Setting priority conservation management regions to reverse rapid range decline of a key neotropical forest ungulate

Júlia Emi de Faria Oshima [a,i,*], Maria Luisa S.P. Jorge [b], Thadeu Sobral-Souza [a,c], Luca Börger [d,e], Alexine Keuroghlian [f], Carlos A. Peres [g,h], Maurício Humberto Vancine [a], Ben Collen [i,1], Milton Cezar Ribeiro [a]

[a] Spatial Ecology and Conservation Laboratory (LEEC), Postgraduate Program in Zoology, Ecology Department, Institute of Biosciences, São Paulo State University (UNESP), Rio Claro, SP 13506-900, Brazil
[b] Department of Earth and Environmental Science, Vanderbilt University, 5726 Stevenson Center; 7th floor, Nashville, TENN 37240, USA
[c] Department of Botany and Ecology, Institute of Bioscience (IB), Universidade Federal de Mato Grosso, UFMT – Cuiabá, MT 78060-900, Brazil
[d] Department of Biosciences, Swansea University, Swansea SA2 8PP, UK
[e] Centre for Biomathematics, Swansea University, Swansea SA2 8PP, UK
[f] Peccary Project/IUCN/SSC Peccary Specialist Group, Campo Grande, 79052-070. Brazil
[g] School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK
[h] Instituto Juruá, Rua das Papoulas 97, Manaus, Brazil
[i] Centre for Biodiversity & Environment Research, Department of Genetics, Evolution & Environment, University College London, London WC1E 6BT, UK

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ABSTRACT

Mammals are important components of biodiversity that have been drastically and rapidly impacted by climate change, habitat loss, and anthropogenic pressure. Understanding key species distribution to optimize conservation targets is both urgent and necessary to reverse the current biodiversity crisis. Herein, we applied habitat suitability models for a key Neotropical forest ungulate, the white-lipped peccary (WLP *Tayassu pecari*), to investigate the effects of climate and landscape modifications on its distribution, which has been drastically reduced in Brazil. We used 318 primary records of WLP to derive habitat suitability maps across Brazil. Our models included bioclimatic, topographic, landscape, and human influence predictors in two modelling approaches. Models including all categories of predictors obtained the highest predictive ability and showed prevalence of suitable areas in forested regions of the country, covering 49% of the Brazilian territory. Filtering out small forest fragments (<2050 ha) reduced the suitable area by 5%, with a further reduction of 4% that was caused by deforestation until 2020, therefore until 2020, the species has suffered a reduction of ~60% from its historical range in Brazil. Of the 40% of the Brazilian territory suitable to WLP, only 12% is protected. In the Atlantic Forest, only half of all protected areas have suitable habitat for WLP and even less in Pantanal (44%), Cerrado (14%) and Caatinga (7%). In a second modelling approach, mapping the areas with suitable climate and those with suitable landscapes separately, allowed us to identify four categories of

* Correspondence to: Laboratório de Ecologia de Movimento, Instituto de Biociências, Departamento de Ecologia, Universidade de São Paulo, São Paulo, Brazil.
E-mail addresses: juliaoshima@yahoo.com.br (J.E.F. Oshima), maluspj@gmail.com (M.L.S.P. Jorge), thadeusobral@gmail.com (T. Sobral-Souza), l.borger@swansea.ac.uk (L. Börger), alexinek@hotmail.com (A. Keuroghlian), c.peres@uea.ac.uk (C.A. Peres), mauricio.vancine@gmail.com (M.H. Vancine), miltinho.astronauta@gmail.com (M.C. Ribeiro).
[1] In memory of Dr. Ben Collen.

conservation values, and showed that only 17% of the Brazilian territory has both high landscape and climatic suitability for WLP. Our models can help inform complementary conservation management strategies and actions that could be essential in slowing down and possibly reversing current trends of population and geographic range reductions for the species, thereby averting a possible future collapse of forest ecosystem functioning in the Neotropical region.

1. Introduction

Climate change and landscape modifications are major causes of biodiversity loss worldwide (e.g. Newbold, 2018; Newbold et al., 2015; Urban, 2015). However, identifying species responses to climate change, land cover modifications, habitat loss, forest fragmentation, and other antropic pressures (such as hunting, creation of artificial barriers and pollution) requires new modelling efforts (e.g. Struve et al., 2010, Barlow et al., 2016, Behr et al., 2017). Habitat Suitability Models (HSMs) have been used to assess the effects of climate change and landscape modification on biodiversity (Elith and Leathwick, 2009) and predict future biodiversity responses to environmental changes at multiple scales (see Guisan and Rahbek, 2011), thus defining goals and regions where conservation management actions could be most effectively applied (e.g. Crouzeilles et al., 2015; Newbold, 2018).

Mammals play key roles in forest ecosystems (Schipper et al., 2008) and are important components of biodiversity, and currently, over 27% of all mammal species are threatened (Schipper et al., 2008), Defaunation induced by hunting pressure (Antunes et al., 2016), and habitat loss and fragmentation (e.g. Fahrig, 2003; Pardini et al., 2017) are considered the new drivers of a mass extinction event (Barnosky et al., 2011; Galetti et al., 2017). Therefore, understanding the effects of those factors on key mammal species distribution can help optimize conservation actions and is both urgent and necessary (Ceballos and Ehrlich, 2006).

