 60% (Fig. 4a). These cells occur all along the Cerrado, being only absent from large

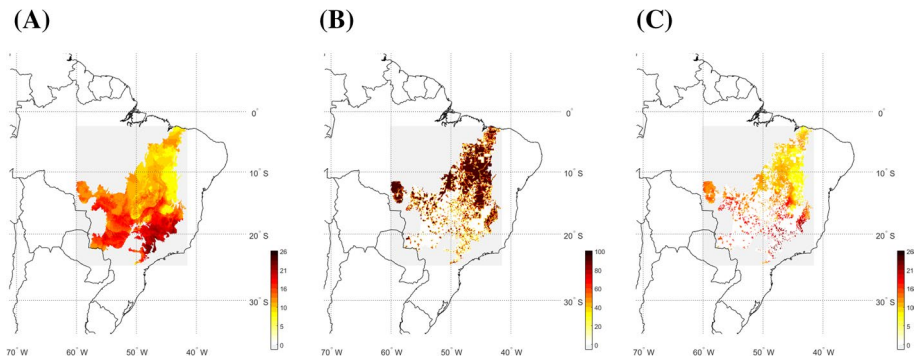


Fig. 1 Habitat remaining, original species richness and remaining species richness of endangered mammals in the Cerrado. **a** Proportion of habitat remaining in Cerrado biome after the impact of agriculture, mining, oil, energy, transportation, rural settlements and urban areas. **b** Original mammal endangered species richness estimated from ecological niche models developed by species at landscape cells of 9×9 km. **c** Remaining mammal endangered species richness as predicted considering habitat remaining in (a) and original species richness in (b), considering a 50% habitat remaining threshold below which the landscape cell is considered unavailable for the species

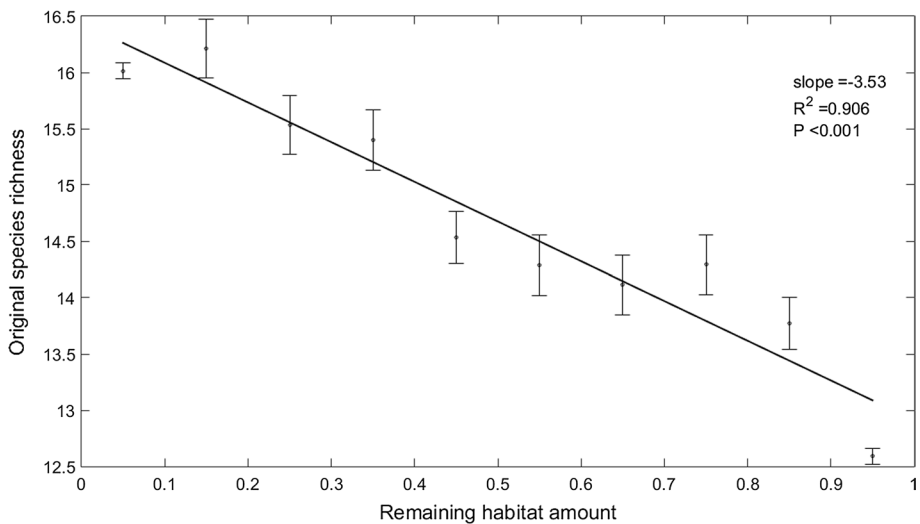


Fig. 2 Relationship between original species richness and proportion of habitat remaining in the Cerrado biome. Due to the large sample size ($n > 24000$), cells are grouped in ten classes of remaining habitat and the regression line is estimated over the averages of these classes. For each class, mean and 95% confidence interval of species richness is represented

areas with extreme values of land-use conversion (compare Figs. 1a, 4a). In accordance to the overall pattern (Fig. 1b), southern Cerrado cells presents the higher richness. Mean threatened species richness in vulnerable cells (10.45 ± 0.41 , confidence interval) is similar to the species richness along all the landscape cells of Cerrado (11.63 ± 0.07).

Species show a large variation in the proportion of their EOO that is preserved, varying from 7% (*Sapajus cay*) to 72% (*Tolypeutes tricinctus*). There is also a large variation in

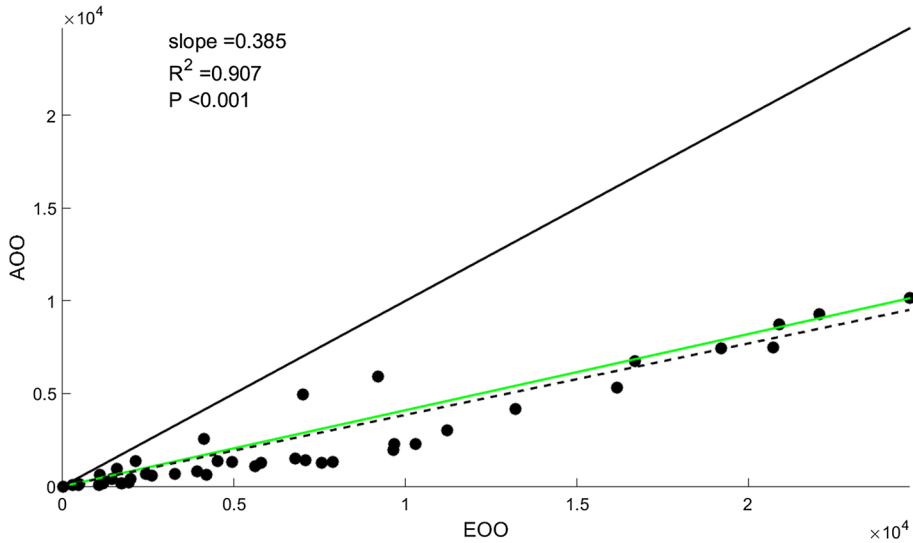


Fig. 3 Relationship between AOO and EOO of threatened mammal species of Cerrado biome, considering habitat remaining after the impact of human activities. Each point represents a threatened mammal species (see Table 1). EOO is estimated based on ecological niche models using the ROC threshold. AOO is estimated considering a 50% habitat remaining threshold, below which the landscape cell is considered unavailable for the species. Solid black line represents the expected results for no change in EOO (extent of occupancy) before and after habitat loss. Dash-dotted black line represents a regression line constrained to a zero intercept; the slope of this line being the average AOO (area of occupancy) of species. Solid green line represents the expected AOO if species distributions were randomly distributed along the Cerrado; the slope of this line being the average remaining habitat in the biome. (Color figure online)

the original EOO, which varies from 3859 to 2,106,976 km² (45–24,625 landscape cells), the last one comprising almost all Cerrado. A clear pattern is observed between these two variables, as there is a tendency of species with original smaller EOO to show a larger variation in the proportion of AOO (Fig. 5).

