Research Article

Evaluating landscape suitability for golden-headed lion tamarins (*Leontopithecus chrysomelas*) and Wied's black tufted-ear marmosets (*Callithrix kuhlii*) in the Bahian Atlantic Forest

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Abstract

In southern Bahia, Brazil, rapid deforestation of the Atlantic Forest threatens a variety of endemic wildlife, including the Endangered golden-headed lion tamarin (GHLT; *Leontopithecus chrysomelas*) and the Near Threatened Wied's black-tufted-ear marmoset (Wied's marmoset; *Callithrix kuhlii*). Identifying high quality areas in the landscape is critical for mounting efficient conservation programs for these primates. We constructed ecological niche models (ENMs) for GHLTs and Wied's marmosets using the presence-only algorithm Maxent to (1) locate suitable areas for each species, (2) examine the overlap in these areas, and (3) determine the amount of suitable habitat in protected areas. Our models indicate that 36% (10, 659 km^2) of the study area is suitable for GHLTs and 53% (15, 642 km^2) for Wied's marmosets. Suitable areas were strongly defined by presence of neighboring forest cover for both species, as well as annual temperature range for GHLTs and distance from urban areas for Wied's marmosets. Thirty-three percent of the landscape (9,809 km^2) is overlapping suitable habitat. Given that the focal species form mixed-species groups, these areas of shared suitability may be key locations for preserving this important behavioral interaction. Protected areas contained 6% (651 km^2) of all suitable habitat for GHLTs and 4% (682 km^2) for Wied's marmosets. All protected areas were suitable for the focal species, excepting Serra do Conduru, which had low suitability for GHLTs. Our results highlight that suitable habitat for GHLTs and Wied's marmosets is limited and largely unprotected. Conservation action to protect additional suitable areas will be critical for their persistence.

Keywords: ecological niche modeling, habitat suitability, primate conservation, Atlantic Forest

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Introduction

Habitat loss is a major driver of biodiversity decline in the tropics, where human population growth and development cause high rates of habitat reduction [1]. The Atlantic Forest of Brazil, home to over 8,000 endemic species, retains only 12% of its original forest cover in numerous isolated patches [2–5]. In certain centers of endemism, estimated rates of habitat loss approach and exceed 90% [5]. This habitat loss is driven by activities such as logging of forests for timber, clearing of land for cattle pasture, and the intensification of traditional farming practices [6,7]. Further deforestation and fragmentation throughout the Atlantic Forest are likely [8–10] and threaten many species. Strategies that emphasize landscape management, connectivity, and protection of representative areas in future conservation efforts are critical and necessitate identifying high quality areas of habitat essential for species persistence.

Two species threatened by continued deforestation are the Endangered golden-headed lion tamarin (GHLT; *Leontopithecus chrysomelas*) and the Near Threatened Wied's black tufted-ear marmoset (Wied's marmoset; *Callithrix kuhlii*; [11,12]). Both are cooperatively-breeding, small-bodied arboreal primates in the family Callitrichidae. Endemic to the southern Bahia region of the Atlantic forest (Fig 1), they share many of their ecological needs, require continuous forest cover to maintain home ranges, and form non-random associations whereby both species travel, forage and rest closely together for periods of up to several hours [13–15]. In the west of their distributions, remaining forest fragments are small and isolated [16]. In the east, forest cover is still relatively well maintained and several protected areas exist, including national and state parks, biological reserves, and numerous privately owned reserves. However, land use intensification, conversion of shade cocoa to other forms of agriculture, and selective removal of trees continue to degrade and eliminate habitat in the east [6,7]. Given the likelihood of future deforestation throughout the Atlantic forest [8–10], there is a need to locate and preserve additional suitable areas for GHLTs and Wied's marmosets.

Prior analyses to identify suitable areas in the landscape have relied on presence-absence methods [16], a combination of population viability and landscape analysis [17], and a prioritization of key habitat patches [18]. These studies addressed landscape suitability for GHLTs, identifying a limited number of fragments capable of supporting self-sustaining populations in the long term [17,18]. While prior approaches have identified landscape characteristics necessary for the persistence of GHLTs, knowledge of local regions of suitability for both primates is needed.

Given the increasing isolation of forest fragments and land-use intensification in Southern Bahia, we constructed Ecological Niche Models (ENMs) to identify regions of localized high quality habitat for GHLT's and Wied's marmosets. Specifically, we used our ENMs to: (1) identify suitable areas in the landscape for each species, (2) examine the overlap in suitable habitat for these two species, and (3) determine the amount of suitable habitat in protected areas.

Methods

Study Area

We focused on the southern Bahia region of the Brazilian Atlantic Forest (Fig 1). The western portion of this area contains highly fragmented, semi-deciduous tropical rainforest, while more continuous coastal evergreen rainforest dominates the landscape in the east [17]. Remaining forest can be broadly characterized as mature forest, regenerating secondary forest, or shade-cocoa agroforest [16]. Shade-cocoa is an agroforestry system in which middle and understory trees are removed and replaced with cocoa trees [19]. All three of these habitat types are used by our focal species [14,20,21]. We defined our focal area by extending the proposed geographic range for GHLTs (Raboy *et al.* unpublished data) to natural geographic barriers. Northern and southern limits were demarcated by major waterways, Rio de Contas in the north and Rio Jequitinhonha in the south. To the east, the study area extended to the Atlantic Ocean, while the western limit was defined by the 700m elevation line, reflecting the altitudinal limit for GHLTs [22]. Wied's marmosets are believed to occupy most of this region [23] and possibly further northwest, southwest, and south [11].

Species Occurrence Data

We gathered presence records for GHLTs and Wied's marmosets from prior studies conducted by the authors between 2005-2014 that made direct observations (by sightings or camera-trapping) of naturally occurring populations. When datasets contained multiple observations of the same social group tracked over time, we included only the first recorded observation. Occurrence records were filtered using the spatial rarefaction tool in the SDMtoolbox extension [24] for ArcGIS 10.1 [25]. Rarefaction distances were chosen to reflect the average minimum distance between two conspecific groups, based on approximate home range radius (455m for GHLTs, calculated based on Oliveira *et al.* [19]; and 265m for Wied's marmoset, calculated based on Raboy *et al.* [14] and Rylands [26]). Our final occurrence datasets contained 133 points for GHLTs and 121 points for Wied's marmosets, all converted to Corrego Alegre Universal Transverse Mercator (UTM) Zone 24S.