White-lipped peccaries (WLP; *Tayassu pecari*) are the only Neotropical forest ungulates that form large herds (hundreds and up to thousands of individuals, see Keuroghlian et al., 2013; Sowls, 1997) and exert strong local top-down effects on forest ecosystems (Keuroghlian et al., 2009). Their extirpation from native areas may cause additional biodiversity losses through cascading effects (e.g. Altrichter and Almeida, 2002; Keuroghlian et al., 2009), which makes them a key species for the conservation of Neotropical forests. Due to the impacts of WLP herds on soil, litter, plant recruitment and dispersal, the species directly and indirectly alters its environment, with associated effects on local communities (Beck, 2006; Keuroghlian and Eaton, 2009), and functions as ecosystem engineers (Beck et al., 2010; Ringler et al., 2015). The selective habitat use associated with extensive home ranges and movements (Altrichter and Almeida, 2002; Fragoso, 1998; Hofman et al., 2016; Jorge et al., 2021, 2019; Keuroghlian et al., 2015; Reyna-Hurtado et al., 2009) renders WLPs an ideal species to investigate how landscape changes affect their spatial distribution.

Due to habitat loss and hunting (e.g. Antunes et al., 2016; Keuroghlian et al., 2013; Peres, 1996), WLPs have shown reduced abundance and low probability of long-term survival within 48% of their current distribution, which was estimated in 2012 as 11,177, 435 km^2 (79% of the historical range, see Altrichter et al., 2012), thereby being classified as Vulnerable on the IUCN Red List. In Brazil, WLP population had a reduction that reached more than 30% in the last decade, the species has been virtually extirpated from the northern Atlantic Forest region (Canale et al., 2012) and the arid Caatinga biome, where it is mainly threatened by landscape modification, deforestation and hunting, and it only occurs in specific protected areas (Keuroghlian et al., 2012). Additionally, WLPs in Brazil suffered impacts of livestock, including infectious diseases (de Freitas et al., 2010; Fragoso, 2004). Recent studies indicate that a reduction in WLP abundance and geographic distribution will continue for the next three generations (Keuroghlian et al., 2013). Thus, identifying threats influencing the persistence of WLP within different biomes will allow prioritizing areas for conservation actions, which will in turn benefit regional biodiversity.

Fig. 1. The white-lipped peccary, *Tayassu pecari,* in Brazil.

For this purpose, we quantified the amount of remaining suitable habitat areas for WLPs in Brazil, the country with the largest portion of the species current range ($\sim$ 65% or 7336,197 km^2) (Altrichter et al., 2012). Furthermore, we explored how landscape and climate predicted WLP suitability, and how the remaining suitable areas were distributed across different Brazilian biomes. Finally, we discuss how forest loss in Brazil in recent years (until 2020) has affected the amount of suitable habitat available for the species.

2. Material and methods

2.1. Model species

The White-lipped peccary (WLP; *Tayassu pecari*) (Link, 1795) is one of three species belonging to the Tayassuidae family, in the superorder Cetartiodactyla. This social, frugivorous–omnivorous ungulate is distributed across the Americas from southeastern Mexico to northern Argentina and southern Brazil (Sowls, 1997). The species presents some plasticity in occupying different vegetation habitats (e.g. rainforests, dry forests, savannahs, and wetlands), but preferentially uses forest habitats and riparian zones (Fragoso, 1999; Keuroghlian and Eaton, 2008a). WLP is a highly social species (Fig. 1) with a promiscuous mating system (Biondo et al., 2011; Leite et al., 2018) and their fusion-fission social structure is characterized by the formation of herds that are divided into sub-herds, with frequent exchange of individuals (Biondo et al., 2011; Keuroghlian et al., 2004). Adults weigh 30 kg on average, WLP represent the largest mammal biomass in the Neotropical forests where they are present (e.g. Beck, 2006; Eisenberg, 1980; Peres, 1996). WLP have key ecological roles: as prey for large carnivores (e.g. the jaguar, *Panthera onca,* and the cougar, *Puma concolor*), as seed predators and dispersers, and as ecosystem engineers due to their impacts on forest soil and plant trampling (Keuroghlian and Eaton, 2009; Kiltie and Terborgh, 1983; Ringler et al., 2015).

2.2. Presence records

A database with geographic locations of 318 presence records of WLPs in Brazil was compiled via literature review and specialists databases. Only direct observations, camera trap data and signs (e.g. footprints and hair) collected between 1987 and 2017 were considered (for details please see Supplementary material section SM1).

2.3. Environmental predictors

Four sets of environmental layers were used to model habitat suitability for WLP: a) bioclimatic (Isothermality, Mean Temperature of Warmest Quarter, Precipitation of Wettest Quarter, and Precipitation of Driest Quarter, see Karger et al., 2017); b) topographic (Terrain slope, see Valeriano and Rossetti, 2012); c) landscape (Percentage of tree canopy cover, see Hansen et al., 2013), Spatial heterogeneity/habitat diversity, see Tuanmu and Jetz (2015), Inland surface water frequency dataset, see Feng et al. (2016); and d) Human influence (Human density, see Brazilian Demographic data at www.ibge.gov.br). For details, please see Supplementary material section SM2.

All predictors were calculated or spatially rescaled for a resolution of approximately 1 km^2 (0.00833º) and projected to the WGS 84 geographic system using ArcGIS 10.2 (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). We used a factorial analysis to group climatic variables into a smaller set of meaningful variables, and looked for collinearity among all layers using bivariate Pearson correlations, excluding correlated variables with rho > 0.7 (Supplementary material SM3).