Habitat loss in the Cerrado biome seems to be mainly driven by agriculture and transport infrastructures, which are found in more than 45% of Cerrado landscapes each (Fig. 6a). These levels of occupation are far from those of other human activities. However, the relative impact of different human activities shows slight differences depending on the level of landscape habitat remaining. When looking at cells with habitat remaining below 50%, agriculture slightly stands out above transport infrastructures, while other activities have minor importance (Fig. 6b). Nevertheless, the occupation of vulnerable cells with habitat remaining between 50% and 60% is driven by a larger variety of activities and, in this case, transport slightly stands out above agriculture (Fig. 6c).

Discussion

There is a strong spatial congruence between current human activities and predicted richness of threatened mammals in Cerrado. This result highlights the importance of conservation programs to ensure the survival of those populations in impacted landscapes.

At a larger scale it has been pointed that South America, China and Eastern Africa have high spatial congruence between agriculture intensity and mammal endemic species richness (Kehoe et al. 2015). Climate and topography are important to determine species suitability (Andrews and O'Brien 2000; Martinez-Meyer et al. 2004), while they are also key features driving the establishment of dominant economic activities in the Cerrado. Lowland areas may exhibit the desirable topography for agriculture conversion; Sugarcane plantations, for example, are restricted to slopes lower than 12 degrees (Aguiar et al. 2011). Topography also strongly determines the distribution of natural remnants in Cerrado (Carvalho et al. 2009). Correspondingly, mammal species distribution in Cerrado is driven by the climate (Diniz-Filho et al. 2008). Then, the observed overlap between species richness and remaining habitat could partially derive from the fact that both distributions are determined by the same environmental features. It is important to note that this relationship may not be static; while species distribution and evolutionary adaptation leading to range shifts are gradual, technological development capable to turn previously unused lands into adequate areas quickly revamp landscapes. Thus, even areas that have escaped degradation until now due to their lack of economic interest may rapidly turn profitable and be invaded by human activities.

There is another possible explanation for the spatial overlap between threatened species richness and habitat loss. Species with original distributions overlapping economic activities have higher chances of becoming threatened, especially those with original restricted distributions (Cardillo et al. 2008). IUCN guidelines explicitly point that species are only considered threatened if there are confirmed impacts within their distribution capable to disrupt their populations (IUCN Standards and Petitions Subcommittee 2014). This increases the chance of finding threatened species exactly in the regions with higher impacts. In the Brazilian Cerrado, the environmental impact increases towards the largest economic centers of the country in the south (Sano et al. 2010). Economic activities such as soybean plantations and sugarcane are moving northwards mostly due to the competition for land, costs of southern landscapes, and improved transport infrastructure (Martinelli and Filoso 2008; De Souza et al. 2013; Alkimim et al. 2015). Specifically, this seems to be the ongoing process in the MATOPIBA region, northern Cerrado, which recently became the new agricultural frontier of Brazil (Spera et al. 2016).

The spatial aggregation of human activities has another consequence on the predictability of species vulnerability: species with restricted distributions show a higher variability in their AOO than species with larger distributions. Species with distributions covering a large part of the Cerrado show AOO values close to habitat remaining levels in Cerrado itself. However, species with restricted areas have a higher variability on the spatial overlap of their distribution with impacted areas and thus show higher variability of AOO. In this case, species with small distributions in northern Cerrado regions will be proportionally less affected by land-use changes than species with small distributions in southern Cerrado. Small distribution is generally accepted as the best surrogate of extinction risk (Purvis et al. 2000; Harcourt et al. 2002; Fritz et al. 2009; Fordham et al. 2013). Nevertheless, under an uneven spatial distribution of impacts, as it is the case in Cerrado, the position of the species in the geographic space is also indispensable for predicting their vulnerability. The observed high variation among small-distribution species may simply result from the chance component of exposition of each species to human activities.