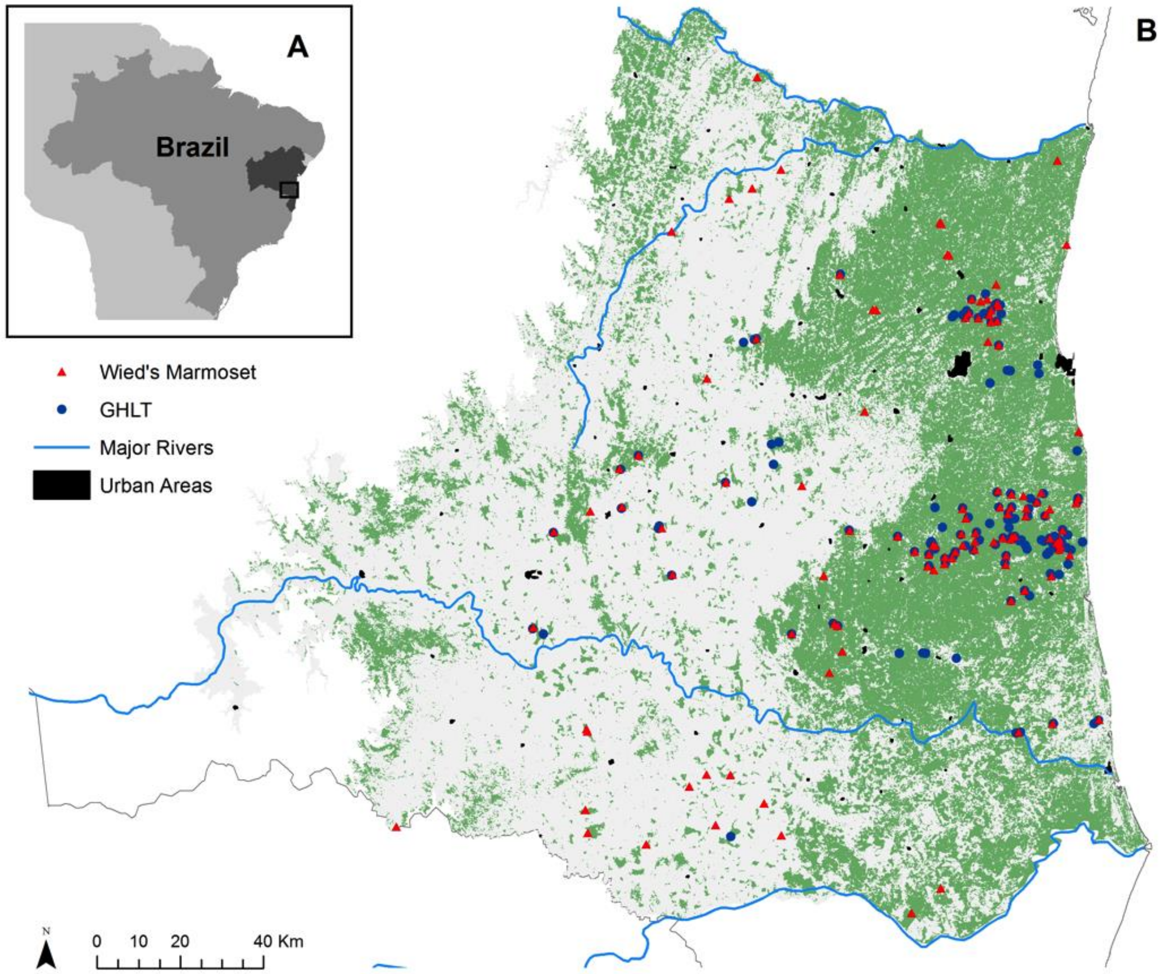

Fig. 1 Location of study area in southern Bahia, Brazil. A) Scale map of southern Bahia. Black rectangle indicates the location of the study area. B) The study area. The shaded region is the landscape analyzed in this study. Green represents forest, light grey deforested areas. Presence-points used to construct ENMs are also displayed.

Environmental Layers

We considered 24 environmental, climatic, and anthropogenic variables for inclusion in our analysis (Appendix 1). From those we prioritized the most relevant to our study species on the basis of expert opinion, further excluding variables due to high correlation (Pearson correlation coefficient ≥ 0.75). Ultimately, six environmental variables were included in our final models: distance to urban areas, neighboring forest cover, average annual temperature, elevation, annual temperature range, and precipitation in the wettest quarter. All environmental variables were resampled to a spatial resolution of 90 m, chosen to match the scale of our finest resolution variable, which was elevation. All variables were converted to Corrego Alegre UTM Zone 24S. Manipulations of environmental variables were performed in ArcGIS 10.1.

We used a forest cover map, characterizing areas of non-forest and forest, previously generated by Zeigler *et al*. [17], and further adapted it by performing a neighborhood analysis. This created a map of average forest cover smoothed over a larger area, to get a broader sense of the amount of forest bordering each pixel. Our neighborhood was defined as a circle with a radius of 1,753 m, the average daily path length of GHLTs [21].

Spatial data on urban centers were obtained from the Biodiversity Corridors in the Atlantic Forest of southern Bahia database [27]. We created a Euclidean distance surface map for urban areas. Elevation data were available from NASA's SRTM mission [28]. Climate data were obtained from the BioClim global climate datasets developed by Hijmans *et al.* [29].

Ecological Niche Models (ENMs)

We used the presence-only algorithm Maxent to produce ENMs (version 3.3.3k, [30–32]). Ecological niche models use environmental data and species occurrence records to produce probability surface maps that highlight the likelihood of species' occurrence/suitable conditions in a given area [33,34]. We optimized settings as recommended by Merow, Smith & Silander [35] in order to reflect species-specific considerations. The regularization parameters (GHLTs β=1.8, Wied's marmoset β=3.4) were calculated following Warren & Seifert [36] using ENMTools (version 1.4.3, [37]). Hinge features (i.e. use of linear threshold functions) were excluded to reduce model complexity and avoid redundancy with the linear features option [32,35]. Additionally, we included a bias grid to account for varied sampling efforts throughout the region (Appendix 3). Relative sampling weights were assigned based on the number of species occurrences, amount of survey work, and number of long term tracking studies of our focal species in these areas.