2.4. Removing sampling bias from occurrence data

In HSMs, identifying and removing sampling bias from occurrence data is important (Elith et al., 2011), as it can significantly affect model predictions (Araújo et al., 2019; Merow et al., 2013). To do so, we filtered occurrences with similar environmental information or spatially clumped, as well as removed possible duplicated data (Supplementary Material SM4) using the SDMtoolbox (Brown, 2014) in ArcGIS 10.2. We retained 278 occurrence records after the filtering. Following the methods proposed by (Fitzpatrick et al., 2013) we checked if the use of accessibility bias masks would improve modelling results, which it did not (see Supplementary material SM5). Therefore we corrected bias for clumped data using the filtering procedure only.

2.5. Modelling methods

Four algorithms (Bioclim, Gower Distance, Support Vector Machines and MaxEnt) based on presence-only and presence-background data were tested to infer habitat suitability for WLP using the packages dismo (Hijmans et al., 2017) and kernlab (Karatzoglou and Feinerer, 2010) in R. We fitted all models using a partitioning criterion to randomly select 75% of data for training and 25% for the test, with 10 replications per algorithm. We calculated the frequency map for each algorithm, as well as the mean and standard deviation of all models of all algorithms (Supplementary Material SM9).

To measure predictions accuracy, we used the area under the receiver operating curve (AUC) with a threshold of AUC > 0.7. As only MaxEnt models achieved such standards for the 2 modelling approaches we opted to use only the MaxEnt algorithm results for our final analysis. We used MaxEnt defaults as set in R in the dismo package (Hijmans et al., 2017), and the logistic outputs for the suitability models, but we set the jackknife of regularized training gain to true to calculate the predictors' percent of contribution, and set 10,000 background points and 500 iterations for the runs.

To derive binary (suitable/unsuitable) raster maps from the model predictions, we used the *maximum training sensitivity and specificity* thresholds (Liu et al., 2013), and converted each cell to values of 0 (unsuitable) or 1 (suitable). We then summed the output raster maps and divided the cell values by the number of summed maps to set the values to a scale of 0–1 and determined the frequency in which each cell was predicted as suitable. We used a 10 percentile threshold for model cut-off for the different models, and computed the final predicted binary maps (Pearson et al., 2007).

We first modeled the habitat suitability for WLP using all the predictors together in a so-called *Full model*, which was the base model to determine suitable areas for the species and for further analysis of forest cover loss impacts (Fig. 2). The importance of each environmental variable to determine habitat suitability for WLPs was explored assessing the Jackknife training gain results for the
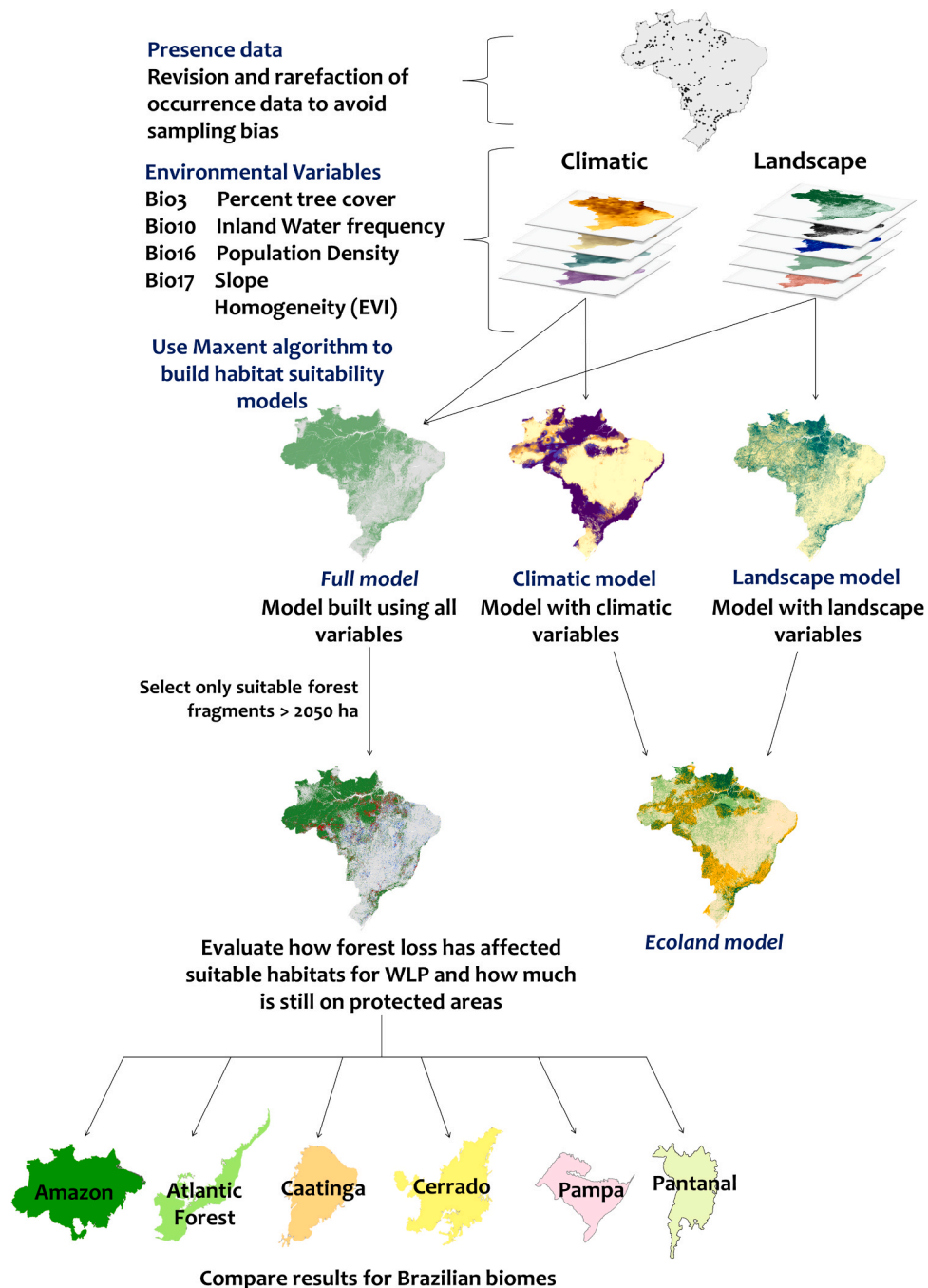
Fig. 2. A conceptual framework for the Full and Ecoland models used to analyze habitat suitability for *Tayassu pecari* in Brazil, with the spatial analysis steps used to quantify the impact of forest loss on its distribution.