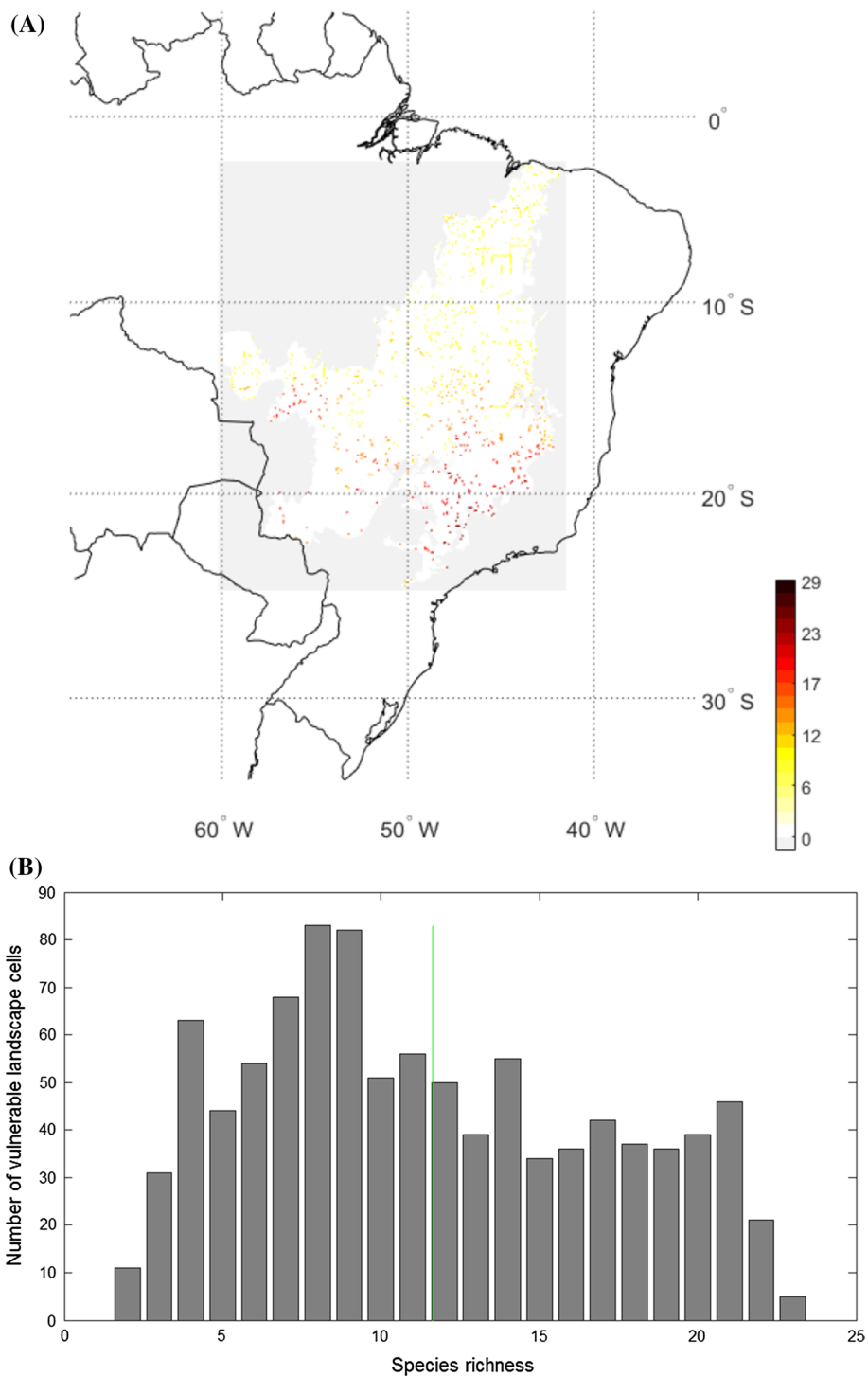
Fig. 4 Spatial distribution and species richness of vulnerable landscape cells on the Cerrado biome. **a** Vulnerable landscape cells in the Cerrado biome, identified from light yellow (low species richness), to orange-red (intermediate species richness) and black (high species richness). **b** Frequency distribution of species richness in vulnerable landscape cells. The dashed green line represents the mean species richness of endangered mammals considering the whole Cerrado. Vulnerable cells are defined as 9.25×9.25 km cells with habitat remaining between 40 and 50% and considered to be close to become unavailable for species under the logic of occupancy above 50% of landscape habitat remaining. (Color figure online)

Vulnerable landscapes: moving from a reactive towards a proactive approach

We observed a smaller remaining area to support biodiversity (41%) than previous studies (Klink and Machado 2005; Brasil 2015). This difference is probably due to our conservative approach of considering landscapes with less than 50% of remaining natural vegetation as unsuitable for threatened species populations. We based this value on previous studies that encountered biological responses to habitat loss at levels of habitat remaining up to 50% of the landscape (Betts et al. 2010; Rueda et al. 2013; Muylaert et al. 2016; Mendes and De Marco 2017). We are not only evaluating the current overlap of human use and species distribution, but also predicting available remaining area for mammals, assuming that in landscapes with less than 50% of remaining habitat species are expected to be lost at the long run. This is important since there is an expected extinction time lag between habitat loss and species extinction (Tilman et al. 1994; Metzger et al. 2009). In spite of the southern parts of the Cerrado having been converted for decades, many landscapes are suffering only a recent increase in land-use conversion, mostly related to the expansion of soybean (Morton et al. 2006; Barreto et al. 2012) and sugarcane (Lapola et al. 2010). These ongoing processes may imply that actual species losses would be noticed only in a few years. We believe that our method based on buffers around known economic and infra-structure elements may be even considered conservative.

We recognize that landscapes with higher intensity of human activities and, thus, with low probability of species persistence will be hardly restored. Changing those landscapes to increase habitat amount could be a very difficult task, especially considering that the conflict for space is with agriculture (Dobrovolski et al. 2011b). The intense local and global pressure to increase grain production turns this kind of discussion unproductive. Nevertheless, it is necessary to consider that those cells require the implementation of reactive conservation actions to affect species ecological sustainability. The most profitable action is the expansion of original vegetation restoration in areas where the current legal scenario enforces its maintenance. Even with the recent changes in the Brazilian Forest Code, which cut down the required extension of riparian forests (Soares-Filho et al. 2014), restoration is still necessary in some landscapes to accomplish minimal legal requirements of the new Forest Code.

Proactive conservation management aims to show solutions for conservation issues before they happen. We pointed landscapes with 40–50% of habitat loss, as landscapes at which mammal population's persistence is still ensured but would be threatened with only small further habitat losses. We propose that such landscapes should be considered the most vulnerable, and new infrastructure or economic projects should be avoided in these areas. These landscapes are potential targets for a proactive conservation management (Dobrovolski et al. 2011a) designed to induce the negotiation around the conservation objectives in them. We were able to identify more than 900 cells under these criteria many of them with than 15 threatened mammal species, which reinforce their strategic importance.