Final ENMs were based on 100-subsampled replicates, constructed using 70% of species occurrence records. The remaining 30% of records were used for model evaluation. Only the logistic outputs, displaying suitability on a scale ranging from 0 (unsuitable) to 1 (suitable), were considered [32].

Landscape Calculations and Protected Area Evaluation

Final ENMs for GHLTs and Wied's marmosets were reclassified into suitable and unsuitable areas. Chosen thresholds for species presence were based on a modified lowest presence threshold approach (LPT, [38,39]). Due to isolation of habitat patches in the west, deforestation throughout the region, and the nine-year period of occurrence data collection, we assumed that local extinctions for either species were possible. To account for this, we used a 10% omission rate. With 10% omission, 90% of all occurrences were assumed to fall into suitable habitat ($LPT_{10\%,GHLT}$=0.3, $LPT_{10\%,Weid's}$= 0.41) (Fig 2). Additionally, within suitable regions, we distinguished 'highly suitable' areas from 'moderately suitable' areas using a more stringent 40% omission threshold, given that some metapopulations may be persisting in suboptimal habitat ($LPT_{40\%,GHLT}$= 0.67, $LPT_{40\%,Wied's}$= 0.55) (Fig 2). The amount of moderately and highly suitable habitat for GHLTs and Wied's marmosets, as well as overlapping moderately and highly suitable habitat, was measured on maps reclassified based on LPT thresholds.

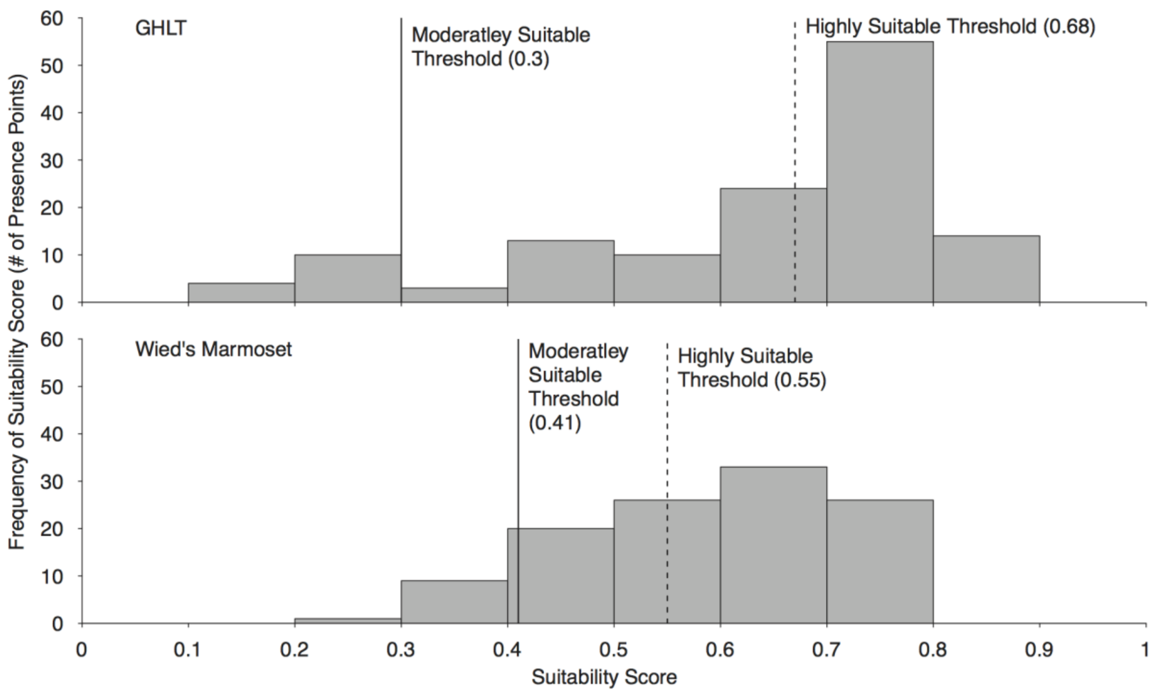

Fig. 2 Suitability values associated with species' occurrence points from logistic ENM outputs. Vertical lines represent suitability thresholds based on a modified LPT assuming 10% omission rate (solid line) and 40% omission rate (dashed line). Above these values, habitat is assumed to be suitable and highly suitable, respectively, for species. Suitability value histograms are labeled with respective species names and LPT values.

We evaluated the suitability of protected areas in the study region with IUCN classifications I-III (large natural areas set aside to preserve biodiversity or ecological processes [40]). This included four areas: Una Biological Reserve, Una Wildlife Refuge, Serra das Lontras National Park, and Serra do Conduru State Park. Additionally, we assessed a cluster of privately owned reserves belonging to the company Veracel, which have served as recent reintroduction sites for GHLTs.

Finally, using the raw logistic Maxent outputs, we calculated the average suitability of habitat inside protected areas for GHLTs and Wied's marmosets using all raster pixel values inside reserve boundaries. To examine differences in average suitability, confidence intervals based on standard deviation were compared among protected areas. Using reclassified LPT maps, we also measured the amount of suitable habitat and overlapping suitable habitat for each species within protected area boundaries.

Table 1 Amounts and percentages of suitable habitat in the landscape and protected areas for GHLTs and Wied's marmosets.