MaxEnt models and with a principal component analysis to verify how the magnitude of values varied among the four Brazilian biomes where the species still occurs (Atlantic Forest, Cerrado, Pantanal and the Amazon) (Janekovi and Novak, 2012; Moreira et al., 2014).

In a second approach (*Ecoland model*), we modeled the climatic suitability for WLP using only the four bioclimatic variables as predictors (*Climatic model*) and the landscape suitability using only the landscape, topographic and anthropogenic variables (percent of tree cover, homogeneity, inland water frequency, terrain slope and human density) (*Landscape model*).

2.6. Ecoland model

For the *Ecoland* modelling approach (Santos et al., 2020; Sobral-Souza et al., 2021) we ran the climatic and landscape models separately at first and then combined the two outputs. This approach allowed us to disentangle and map the consensus and disagreement areas between the two model predictions. We repeated the modelling approach described for the *Full model* for each set of predictors separately and used the binary maps from five MaxEnt climatic models and five MaxEnt landscape models with highest AUC > 0.7. We then quantified the level of consensus/disagreement into four categories, using 50% threshold to separate low suitability regions from high suitability ones (Fig. 2).

Specifically, we defined four different classes of habitat suitability: i) high climatic and landscape suitability - more than 0.5 for both model outputs, ii) high climatic and low landscape suitability - more than 0.5 for climatic and less or equal 0.5 for landscape model, iii) high landscape and low climatic suitability values - more than 0.5 for landscape and less or equal than 0.5 for climatic model, iv) low climatic and low landscape suitability – less or equal than 0.5 for both model outputs. With that procedure, it was possible to identify areas where both climatic and landscape were suitable for WLP, and areas with high climatic suitability and low landscape suitability, or vice-versa.

2.7. Suitable forest fragments, forest loss effects and protection status

We used the results from the *Full model* with a resolution of 1 km², projected to South America Albers Equal Area Conic projection system (Datum SAD69), to calculate the suitable area for WLP in Brazil. We then evaluated how much of the suitable areas were too small to retain viable populations of WLP, based on the size of the available forest patches and information about WLP home range size
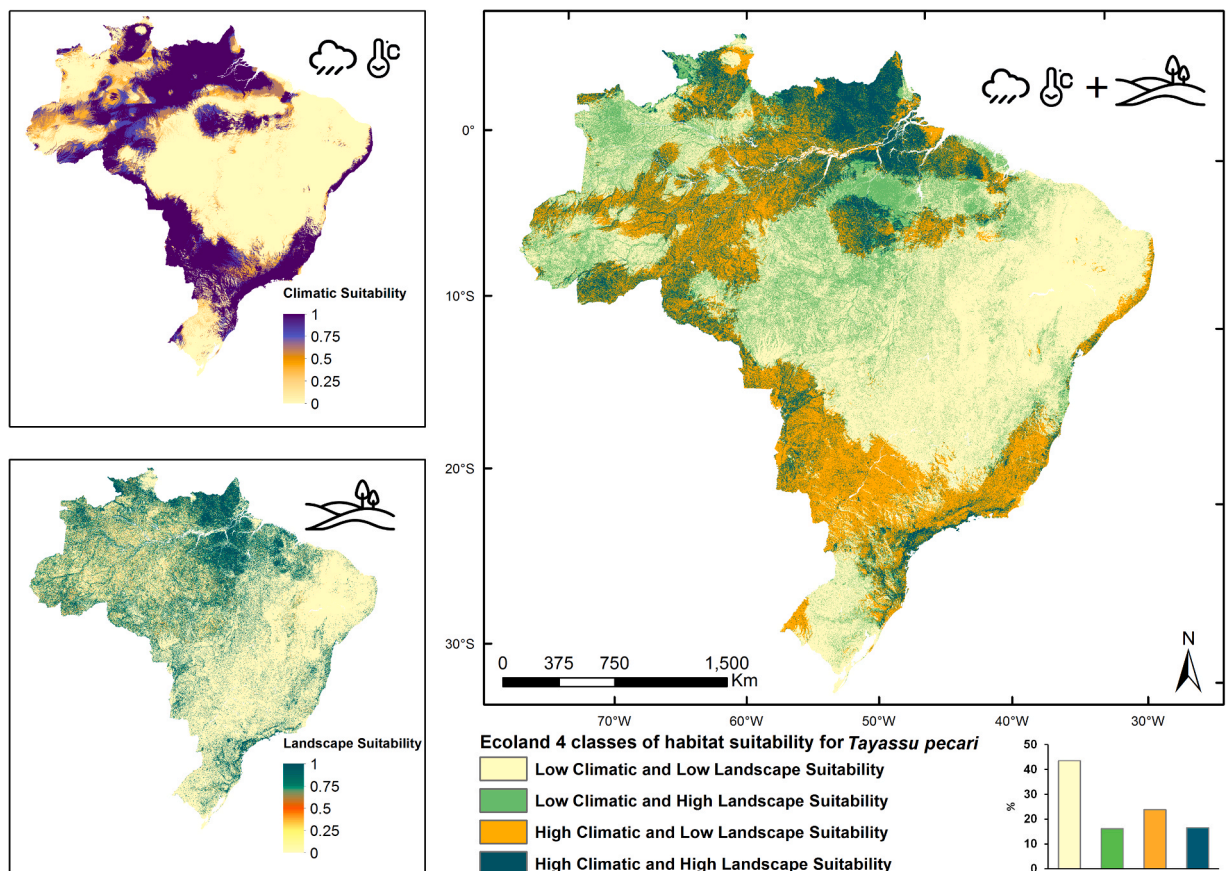