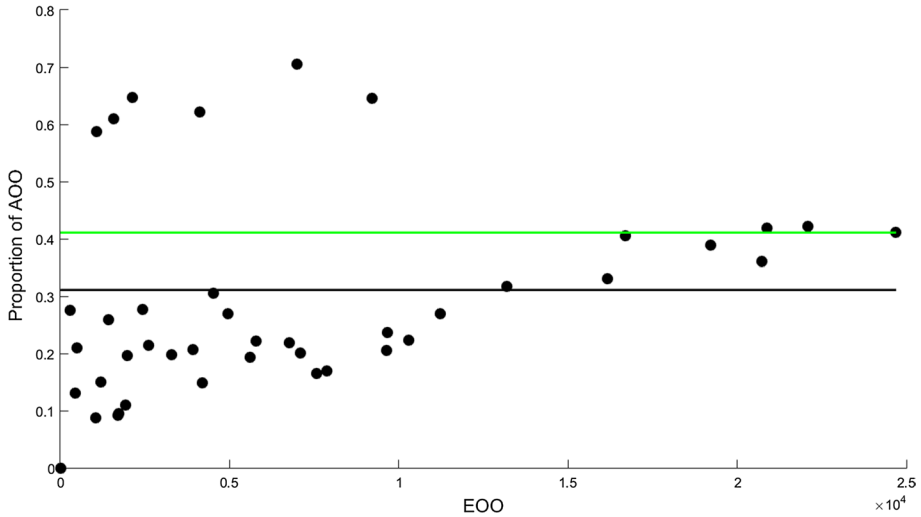


Fig. 5 Relationship between EOO (extent of occurrence) and proportion of AOO of threatened mammal species in Cerrado biome. Each point represents a species. Black solid line represents the mean proportion of AOO (area of occupancy) across species. Green solid line is the current proportion of remaining habitat in Cerrado. (Color figure online)

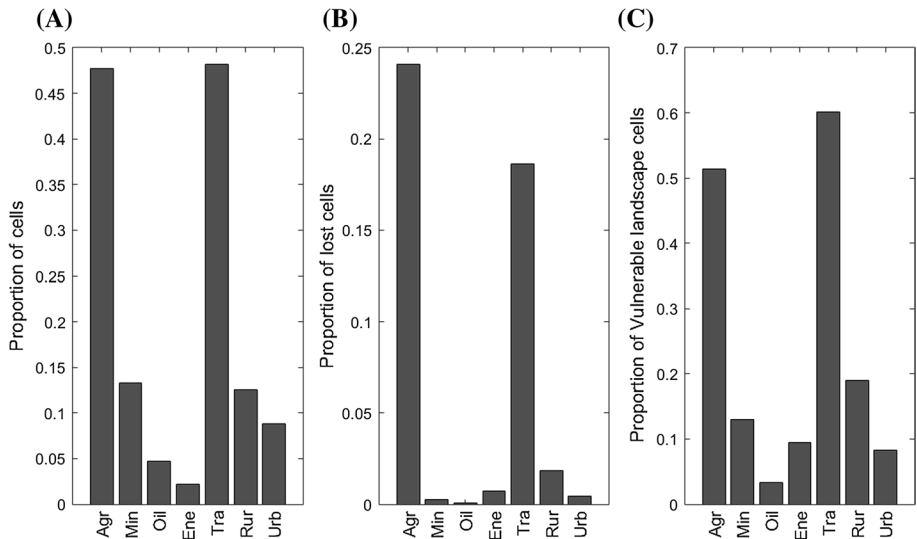


Fig. 6 Proportion of landscape cells affected by each human activity in the whole Cerrado biome (a), in lost landscape cells with habitat remaining below 50% (b) and in vulnerable landscape cells with habitat remaining between 50% and 60% (c). Agr: agriculture; Min: mining; Oil: oil reserves; Ene: energy production and power lines; Tra: transport infrastructure; Rur: rural settlements; Urb: urban areas

Established land-use in Cerrado will hardly change even if it causes a strong negative effect on current species vulnerability. The most profitable conservation actions will be the negotiation of planned infrastructure or control policies over economic actions in

the near future. Recent governmental planning in Brazil was led by the “Accelerated Development Programs” (In Portuguese “Programas de Aceleração do Crescimento—PAC”), which are at least partially transparent (Lemos and Roberts 2008; Fearnside and Laurance 2012). The existence of such information opens the possibility to evaluate the possible threats derived from the implantation of those plans where biodiversity is already vulnerable.

Agriculture and transport infrastructure dominate the Cerrado

Habitat loss for mammal species in the Cerrado is driven by a combination of multiple human activities, although two activities stand out: agriculture and transport infrastructure. Agriculture is responsible for a large portion of the economic input in the Cerrado region, and the expansion of this activity was highly encouraged in past decades (Brannstrom et al. 2008). Our results show that it is the most important current activity in highly impacted landscapes that are considered already unsuitable for mammals. There are at least three different activities under this theme. Sugarcane and soybean production represent a large portion of these areas and their preponderance is expected to largely increase (Fearnside 2001; Rudorff et al. 2010). Cattle farming is the other main economic activity in those areas, but at least partially under pressure to conversion to more profitable activities (most sugarcane and soybean) as occurred in Amazonia (Santos et al. 2004; De Souza et al. 2013). From a landscape perspective, pastures maintain less fragmented landscapes with more remnant habitat than crops (Carvalho et al. 2009). Thus, the dynamics of spatial interchanges among those activities may directly affect mammal persistence.

Transportation infrastructure is both a direct cause of habitat loss (Laurance et al. 2002; Freitas et al. 2010) and essential to the further development of croplands. Transportation is key to the definition of current vulnerable cells, possibly with some level of autocorrelation with croplands. Pressure to increase Cerrado grain production directly reflects in the improvement and extension of the roads network and development of other kinds of transportation. Some threatened mammal species in Cerrado, such as *Myrmecophaga tridactyla*, are specially prone to becoming roadkill (Diniz and Brito 2013). There is no complete account of the importance of roadkill as a threat in Cerrado, but many local studies show that a large portion of biodiversity, including threatened mammals, is highly vulnerable (Cáceres et al. 2010; Cunha et al. 2010; Saranholi et al. 2016). Finding the best possible conservation plan to minimize the effects of habitat conversion under unprecedented rates on the Cerrado biodiversity is critical since we may be facing a last-chance opportunity to apply it.