Suitability Category	Amount of Habitat (km^2) and Percentage of Landscape						Amount Under Protection	
	Landscape[2]			Protected Areas[3]				
	GHLT	WM	Overlap	GHLT	WM	Overlap	GHLT	WM
Moderately Suitable	9,115 (31%)	10,667 (36%)	4995 (17%)	336 (47%)	194 (27%)	170 (24%)	3%	2%
Highly Suitable	1,544 (5%)	4,975 (17%)	1474 (5%)	316 (44%)	488 (68%)	313 (43%)	20%	9%
Suitable[1]	10,659 (36%)	15,642 (53%)	9809 (33%)	651 (90%)	682 (95%)	634 (88%)	6%	4%

[1]Suitable = combined moderately and highly suitable habitat
[2]Percentages based on total study area
[3]Percentages based on combined area of all protected areas in the landscape

Results

Landscape Patterns of Suitability

Ecological niche models had Area Under the Curve (AUC) values of 0.872 (± 0.024SD) for GHLTs and 0.782 (± 0.032SD) for Wied's marmosets. The minimum training presence logistic threshold for ENMs was 0.147 (± 0.026SD) for GHLTs and 0.302 (± 0.035SD) for Wied's marmosets. Based on percent contribution (PC), the environmental variables that contributed most to the final models for GHLTs were neighboring forest cover (PC=72.6%) and annual temperature range (PC=10.9%) (Appendix 2). Response curves indicated that suitability of habitat increased with increasing neighboring forest cover and decreased at low values of annual temperature range (Appendix 4). The environmental variables that contributed most to final models for Wied's marmosets were neighboring forest cover (PC=70.2%) and distance to urban areas (PC=17.8%) (Appendix 2). Response curves suggested that the most suitable areas were those with more neighboring forest cover located farther away from urban areas (Appendix 5).

Reclassified models based on modified LTP-thresholds indicated differing amounts of suitable habitat in the landscape for the two primate species (Fig 3, Table 1). Thirty-six percent of the study area (10,659 km^2) was suitable for GHLTs, of which 14% (5% of the study area, 1,544 km^2) was highly suitable habitat. Suitability scores associated with GHLT presence points took on a wide range of values (Fig 2). Models for Weid's marmosets indicated that 53% of the study area (15,642 km^2) was suitable for the species, of which 31% (17% of the study area, 4,975 km^2) was highly suitable habitat. The distribution of suitability scores for Weid's marmosets' presence points was narrower than that for GHLTs (Fig 2).

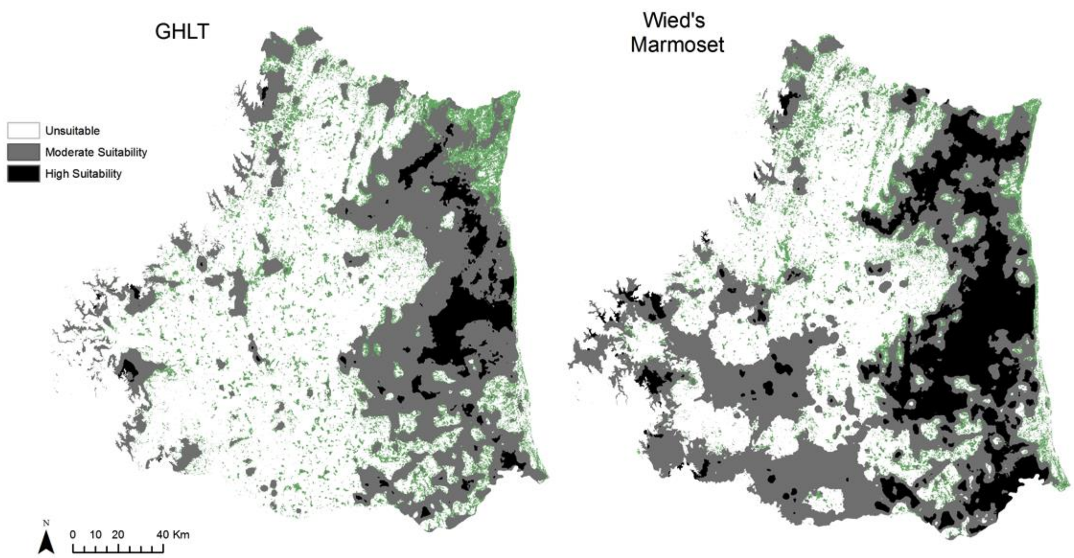

Fig. 3 Reclassified ENMs for GHLTs and Wied's marmosets. Maps display areas classified as both moderately suitable and highly suitable. Forest cover is displayed in green for reference.

Presence of GHLTs and Wied's marmosets was most strongly defined by neighboring forest cover. The majority of suitable areas for both species were confined to the eastern part of the study area, within remaining regions of continuous forest cover. Additional suitable areas for GHLTs and Wied's marmosets were also identified in the west, in some of the larger remaining forest fragments. The largest dissimilarities in suitable habitat were the northeast and southwest regions of the study area. Here, large portions of habitat were suitable for Wied's marmosets, but not for GHLTs (Fig 3). Despite dissimilarities in suitable regions for both species, 33% percent of the study area (9,809 km^2) was overlapping suitable habitat (Fig 4). Of this, 15% was overlapping highly suitable habitat (5% of the study area, 1,474 km^2).

Table 2 Amount and percentages of protected areas considered suitable for GHLTs and Wied's marmosets. The amount of overlapping suitable habitat inside the boundaries of each protected area is also reported.

Protected Area	Amount of Protected Area (km^2)					
	Moderately Suitable			Highly Suitable		
	GHLT	WM	Overlap	GHLT	WM	Overlap
Una Biological Reserve	39 (21%)	12 (6%)	10 (6%)	145 (79%)	172 (93%)	143 (77%)
Una Wildlife Refuge	95 (41%)	62 (26%)	60 (26%)	121 (52%)	151 (64%)	120 (51%)
Serra das Lontras National Park	123 (74%)	69 (42%)	68 (41%)	40 (24%)	83 (50%)	40 (25%)
Serra do Conduru State Park	49 (52%)	36 (38%)	17 (19%)	0	58 (62%)	0
Veracel Reintroduction Sites	30 (72%)	17 (39%)	15 (34%)	9 (22%)	25 (60%)	9 (22%)

Suitability of Protected Areas

Protected areas preserved suitable habitat for both GHLTs and Wied's marmosets (Fig 4). There were high amounts of moderately and highly suitable habitat for both species in Una Biological Reserve, Una Wildlife Refuge, Serra das Lontras National Park, and the reintroduction sites (Table 2). These conservation units also contained large amounts of overlapping suitable habitat (Fig 4). In contrast, Serra do Conduru State Park contained considerably less suitable habitat for GHLTs than for Wied's marmosets.