Fig. 3. Climatic, Landscape, and Ecoland models of habitat suitability for white-lipped peccaries (*Tayassu pecari*) in Brazil.

(Fragoso, 1998; Jácomo et al., 2013; Jorge et al., 2019; Keuroghlian et al., 2015). We established a threshold of 2050 ha (20.5 km^2), which also concurs with Magioli et al. (2015) that found the same threshold area for sensitive species, such as WLPs, of the Neotropical forests. We used the patch size raster to identify forest fragments that were larger than 2050 ha and also suitable for WLP.

After that, we calculated how much forest cover loss affected suitable areas between 2000 and 2020. We identified the percentage of forest area loss, using data of the total area of gross forest cover loss available from the Global Forest Change dataset (Hansen et al., 2013) with the resolution rescaled to 1 km^2. We did this for each one of the biomes (Amazon, Atlantic Forest, Caatinga, Cerrado, Pampa and Pantanal), using the delimitation provided by IBGE 2016, to make a new evaluation of the suitable areas not affected by loss during this period.

Finally we quantified how much of these suitable areas were inside protected areas, using the delimitation shapefile of the Brazilian Environment Ministry (available at http://mapas.mma.gov.br/i3geo/datadownload.htm) as a mask. The input occurrence data and models results are available at https://github.com/LEEClab/Tayassupecari_HabitatSuitability.
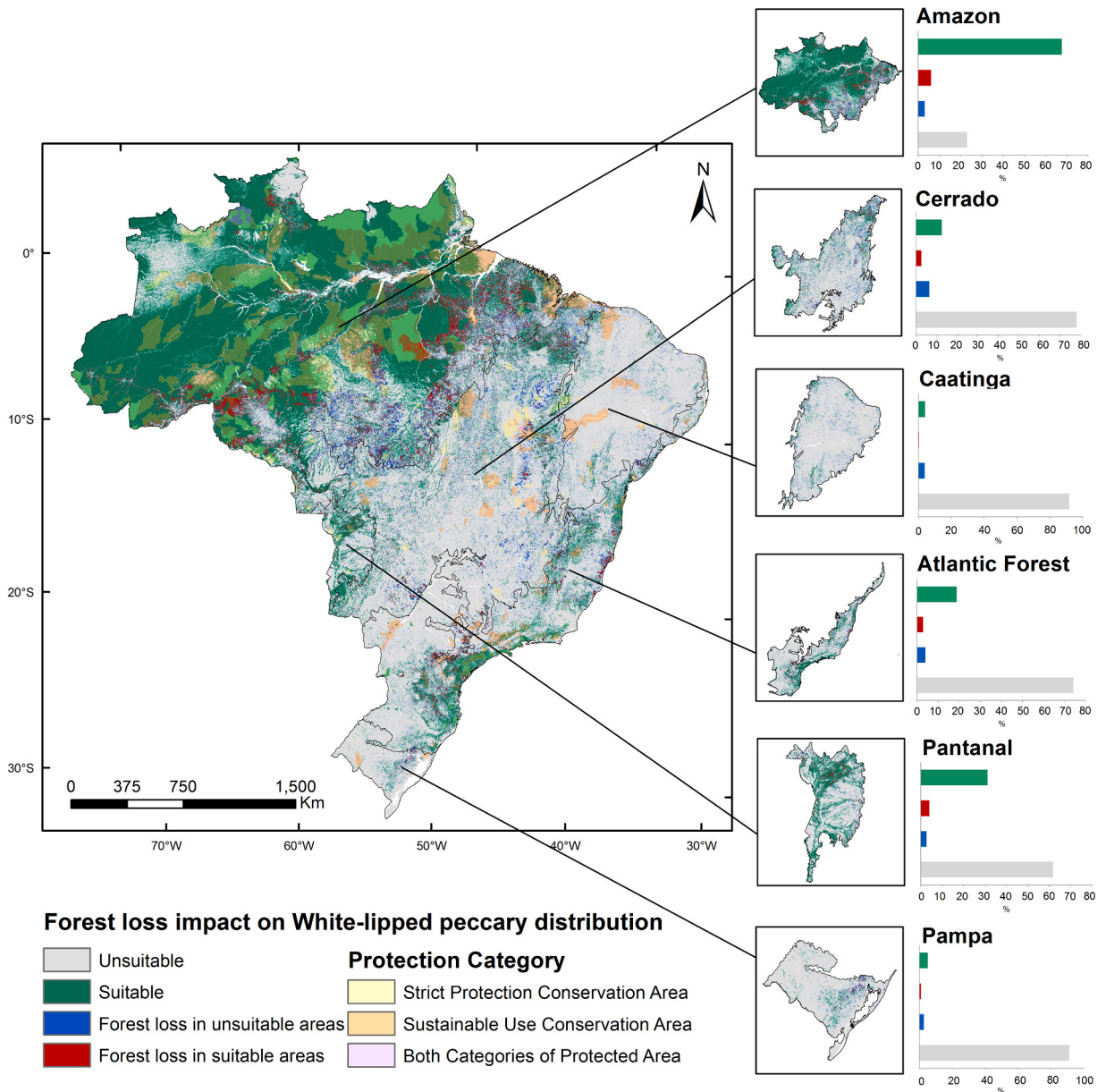