Finally, we argue that the interpretation of “which economic activity is causing the major threat to biodiversity?” needs a broad review. The evaluation of the exposure to a single economic activity (e.g., mining operations) on biodiversity could be misleading, since economic activities may present complex synergistic effects. A landscape perspective, that allows integrating those effects in a single analysis, is clearly able to produce a more realistic prediction of species and landscape vulnerability.

Acknowledgements This contribution is part of the cooperative program UFG-ICMBIO entitled “Mapa de vulnerabilidade das espécies brasileiras ameaçadas de extinção”. Paulo De Marco is supported by continuous CNPq productivity Grant (308694/2015-5). Sara Villén-Pérez is supported by a Young Talent Attraction CNPq fellowship (401408/2014-0). Poliana Mendes is supported by a CNPq fellowship (403347/2014-9).

References

- Aguiar DA, Rudorff BFT, Silva WF et al (2011) Remote sensing images in support of environmental protocol: monitoring the sugarcane harvest in São Paulo State, Brazil. *Remote Sens* 3:2682–2703. <https://doi.org/10.3390/rs3122682>
- Aguirre-Gutierrez J, Carvalheiro LGLG, Polce C et al (2013) Fit-for-purpose: species distribution model performance depends on evaluation criteria—dutch hoverflies as a case study. *PLoS ONE* 8:e63708
- Alkimim A, Sparovek G, Clarke KC (2015) Converting Brazil's pastures to cropland: an alternative way to meet sugarcane demand and to spare forestlands. *Appl Geogr* 62:75–84. <https://doi.org/10.1016/j.apgeog.2015.04.008>
- Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J Appl Ecol* 43:1223–1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>
- Allouche O, Steinitz O, Rotem D et al (2008) Incorporating distance constraints into species distribution models. *J Appl Ecol* 45:599–609. <https://doi.org/10.1111/j.1365-2664.2007.01445.x>
- Anderson RP, Gonzalez I (2011) Species-specific tuning increases robustness to sampling bias in models of species distributions: An implementation with Maxent. *Ecol Modell* 222:2796–2811. <https://doi.org/10.1016/j.ecolmodel.2011.04.011>
- 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. <https://doi.org/10.2307/3545823>
- Andrews P, O'Brien EM (2000) Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *J Zool* 251:205–231
- Araujo MB, New M (2006) Ensemble forecasting of species distributions. *Trends Ecol Evol* 22:42–47
- Attorre F, De Sanctis M, Farcomeni A et al (2013) The use of spatial ecological modelling as a tool for improving the assessment of geographic range size of threatened species. *J Nat Conserv* 21:48–55. <https://doi.org/10.1016/j.jnc.2012.10.001>
- Barreto L, Van Eupen M, Kok K et al (2012) The impact of soybean expansion on mammal and bird, in the Balsas region, north Brazilian Cerrado. *J Nat Conserv* 20:374–383
- Barve N, Barve V, Jimenez-Valverde A et al (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol Modell* 222:1810–1819. <https://doi.org/10.1016/j.ecolmodel.2011.02.011>
- Bascompte J, Sole RV (1996) Habitat fragmentation and extinction thresholds in spatially explicit models. *J Anim Ecol* 65:465–473
- Bellard C, Leclerc C, Leroy B et al (2014) Vulnerability of biodiversity hotspots to global change. *Glob Ecol Biogeogr* 23:1376–1386. <https://doi.org/10.1111/geb.12228>
- Betts MG, Hagar JC, Rivers JW et al (2010) Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. *Ecol Appl* 20:2116–2130. <https://doi.org/10.1890/09-1305.1>
- Boukal DS, Berecz L (2002) Single-species models of the allee effect: extinction boundaries, sex ratios and mate encounters. *J Theor Biol* 218:375–394
- Brannstrom C, Jepson W, Filippi AM et al (2008) Land change in the Brazilian Savanna (Cerrado), 1986–2002: Comparative analysis and implications for land-use policy. *Land use policy* 25:579–595. <https://doi.org/10.1016/j.landusepol.2007.11.008>
- Brasil (2014) Lista brasileira de espécies ameaçadas de extinção. Diário Oficial da União, Brasília, DF
- Brasil (2015) Mapeamento do Uso e Cobertura do Cerrado: Projeto Terra Class Cerrado 2013. Brasília, DF
- Cáceres NC, Hannibal W, Freitas DR et al (2010) Mammal occurrence and roadkill in two adjacent ecoregions (Atlantic Forest and Cerrado) in south-western Brazil. *Zoologia* 27:709–717. <https://doi.org/10.1590/S1984-46702010000500007>
- Carvalho FMV, De Marco P, Ferreira LG (2009) The Cerrado into-pieces: Habitat fragmentation as a function of landscape use in the savannas of central Brazil. *Biol Conserv* 142:1392–1403. <https://doi.org/10.1016/j.biocon.2009.01.031>
- Cunha HF, Moreira FGA, Silva SS (2010) Roadkill of wild vertebrates along the GO-060 road between Goiânia and Iporá, Goiás State, Brazil. *Acta Sci Biol Sci* 32:257–263. <https://doi.org/10.4025/actasbiolsci.v32i3.4752>
- Dawson TPT, Jackson ST, House JJJ, et al (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science* (80-) 332:53–58. <https://doi.org/10.1126/science.1200303>
- De Marco P Jr, Diniz-Filho JAF, Bini LM (2008) Spatial analysis improves species distribution modelling during range expansion. *Biol Lett* 4:577–580. <https://doi.org/10.1098/rsbl.2008.0210>
- de Pena JCC, Kamino LHY, Rodrigues M, et al (2014) Assessing the conservation status of species with limited available data and disjunct distribution. *Biol Conserv* 170:130–136