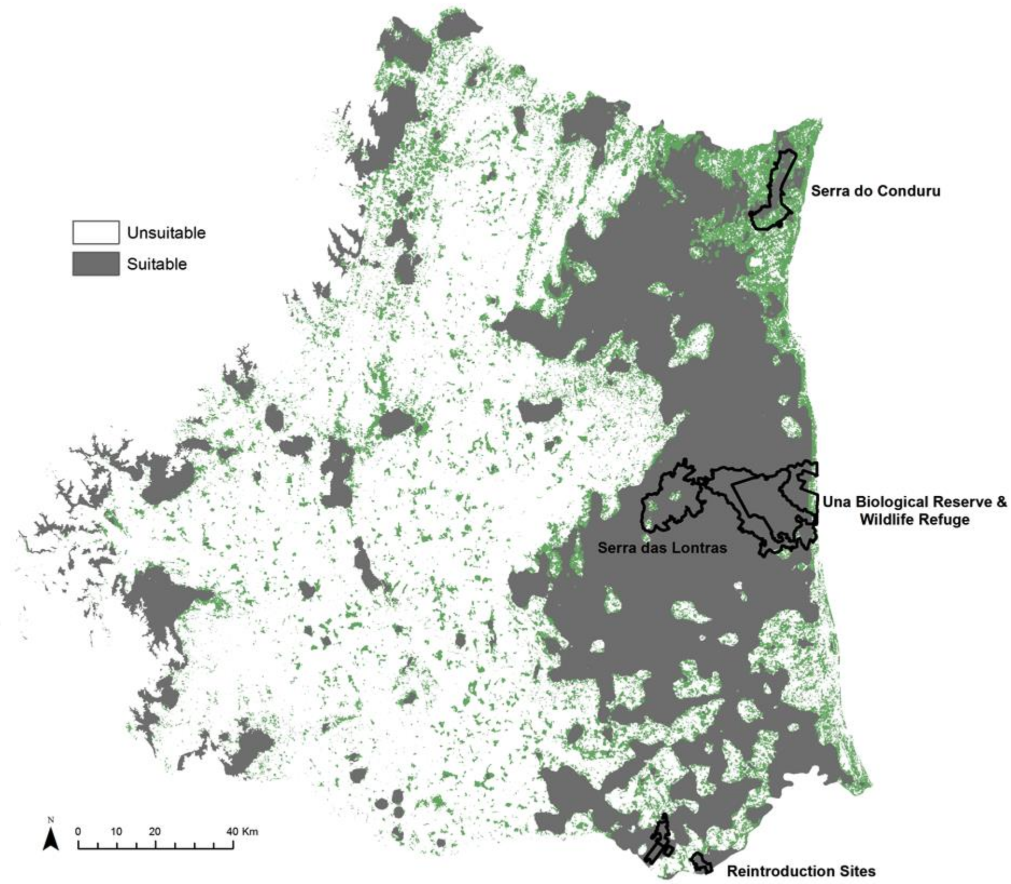

Fig. 4 Overlapping suitable habitat in the study area for GHLTs and Wied's marmosets. Areas of overlap represent combined moderately and highly suitable classes. Protected areas are indicated. Forest cover is displayed in green.

Average suitability measures for each protected area indicated that all of these areas were suitable for both species (*i.e.,* average suitability and confidence intervals fell above or overlapped with the minimum suitability threshold) (Fig 5). Average suitability scores of protected areas ranged between 0.29 (±0.18SD) and 0.73 (±0.08SD) for GHLTs. Average suitability scores of protected areas for Wied's marmosets ranged between 0.43 (±0.12SD) and 0.67 (±0.07SD). Serra do Conduru State Park had a much lower average suitability for GHLTs than the other protected areas. Average suitability scores within protected areas were similar between species for all reserves, except Serra do Conduru, where average suitability was lower for GHLTs (based on confidence intervals).

Although well represented in protected areas, only 3% of all moderately suitable and 20% of all highly suitable habitat in the study area was protected for GHLTs (Table 1). For Wied's marmosets 2% of moderately suitable and 9% of highly suitable habitat was protected (Table 1). Considering total suitability (moderately and highly suitable habitat combined), protected areas contained only 6% of suitable GHLT habitat and 4% of suitable Wied's marmoset habitat (Table 1).

Discussion

Species Distribution

Our models demonstrate that suitable habitat for GHLTs and Wied's marmosets is limited and mostly unprotected. Model predictions were largely consistent with expectations based on the ecological needs of these sympatric arboreal primates. Neighboring forest cover was the strongest contributing variable to models, and the most suitable habitat for both species was located in the largest block of contiguous forest in the study area. This is the only fragment thought capable of supporting a genetically viable, self-sustaining population of GHLTs under high-risk scenarios [17]. For both species, comparatively less suitable habitat was identified in the western region of the study area. Here, high rates of habitat conversion have resulted in relatively small, isolated forest fragments surrounded by cattle pasture. The likelihood of extinction is thought to increase in such fragments, which are often not considered large enough to support viable primate populations in the long-term [17,41,42]. Moreover, dispersal between fragments, at least for GHLTs, is thought to be unlikely and infrequent [16].

Within the otherwise suitable eastern forest block, there was an absence of suitable habitat for GHLTs in the northeast corner. This region, in and around Serra do Conduru State Park (Figure 4), was noted as a lacuna by Pinto and Rylands [43] in their 1991-93 survey. Disagreement exists about whether it is a natural gap in the GHLT distribution or a result of more recent anthropogenic changes [43]. It has been a long-standing enigma for lion tamarin biologists, as the region contains forest types thought to be good habitat for GHLTs [15,19–21,44]. Additionally, researchers recently identified a high density of *Aechmea* and *Hohenbergia* bromeliads in this region [45], known to be important resources for GHLTs [21,46,47]. However, despite seemingly ideal habitat, our models indicate GHLT presence may be limited in the northeast by certain climatic factors. On the basis of variable response curves (Fig S2), we suggest that high levels of precipitation and/or low variability in annual temperature range might explain the absence of GHLTs, although the reasons why are unclear. These climatic factors could be interacting to limit the diversity of animal prey or another critical resource used by this species. Further research to understand the limitations imposed by climatic conditions on GHLTs in this region is needed.