Fig. 4. Effects of forest loss between 2000 and 2020 in suitable forest fragments (larger than 2050 ha) for white-lipped peccaries (*Tayassu pecari*) in Brazil.

3. Results

3.1. General results

A total area of 4,095,810 km^2 was predicted as suitable using the *Full MaxEnt binary model,* which corresponds to 49% of the Brazilian territory. The *Full model* (based on the combination of all environmental predictors) consistently had higher AUC values than the models built using only climatic or landscape-level predictors, and showed a large prevalence of suitable areas in forested regions with less suitable areas in regions dominated by agricultural crops. In the Caatinga, northeastern region of Brazil, and in the extreme south of the country (Pampas) the model showed lower habitat suitability for the species than the other biomes. The climatic and the landscape models produced divergent predictions for WLP in many regions of the country, showing that climatic and landscape models can provide complementary information for habitat suitability analysis (Fig. 3). The total suitable area predicted with the *Climatic MaxEnt mode*l was 3443,007 km^2 and the total area predicted by the *Landscape MaxEnt model* was 2735,182 km^2.

We also calculated the consensus areas predicted by all four algorithms (Supplementary Material SM7) of the *Full model*, which encompass 2,489,205 km^2 (Supplementary material SM8), as well as mean and standard deviation from those outputs. The use of the four different algorithms allowed for comparisons of the suitable areas and determination of uncertainty (standard deviation map) between predictions, indicating regions where more information about the species occurrence could improve model predictions (Supplementary material SM9).

3.2. Ecoland model

The Ecoland model allowed for comparisons about how climatic and landscape variables can provide different estimates of suitable areas, leading to the identification of four categories of suitable areas for WLP in Brazil (Fig. 3). Around 17% of the total area of Brazil (1,382,008 km^2 – dark green in Fig. 3) has high suitability in both climatic and landscape models. Areas with high climatic suitability values and medium/low current landscape suitability cover 24% of Brazil (1,994,341 km^2 – orange colour in Fig. 3) and represent those most affected by habitat loss and anthropogenic alteration. Approximately 16% of Brazil (1,352,077 km^2 – light green colour in Fig. 3) has high landscape suitability but low climatic suitability for WLP, especially in specific regions in the South, and in some regions of the nothwest of the Amazon, and in its ecotone with the Cerrado. Finally, 44% of Brazil (3,643,425 km^2 – yellow colour in Fig. 3) is neither climatic nor has landscape suitable for WLPs. These areas are characterized by a predominance of shrubland vegetation and dry rainfall regime in the northeast (Caatinga), areas of grassland and low seasonal temperature in the south (Pampas) (representing drier and colder regions), and areas with high land-use change, used mainly for agriculture within the "dry diagonal" in the center of the country (Cerrado).

3.3. Suitable forest fragments, forest loss effects and protection status

Filtering out fragments smaller than 2050 ha (based on average home range size and threshold for forest patch size) reduced suitable areas by 5% (from 4,095,810 km^2 to 3,683,796 km^2). Forest cover loss between 2000 and 2020 (Hansen et al., 2013) removed a further 4% of suitable areas (350,701 km^2) for WLP. Considering both aspects (patch size and forest loss) resulted in 40% of Brazilian territory (3,333,094 km^2) suitable for the species (Fig. 4). The suitable forest areas estimated per biome varied between 8,242 km^2 for the Pampa (where the species is currently considered extinct) and 2,782,287 km^2 for the Amazon (Fig. 4 and Supplementary Material SM12).

Finally, only 12% of Brazil territory has suitable habitats for WLP within protected regions (992,546 km^2), of which 389,123 km^2 is in strictly protected areas and 603,423 km^2 is in sustainable use areas (Fig. 4), albeit with strong regional variation (Supplementary Material SM14). Most protected regions in the Amazon biome (83%) are suitable for the species, whereas in the Atlantic Forest, this value is close to 50%, in the Pantanal, 44%, in the Cerrado, 14%, only 7% in the Caatinga, and in the Pampas only 6%, where the species is currently considered regionally extinct (Supplementary Material SM13).