- de Souza RA, De Marco P (2014) The use of species distribution models to predict the spatial distribution of deforestation in the western Brazilian Amazon. *Ecol Modell* 291:250–259. <https://doi.org/10.1016/j.ecolmodel.2014.07.007>
- De Souza RA, Mizziara F, De Marco Junior P (2013) Spatial variation of deforestation rates in the Brazilian Amazon: A complex theater for agrarian technology, agrarian structure and governance by surveillance. *Land Use Policy* 30:915–924. <https://doi.org/10.1016/j.landusepol.2012.07.001>
- Diniz MF, Brito D (2013) Threats to and viability of the giant anteater, *Myrmecophaga tridactyla* (Pilosa: Myrmecophagidae), in a protected Cerrado remnant encroached by urban expansion in central Brazil. *Zoologia* 30(2):151–156. <https://doi.org/10.1590/S1984-46702013000200005>
- Diniz-Filho J, Bini LM, Vieira CM et al (2008) Spatial patterns of terrestrial vertebrate species richness in the Brazilian Cerrado. *Zool Stud* 47:146–157
- Diniz-Filho JAF, Mauricio Bini L, Fernando Rangel T et al (2009) Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. *Ecography (Cop)* 32:897–906. <https://doi.org/10.1111/j.1600-0587.2009.06196.x>
- Dobrovolski R, Diniz JAF, Loyola RD et al (2011a) Agricultural expansion and the fate of global conservation priorities. *Biodivers Conserv* 20:2445–2459. <https://doi.org/10.1007/s10531-011-9997-z>
- Dobrovolski R, Loyola RD, de Marco P, Diniz JAF (2011b) Agricultural expansion can menace Brazilian protected areas during the 21st century. *Nat Conserv* 9:208–213
- Dormann CF, Purschke O, Marquez JR et al (2008) Components of uncertainty in species distribution analysis: a case study of the great grey shrike. *Ecology* 89:3371–3386
- Dupin M, Reynaud P, Jarosik V et al (2011) Effects of the training dataset characteristics on the performance of nine species distribution models: application to *Diabrotica virgifera virgifera*. *PLoS ONE* 6:e20957. <https://doi.org/10.1371/journal.pone.0020957>
- Elith J, Graham CH, Anderson RP et al (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography (Cop)* 29:129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Elith J, Phillips SJ, Hastie T et al (2011) A statistical explanation of MaxEnt for ecologists: statistical explanation of MaxEnt. *Divers Distrib* 17:43–57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
- Fahrig L (2001) How much habitat is enough. *Biol Conserv* 100:65–74
- Fearnside PM (2001) Soybean cultivation as a threat to the environment in Brazil. *Environ Conserv* 28:23–38
- Fearnside PM, Laurance WF (2012) Infraestrutura na Amazônia: As lições dos planos plurianuais. *Cad CRH* 25:87–98. <https://doi.org/10.1590/S0103-49792012000100007>
- Foden WB, Butchart SHM, Stuart SN et al (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0065427>
- Fordham DA, Akçakaya HR, Araújo MB et al (2013) Tools for integrating range change, extinction risk and climate change information into conservation management. *Ecography (Cop)* 36:956–964. <https://doi.org/10.1111/j.1600-0587.2013.00147.x>
- Freitas SR, Hawbaker TJ, Metzger JP (2010) Effects of roads, topography, and land use on forest cover dynamics in the Brazilian Atlantic Forest. *For Ecol Manag* 259:410–417
- Fritz SA, Bininda-Emonds ORP, Purvis A (2009) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol Lett* 12:538–549. <https://doi.org/10.1111/j.1461-0248.2009.01307.x>
- Guillera-Arroita G, Lahoz-Monfort JJ, Elith J et al (2015) Is my species distribution model fit for purpose? Matching data and models to applications. *Glob Ecol Biogeogr* 24:276–292. <https://doi.org/10.1111/geb.12268>
- Harcourt AH, Coppeto SA, Parks SA (2002) Rarity, specialization and extinction in primates. *J Biogeogr* 29:445–456
- Hastie T, Tibshirani R, Friedman JH (2009) The elements of statistical learning: data mining, inference, and prediction, 2nd edn. Springer, New York
- Hijmans RJ, Cameron SE, Parra JL et al (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978
- Hijmans RJ, Phillips S, Leathwick J, Elith J (2017) Species distribution modeling. Package 'dismo.' *dismo Species Distrib. Model. R Packag.* version 1.1–4. <https://CRAN.R-project.org/package=dismo> Version 1
- Huggett AJ (2005) The concept and utility of “ecological thresholds” in biodiversity conservation. *Biol Conserv* 124:301–310
- Humphries MM, Thomas DW, Speakman JR (2002) Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature* 418:313–316. <https://doi.org/10.1038/nature00903.1>