Our models identify several areas in the highly fragmented southwestern region as suitable for Wied's marmosets. This may be contrary to expectation for an arboreal species, but Wied's marmosets exhibit a high degree of ecological and behavioral plasticity [14,26,48]. In fact, they have been observed to colonize urban environments, suggesting an ability to rapidly adapt to changing conditions [48]. The flexibility of Wied's marmosets can be partially attributed to specialized dentition that enables them to extract exudates from trees [14,26,49]. This feeding behavior ensures continued access to stable sources of carbohydrates [49]. Moreover, marmosets have smaller home ranges (average 38.9 ha, range 34-39 ha; Raboy *et al.* [14]) than GHLTs (average 83 ha, range 22-197 ha; Oliveira *et al.* [44]). Wied's marmosets may therefore be better able to maintain the social integrity of their groups in smaller forest patches without suffering social Allee effects. Thus, gummivory and range size are both socioecological factors that may explain why Wied's marmosets are found in smaller, fragmented areas of forest.

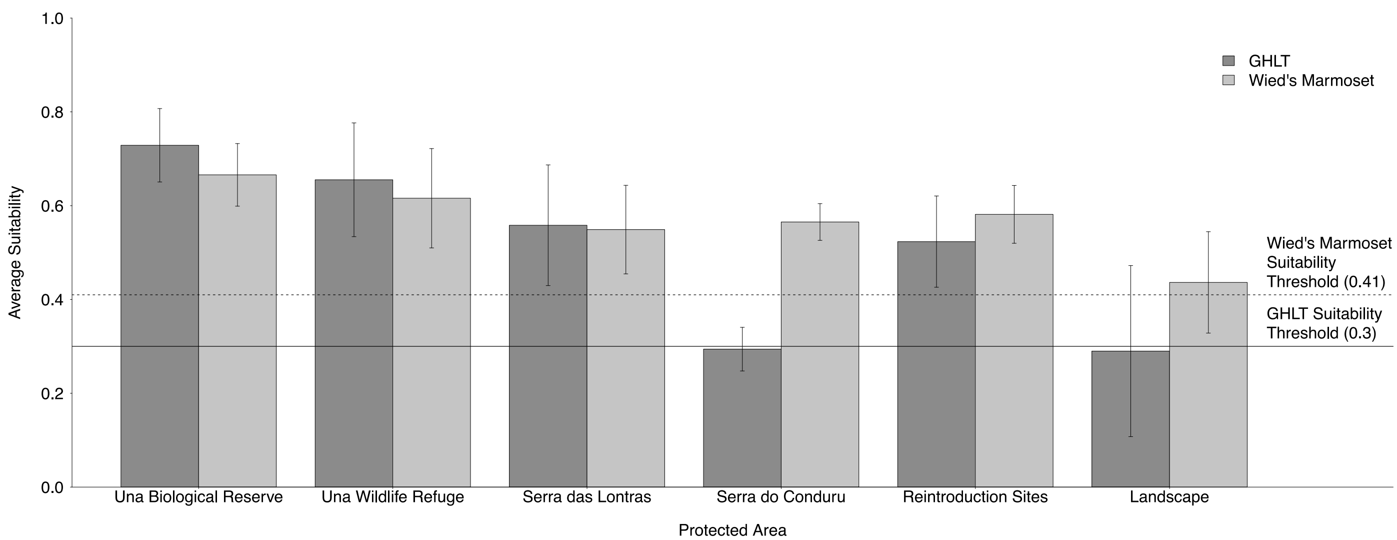

Fig. 5 Average suitability of protected areas for GHLTs and Wied's marmosets. Average suitability for the entire landscape is included for reference on the far right. Values were calculated from raw logistic ENM outputs. Error bars represent standard deviation. Horizontal lines represent suitability thresholds for GHLTs and Wied's marmosets based on a modified LPT assuming 10% omission rate. Above this value, habitat is assumed to be suitable for species.

Protected Areas and Conservation Prospects

Given a growing need for accountability in management decisions, it is important to validate locations of existing reserves. Our models indicate existing protected areas contain large amounts of moderately and highly suitable habitat for GHLTs and Wied's marmosets, with one exception. Serra do Conduru contained minimal suitable habitat for GHLTs. Additionally, our models indicated that the recent reintroduction sites for GHLTs in the southern part of their distribution contained large amounts of moderately and highly suitable habitat for the species. These sites were originally selected on a presumed ability to sustain viable populations and lack of native GHLTs (MCM Kierulff, personal observation). Further assessing these areas for suitability based on environmental and climatic conditions indicates that populations may do well in these areas.

Given concerns about future deforestation in southern Bahia [10], conservation actions to protect as much of the region's suitable habitat as possible would be beneficial for the preservation of GHLTs and Wied's marmosets. Although protected areas contained suitable regions for both species, only 6% of all suitable habitat for GHLTs and 4% for Wied's marmosets is currently protected in the study area. Given the congruence in suitable areas for GHLTs and Wied's marmosets, targeting the regions of overlapping suitable habitat identified in our maps would be an effective way to achieve protection for both primates and other arboreal frugi-faunivore guild members. Moreover, protecting regions of overlapping suitable habitat may help preserve the unique behavioral associations between GHLTs and Wied's marmosets. Prior work suggests these mixed species associations [14,15,26] provide benefits in terms of increased foraging efficiency [13] and predator surveillance [15]. Given the likely survival benefits of forming associations, protecting areas of shared suitability could promote continued interaction and thus facilitate each species' persistence. Currently, only 6% of overlapping suitable habitat in the study area is protected.

Limitations and Future Directions

Although neighboring forest cover was the strongest contributing variable in our final models (Appendix 2), this variable did not distinguish among forest types, which vary in this region. Abundant forest cover in the eastern portion of the study area is composed of shade-cocoa, secondary and mature forests [16], which differ in canopy cover and resources [19,20]. Additionally, these forest types are under different deforestation pressures. While the removal of late secondary and mature forest is largely limited by the Brazilian forest code (Federal Law No. 12651, of May 25, 2012) and "Lei da Mata Atlântica" (Federal Law No. 11.428, of December 22, 2006), tree removal in shade-cocoa agroforest is likely to be authorized (Federal Law No. 12651 of May 25, 2012 and INEMA Ordinance No. 10225 of August 18, 2015). Differences in deforestation and variance in canopy cover and resources are important factors that impact the suitability of habitat for GHLTs and Wied's marmosets. Unfortunately, a reliable map detailing different forest cover types does not exist for our study area. Eventual inclusion of such a map would aid conservation planning. This may be especially important for GHLTs, given their different responses to, and risk in, different forest types [15,21,50].