4. Discussion

4.1. Climatic and landscape suitability and WLP conservation

Our modelling approach allows us to identify areas that require different conservation prioritization. It is critical that forest areas with high suitability of both climate and landscape, have protection and connectivity assured by environmental laws, such as the Brazilian Forest Code (Azevedo et al., 2017; Soares-Filho et al., 2014). Deforestation monitoring through remote sensing coupled with ground truthing inspections through national programs such as MapBiomas (http://mapbiomas.org) and the "SiCAR" system (Sistema Nacional de Cadastro Ambiental Rural) (Alix-Garcia et al., 2018) can help identify land-use violations at the landholding scale to levy appropriate fines. It is also important to provide protection to those areas identified as high climate and landscape suitability, enhancing connectivity and enforcing surveillance to avoid illegal hunting and deforestation. Besides those national initiatives, environmental education is important to reduce illegal hunting locally and regionally in the biomes where the species is largely threatened – Atlantic Forest and Cerrado (Keuroghlian et al., 2013), and in south Amazon in the "arc of deforestation" where hunting acting synergistically with forest loss can have dramatic effects on WLP populations (Antunes et al., 2016).

Areas with high climatic suitability and low landscape suitability can be targeted for restoration and wildlife corridors, promoting

greater landscape suitability and connectivity where climatic conditions are favorable. Moreover, these regions are also important ecotones and may be used strategically to favor gene flow among populations across different biomes. Recent studies show that large mammals, including WLPs, can occupy secondary savannahs regenerated from clear-cutting in areas of protected Cerrado, suggesting a potential reversal of the non-habitat matrix to suitable habitats for WLPs and other forest-dwelling species occupying regenerated landscapes (Ferreira et al., 2017).

Areas with low climatic suitability and high landscape suitability areas (south, northeast and some specific regions of the Amazon) should be monitored especially for climate change effects. As discussed by Keuroghlian et al. (2015), extreme droughts can affect resource availability, change activity patterns (Hofmann et al., 2016), and increase the impacts of land-use change on WLPs. It is predicted that synergetic effects of climate change and land use change will increase species losses in tropical savannahs, grasslands and forests, and result in significant alteration in the structure of ecological communities by 2070 (Newbold, 2018). WLP populations in these are likely to be strongly affected by climate change and rely on appropriate landscape suitability to survive. New survey efforts in the Amazon and continued monitoring could help to increase the understanding of WLP presence and distribution in the region, especially in the areas where uncertainty was high (standard deviation map in Supplementary material SM9).

Although the species' historical ecological distribution (Altrichter et al., 2012) suggests that WLPs exhibit considerable plasticity in habitat use at a local scale, from a macroecological perspective, such plasticity is climatically restricted to the warmer regions of the Neotropics. Conservation strategies are critical for retaining suitable forest fragments for the species in areas where climatic suitability is high, since climate change and range shifts might require evolutionary adaptations and phenotypic plasticity that lack for most medium and large mammals (Hetem et al., 2014), including WLPs. This is further hindered by land-use change and anthropogenic barriers that limit movements and dispersal of organisms (Shepard et al., 2008).

4.2. Forest loss and WLP conservation

In 2012, Altrichter et al. (2012) showed that WLP had a reduction of 13% of its historical range in Brazil. Our study shows that this reduction increased to 60% in 2020. Although each study used different modeling approaches, both show a rapid range decline for WLP. Between 2000 and 2020, the suitable areas for WLP affected by forest loss in Brazil represent 4.2% of the total country area, which is larger than the predicted range size for the species in most countries of Mesoamerica (see Altrichter et al., 2012). Recent studies have shown that a rapid population decline may also be occurring in Mesoamerica, suggesting a range reduction of 63% from the current IUCN distribution and 87% from WLP historical distribution for that region (Thornton et al., 2020). WLPs depend mostly on forest areas to acquire food resources (Desbiez et al., 2009; Keuroghlian and Eaton, 2008b) and reduce thermoregulation costs (Hofmann et al., 2016), hence urgent, and more effective than hitherto, conservation actions are urgently needed for the species and similar forest-dependent species in Brazil. However, because the conservation status of WLP populations is highly variable across the Neotropics, ranging from virtually extirpated to hyper-abundant in different regions, it can be misleading, and the species can be considered not threatened by local communities and landowners. For example, WLP herds are considered extremely abundant agricultural pests throughout the southern Amazonian soybean frontier, where they are being poisoned or shot by the thousands in retaliation for crop-raiding losses (Lima et al., 2018).

Our suitability maps for WLP also reflect how land-use change has affected the species in different regions of Brazil. In the biomes where the conservation status of WLPs is currently considered less critical – Pantanal and Amazon (Keuroghlian et al., 2013), forest loss occurs mostly at the edges of the biomes and the land is predominantly used for cattle-ranching. Reduced human density and reduced access through roads (Oliveira et al., 2016) help prevent larger anthropogenic impacts in those regions. In the Cerrado, expansion of cropland and cattle-ranching are the main land-use changes (Carvalho et al., 2009; Roque et al., 2016). Moreover, in some regions of the Cerrado, the matrix consists of corn cropland that is attractive to WLP and the fertilizer used in the soil is a second attractive factor (Morato personal communication), which can increase human conflicts and consequently illegal hunting pressure and human/wildlife conflicts near forest fragments (Lima et al., 2018). One example is Emas National Park, where the main surrounding areas consist of corn monoculture (Jácomo et al., 2013) and there has been increased human-WLPs conflict in the area.