- Illoldi-Rangel P, Sanchez-Cordero V, Peterson AT et al (2004) Predicting distributions of mexican mammals using ecological niche modeling. *J Mammal* 85:658–662. <https://doi.org/10.1644/BER-024>
- International Union for Conservation of Nature [IUCN] (2012) IUCN red list categories and criteria version 3.1 Second Edition. IUCN, Cambridge
- Isaac JL (2009) Effects of climate change on life history: implications for extinction risk in mammals. *Endanger Species Res* 7:115–123. <https://doi.org/10.3354/esr00093>
- Isaac JL, VanDerWal J, Johnson CN, Williams SE (2009) Resistance and resilience: quantifying relative extinction risk in a diverse assemblage of Australian tropical rainforest vertebrates. *Divers Distrib* 15:280–288
- IUCN Standards and Petitions Subcommittee (2014) Guidelines for using the IUCN red list categories and criteria THE IUCN RED LIST OF THREATENED SPECIES™. 11:
- Kamath C (2009) Scientific data mining: a practical perspective. Society for Industrial and Applied Mathematics, Philadelphia
- Karatzoglou A, Smola A, Hornik K, Zeileis A (2004) kernlab—an S4 package for Kernel methods in R. *J Stat Softw* 11:1–20. <https://doi.org/10.1016/j.csda.2009.09.023>
- Kehoe L, Kuemmerle T, Meyer C et al (2015) Global patterns of agricultural land-use intensity and vertebrate diversity. *Divers Distrib* 21:1308–1318. <https://doi.org/10.1111/ddi.12359>
- Klink CA, Machado RB (2005) Conservation of the Brazilian Cerrado. *Conserv Biol* 19:707–713
- Kramer-Schadt S, Niedballa J, Pilgrim JD et al (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. *Divers Distrib* 19:1366–1379. <https://doi.org/10.1111/ddi.12096>
- Kuhn M, Johnson K (2013) Applied predictive modeling. Springer, New York
- Lapola DM, Schaldach R, Alcamo J et al (2010) Indirect land-use changes can overcome carbon savings from biofuels in Brazil. *Proc Natl Acad Sci USA* 107:3388–3393. <https://doi.org/10.1073/pnas.0907318107>
- Laurance WF, Albernaz AKM, Schroth G et al (2002) Predictors of deforestation in the Brazilian Amazon. *J Biogeogr* 29:737–748
- Lemos MC, Roberts JT (2008) Environmental policy-making networks and the future of the Amazon. *Philos Trans R Soc London B Biol Sci* 363:1897–1902. <https://doi.org/10.1098/rstb.2007.0038>
- Liaw A, Wiener M (2002) Classification and regression by random forest. *R News* 2:18–22. <https://doi.org/10.1177/154405910408300516>
- Liu CR, White M, Newell G (2011) Measuring and comparing the accuracy of species distribution models with presence-absence data. *Ecography (Cop)* 34:232–243
- Lobo JM, Jimenez-Valverde A, Real R et al (2008) AUC: a misleading measure of the performance of predictive distribution models. *Glob Ecol Biogeogr* 17:145–151. <https://doi.org/10.1111/j.1466-8238.2007.00358.x>
- Manly BFJ (1994) Multivariate statistical methods: a primer. Chapman and Hall, London
- Marcer A, Sáez L, Molowny-Horas R et al (2013) Using species distribution modelling to disentangle realised versus potential distributions for rare species conservation. *Biol Conserv* 166:221–230. <https://doi.org/10.1016/j.biocon.2013.07.001>
- Marmion M, Parviainen M, Luoto M et al (2009) Evaluation of consensus methods in predictive species distribution modelling. *Divers Distrib* 15:59–69
- Martinelli LA, Filoso S (2008) Expansion of sugarcane ethanol production in Brazil: environmental and social challenges. *Ecol Appl* 18:885–898
- Martinez-Meyer E, Townsend Peterson A, Hargrove WW (2004) Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Glob Ecol Biogeogr* 13:305–314
- Melo GL, Sponchiado J, Cáceres NC, Fahrig L (2017) Testing the habitat amount hypothesis for South American small mammals. *Biol Conserv* 209:304–314. <https://doi.org/10.1016/j.biocon.2017.02.031>
- Mendes P, De Marco P (2017) Bat species vulnerability in Cerrado: integrating climatic suitability with sensitivity to land-use changes. *Environ Conserv*. <https://doi.org/10.1017/S0376892917000194>
- Metzger JP, Martensen AC, Dixo M et al (2009) Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. *Biol Conserv* 142:1166–1177. <https://doi.org/10.1016/j.biocon.2009.01.033>
- Meynard CN, Quinn JF (2007) Predicting species distributions: a critical comparison of the most common statistical models using artificial species. *J Biogeogr* 34:1455–1469. <https://doi.org/10.1111/j.1365-2699.2007.01720.x>
- Morton DC, DeFries RS, Shimabukuro YE et al (2006) Cropland expansion changes deforestation dynamics in the southern Brazilian Amazon. *PNAS* 103:14637–14641
- Muylaert RL, Stevens RD, Ribeiro MC (2016) Threshold effect of habitat loss on bat richness in Cerrado-forest landscapes. *Ecol Appl* 26:1854–1867. <https://doi.org/10.1890/15-1757.1>