Determining the role rainfall or other correlated climatic variables may play in limiting GHLTs in the northeast will be an important avenue of future research. Given the relatively well-preserved status of forest in this region and the existence of a protected area, arguments could be made to consider this area for future reintroductions. We stress the need for thorough evaluation to understand the trophic impacts of high rainfall and low temperature variability on GHLTs or key plant and animal species they rely on, before management action occurs. Furthermore, given the threat of climate change, understanding how rainfall, temperature variation, and other climatic variables may change in the future is a key consideration for management. Recent work indicates that climatically suitable habitat for GHLTs, particularly in the western portion of their range, will greatly decrease under current climate change scenarios [51]. Although the Meyer et al. [51] work did not consider Wied's marmosets, climate change will likely impact them as well. Additionally, changes to climate may interact synergistically with deforestation [52] to further threaten both species, highlighting the need to understand the effects of changing climatic conditions on the distribution of suitable habitat in the landscape.

Investigation of the behavioral plasticity of Wied's marmosets is another valuable research area. Wied's marmosets have been observed to be adept at living in urban areas [48] and are often found in degraded habitat [23]. We caution that these observations do not mean this species does not need high quality forest. Despite the apparent ecological flexibility of Wied's marmosets, response curves (Appendix 5) indicate that the more suitable areas are those with more forest cover, farther away from urban areas. This suggests that natural habitat is ideal where available. It will be useful to compare differences in the behavior of groups living across a spectrum of habitat types (*i.e.,* mature forest, degraded forest, urban areas) to understand this species' capacity for rapid adaptation and the impacts of habitat on their behavior. This information may aid in future management action for this species.

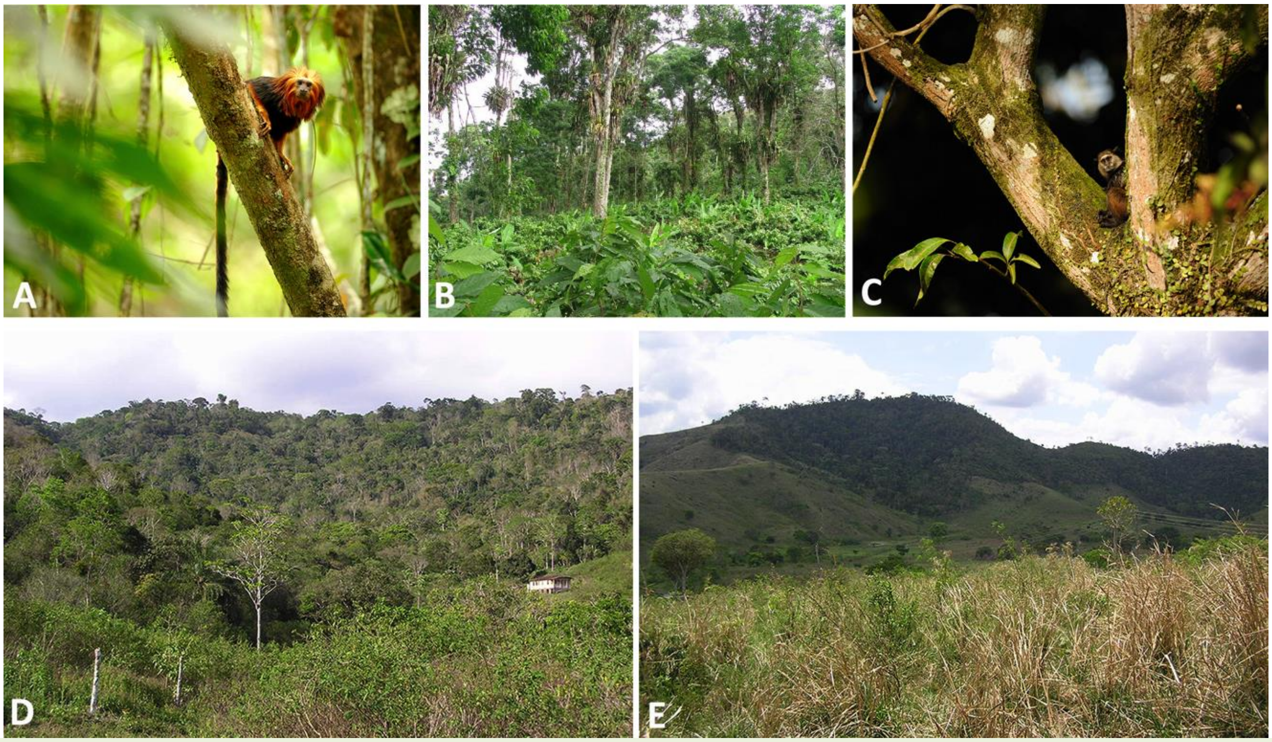

Fig. 6 Study species and landscape. A) Golden-headed lion tamarin. Photo by Kris D´Août. B) Shade-cocoa agroforest. Note the lack of midstory trees. Photo by Leonardo Oliveira. C) Wied's black-tufted ear marmoset. Photo by Kris D´Août. D&E) Fragmented forests typical of the region. Photos by Becky Raboy.

Implications for Conservation

The ENMs we produced for the endangered GHLT and near-threatened Wied's marmoset are a broad approach to understanding habitat suitability and degree of protection in the landscape for these species (Fig 6). This work is a step towards integrating multi-species assessments of suitability into conservation planning for the region. Our studies reveal spatial patterns of suitability useful for developing or enhancing management programs. In particular, many of the unprotected areas of suitable habit for focal species were also regions of overlapping suitable habitat, potentially ideal future conservation targets. Importantly, protecting shared areas of suitability may also help to preserve the beneficial behavioral association between GHLTs and Wied's marmosets. We urge future researchers to make use of techniques considered here and to consider fine-scale habitat variation and population viability analyses among multiple species to further identify areas of importance for Bahian biodiversity.