In the Atlantic Forest, in addition to higher human density in urban areas near the coast, there is a predominance of large tracts of forest fragments in coastal areas, especially in high-elevation areas in the Serra do Mar and Mantiqueira mountain ranges. WLPs are already absent from many protected areas (Jorge et al., 2013) which can generate cascading effects on plants and animals (Galetti et al., 2015; Kurten, 2013). Interior regions of the Atlantic Forest have smaller and more isolated forest remnants (Ribeiro et al., 2009) and some of the remaining WLP populations are very isolated (Keuroghlian et al., 2004), thus it is important to invest in increasing connectivity among populations in this biome following, for example, the guidelines proposed by Ribeiro et al., 2009 and Crouzeilles et al. (2013).

4.3. Other anthropogenic effects that impact WLP populations

Our models highlighted the broad scale impacts of forest loss and fragmentation, climate, and direct human disturbance (human density) on the spatial distribution of suitable areas for WLPs in recent years. Nevertheless, the conservation scenario is more problematic due to other human-driven disturbances, like increasing human activities – light and sounds for example – which have been shown to alter the activity patterns of mammals (Gaynor et al., 2018), create barriers (Shepard et al., 2008), increase poisoning and slaughtering because of human/wildlife conflicts (Lima et al., 2018) and increase hunting pressures (Peres et al., 2016), occurring on the landscape and local scales within forest fragments. These local impacts can highly increase biodiversity loss even where forested areas still remain (Barlow et al., 2016; Galetti et al., 2017; Peres et al., 2016), which could be the case for many regions where the WLPs

occur. Thus, conservation measures derived from our results are urgently required, but will nonetheless need to be complemented by further actions to allow coexistence of WLP and humans, such as identifying key regional stakeholders to propose educational and social projects for conservation, increasing environmental inspection and applying fines to reduce other local impacts within the forest areas. Also, priority areas for conservation, where the species has been locally extirpated due to hunting in past years, could receive translocated animals from areas where human-wildlife conflicts are occurring. This will demand further studies of spatial ecology, genetics and disease ecology but could be a potential solution to conservation management for WLP populations.

4.4. Protected areas and conservation strategies to reduce the impact of forest loss for WLP

Models that predicted habitat suitability for WLP at the landscape scale showed that the presence of protected areas was a very important variable to explain the areas that were most frequently used by WLPs (Norris et al., 2011). Our results show that suitable forest fragments larger than 2050 ha that are currently inside protected areas represent only 11.7% of the historical range for WLP in Brazil (Altrichter et al., 2012). The proportion of suitable areas, i.e. fragments larger than 2050 ha, represents only half of protected areas in the Atlantic Forest, and even less in the Pantanal (44%), Cerrado (14%) and Caatinga (7%). Thus another key conservation outcome from this work is to show that only 39% (389,123 km^2) of the suitable areas for WLP in protected areas are of stricted protection. Unfortunately, even strict protected areas such as National and State Parks are not necessarily a safe place for wildlife, local extinctions of WLPs also occurred in numerous parks in Brazil (Keuroghlian et al., 2012).

Recent changes in legislation that protect the forest fragments in Brazil reduced the extent of areas that should be protected near rivers. Riparian vegetation and small remnants could be further reduced in the near future (Soares-Filho et al., 2014), and these are important habitats for WLP (Keuroghlian and Eaton, 2008a) not located inside protected areas, representing 28% of the Brazilian territory suitable for WLP. Furthermore, applying sustainable agricultural production strategies that minimize forest reduction, such as rotation management systems for cattle and crop production - reducing area requirement and the impact on native trees (Eaton et al., 2011), encouragement for programs of payment for ecosystem services (Pearce, 2001), compliance of the forest code as a criteria for marketing, as well as the use of green certificates for exportation of rural products and reduction of meat consumption (Eisler et al., 2014), will be essential to decrease the impact of food production on white-lipped peccaries and other wild species (Phalan et al., 2011).

4.5. Model limitation and conclusions

We believe that the conservation scenario for WLP might be even more serious than our results suggest because the edges and the shapes of fragments loose definition on a scale of 1 km^2 limiting our model accuracy for the size of the area estimated. That could drive suitable areas to be overestimated for the species due to the model resolution. Nevertheless, although higher resolution could provide a more accurate estimate, our predictions provide the best current overview of the status of suitable areas for WLPs in a country of continental dimensions and a myriad of environments. Testing two different modelling approaches and a range of different environmental variables was important for selecting the final set of variables and providing models that explored divergences between climate and landscape suitability.

Our results represent an important step in evaluating the currently remaining suitable areas for WLPs in Brazil because they provide spatial information about how landscape modifications affect the species persistence. This is essential to evaluate the species current conservation status and to define more efficient conservation actions, such as new areas for population surveys and monitoring, placement of corridors and target regions for educational programs that seek to reduce habitat loss and illegal hunting. Finally, our models showed that WLPs respond to landscape changes and have been losing habitat in recent years. Applying national conservation strategies for WLPs could therefore optimize conservation efforts for other vertebrate species with similar sensitiveness to fragmentation.

CRediT authorship contribution statement

Data availability

https://github.com/LEEClab/Tayassupecari_HabitatSuitability.

Declaration of Competing Interest

The authors declare that they have no known competing interests or personal relationships that could have appeared to influence

the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01796.

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