- Oppel S, Meirinho A, Ramirez I et al (2012) Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biol Conserv* 156:94–104
- Ovaskainen O, Sato K, Bascompte J, Hanski I (2002) Metapopulation models for extinction threshold in spatially correlated landscapes. *J Theor Biol* <https://doi.org/10.1006/jtbi.2001.2502>
- Overbeck GE, Vélez-Martin E, Scarano FR et al (2015) Conservation in Brazil needs to include non-forest ecosystems. *Divers Distrib* 21:1455–1460. <https://doi.org/10.1111/ddi.12380>
- Paglia AP, De Rezende DT, Koch I et al (2012) Modelos de Distribuição de Espécies em Estratégias para a Conservação da Biodiversidade e para Adaptação Baseada em Ecossistemas Frente a Mudanças Climáticas. *Nat Conserv* 10:231–234
- Pardini R, de Bueno AA, Gardner TA et al (2010) Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0013666>
- Peres-Neto PR, Jackson DA, Somers KM (2005) How many principal components? stopping rules for determining the number of non-trivial axes revisited. *Comput Stat Data Anal* 49:974–997
- Peterson AT, Nakazawa Y (2008) Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*. *Glob Ecol Biogeogr* 17:135–144
- Phillips SJ, Dudík M, Schapire RE (2004) A maximum entropy approach to species distribution modeling. In: Proceedings of the twenty-first international conference on Machine learning. ACM, p 83
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Modell* 190:231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Plotnick RE, Gardner RH (2002) A general model for simulating the effects of landscape heterogeneity and disturbance on community patterns. *Ecol Modell* 147:171–197
- Purvis A, Gittleman JL, Cowlshaw G, Mace GM (2000) Predicting extinction risk in declining species. *Proc R Soc London Ser B-Biological Sci* 267:1947–1952
- Rodda GH, Jarnevich CS, Reed RN (2011) Challenges in identifying sites climatically matched to the native ranges of animal invaders. *PLoS ONE* 6:e14670
- Roscioni F, Rebelo H, Russo D et al (2014) A modelling approach to infer the effects of wind farms on landscape connectivity for bats. *Landscape Ecol* 29:891–903. <https://doi.org/10.1007/s10980-014-0030-2>
- Rudorff BFT, de Aguiar DA, da Silva WF et al (2010) Studies on the rapid expansion of sugarcane for ethanol production in São Paulo state (Brazil) using Landsat data. *Remote Sens* 2:1057–1076. <https://doi.org/10.3390/rs2041057>
- Rueda M, Hawkins BA, Morales-Castilla I et al (2013) Does fragmentation increase extinction thresholds? A European-wide test with seven forest birds. *Glob Ecol Biogeogr* 22:1282–1292. <https://doi.org/10.1111/geb.12079>
- Salcedo-Sanz S, Rojo-Álvarez JL, Martínez-Ramón M, Camps-Valls G (2014) Support vector machines in engineering: an overview: Support vector machines in engineering. *Wiley Interdiscip Rev Data Min Knowl Discov* 4:234–267. <https://doi.org/10.1002/widm.1125>
- Sano EE, Rosa R, Brito JLS, Ferreira LG (2010) Land cover mapping of the tropical savanna region in Brazil. *Environ Monit Assess* 166:113–124. <https://doi.org/10.1007/s10661-009-0988-4>
- Santos AJB, Quesada CA, Da Silva GT et al (2004) High rates of net ecosystem carbon assimilation by *Brachiaria* pasture in the Brazilian Cerrado. *Glob Chang Biol* 10:877–885
- Saranholi BH, Bergel MM, Ruffino PHP et al (2016) Roadkill hotspots in a protected area of Cerrado in Brazil: planning actions to conservation. *Rev MVZ Cordoba* 21:5441–5448
- Silva DP, Aguiar AJC, Melo GAR, et al (2013) Amazonian species within the Cerrado savanna: New records and potential distribution for *Aglae caerulea* (Apidae: Euglossini). *Apidologie* 44:673–683. <https://doi.org/10.1007/s13592-013-0216-7>
- Silva D, Gonzalez VH, Melo GA et al (2014) Seeking the flowers for the bees: Integrating biotic interactions into niche models to assess the distribution of the exotic bee species *Lithurgus huberi* in South America. *Ecol Modell* 273:200–209. <https://doi.org/10.1016/j.ecolmodel.2013.11.016>
- Soares-Filho B, Rajão R, Macedo M et al (2014) Cracking Brazil's forest code. *Science* 344:363–364. <https://doi.org/10.1126/science.1246663>
- Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecol Lett* 10:1115–1123. <https://doi.org/10.1111/j.1461-0248.2007.01107.x>
- Spera SA, Galford GL, Coe MT et al (2016) Land-use change affects water recycling in Brazil's last agricultural frontier. *Glob Chang Biol* 22:3405–3413. <https://doi.org/10.1111/gcb.13298>
- Strassburg BBN, Brooks T, Feltran-Barbieri R et al (2017) Moment of truth for the Cerrado hotspot. *Nat Ecol Evol* 1:0099. <https://doi.org/10.1038/s41559-017-0099>
- Swift TL, Hannon SJ (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. *Biol Rev* 85:35–53. <https://doi.org/10.1111/j.1469-185X.2009.00093.x>

- Syfert MM, Joppa L, Smith MJ et al (2014) Using species distribution models to inform IUCN Red List assessments. *Biol Conserv* 177:174–184. <https://doi.org/10.1016/j.biocon.2014.06.012>
- Syphard AD, Franklin J (2009) Differences in spatial predictions among species distribution modeling methods vary with species traits and environmental predictors. *Ecography (Cop)* 32:907–918
- Thornton DH, Branch LC, Sunquist ME (2011) The relative influence of habitat loss and fragmentation: do tropical mammals meet the temperate paradigm? *Ecol Appl* 21:2324–2333. <https://doi.org/10.1890/10-2124.1>
- Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. *Nature* 371:65–66
- Toms JD, Villard M (2015) Threshold detection: matching statistical methodology to ecological questions and conservation planning objectives. *Avian Conserv Ecol* 10:1–8. <https://doi.org/10.5751/ACE-00715-100102>
- van der Hoek Y, Zuckerberg B, Manne LL (2015) Application of habitat thresholds in conservation: considerations, limitations, and future directions. *Glob Ecol Conserv* 3:736–743. <https://doi.org/10.1016/j.gecco.2015.03.010>
- Verbruggen H, Tyberghein L, Belton GS et al (2013) Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. *PLoS ONE* 8:1–14. <https://doi.org/10.1371/journal.pone.0068337>
- Wenger SJ, Olden JD (2012) Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods Ecol Evol* 3:260–267

Affiliations

Paulo De Marco Jr¹  · **Sara Villén¹** · **Poliana Mendes¹** · **Caroline Nóbrega^{1,2}** · **Lara Cortes³** · **Tiago Castro³** · **Rodrigo Souza⁴**

¹ Theory, Metacommunities and Landscape Ecology lab, ICB-V, Universidade Federal de Goiás, Goiânia, Goiás, Brazil

² Instituto de Pesquisa Ambiental da Amazônia, 66035-170 Belém, Pará, Brazil

³ Instituto Chico Mendes de Conservação da Biodiversidade, Brasília, DF, Brazil

⁴ Centro de Sensoriamento Remoto do Instituto Brasileiro do Meio Ambiente (CSR/IBAMA), Trecho 2, Edifício Sede, Bloco F, Brasília, Distrito Federal, Brazil