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Appendix 1: Environmental Variables Originally Evaluated

Table A1 The environmental, climatic, and anthropogenic variables originally considered for inclusion in the analysis with their data sources. Variables included in final models are bolded.

Environmental Variable	Source
Annual Mean Temperature	WorldClim Global Climate Database[1]
Mean Diurnal Range	WorldClim Global Climate Database[1]
Isothermality	WorldClim Global Climate Database[1]
Temperature Seasonality	WorldClim Global Climate Database[1]
Max Temperature of Warmest Month	WorldClim Global Climate Database[1]
Min Temperature of Coldest Month	WorldClim Global Climate Database[1]
Temperature Annual Range	WorldClim Global Climate Database[1]
Mean Temperature of Wettest	WorldClim Global Climate Database[1]
Mean Temperature of Driest Quarter	WorldClim Global Climate Database[1]
Mean Temperature of Warmest	WorldClim Global Climate Database[1]
Mean Temperature of Coldest Quarter	WorldClim Global Climate Database[1]
Annual Precipitation	WorldClim Global Climate Database[1]
Precipitation of Wettest Month	WorldClim Global Climate Database[1]
Precipitation of Driest Month	WorldClim Global Climate Database[1]
Precipitation Seasonality	WorldClim Global Climate Database[1]
Precipitation of Wettest Quarter	WorldClim Global Climate Database[1]
Precipitation of Driest Quarter	WorldClim Global Climate Database[1]
Precipitation of Warmest Quarter	WorldClim Global Climate Database[1]
Precipitation of Coldest Quarter	WorldClim Global Climate Database[1]
Neighboring Forest Cover	Sara L. Zeigler[2]
Distance to Urban Areas	Biodiversity Corridors in the Atlantic Forest of Southern Bahia database[3]
Distance to Waterways	Biodiversity Corridors in the Atlantic Forest of Southern Bahia database[3]
Distance to Roadways	Biodiversity Corridors in the Atlantic Forest of Southern Bahia database[3]
Elevation	NASA's SRTM Mission[4]

[1] Hijimans *et al.* [29]
[2] Zeigler *et al.* [17]
[3] Prado *et al.* [27]
[4] Jarvis *et al.* [28]

Appendix 2: Percent Contribution of Environmental Variables

Table A2 Percent Contribution of environmental variables to final Maxent models for GHLTs and Wied's marmosets.

Environmental Variable	Percent Contribution	
	GHLT	WM
Forest Cover	72.6%	70.2%
Annual Temperature Range	10.9%	3.3%
Distance to Urban Areas	7.7%	17.8%
Average Annual Temperature	5.8%	1.2%
Precipitation in the Wettest Quarter	2%	4.4%
Elevation	1%	3.1%

Appendix 3: Bias Grid

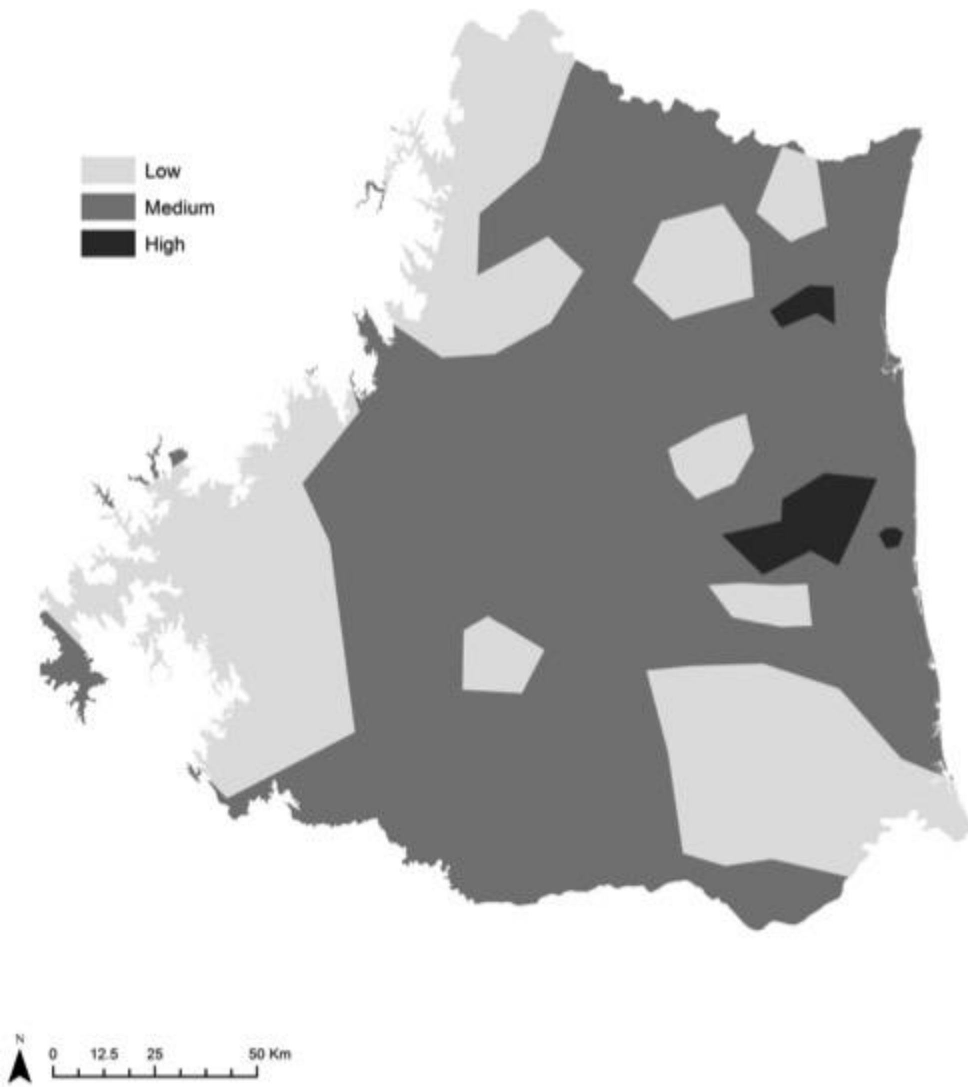

Fig. A3 Bias grid used in analyses. The map delineates three levels of sampling effort for the study region.

Appendix 4: Response Curves for GHLT Models

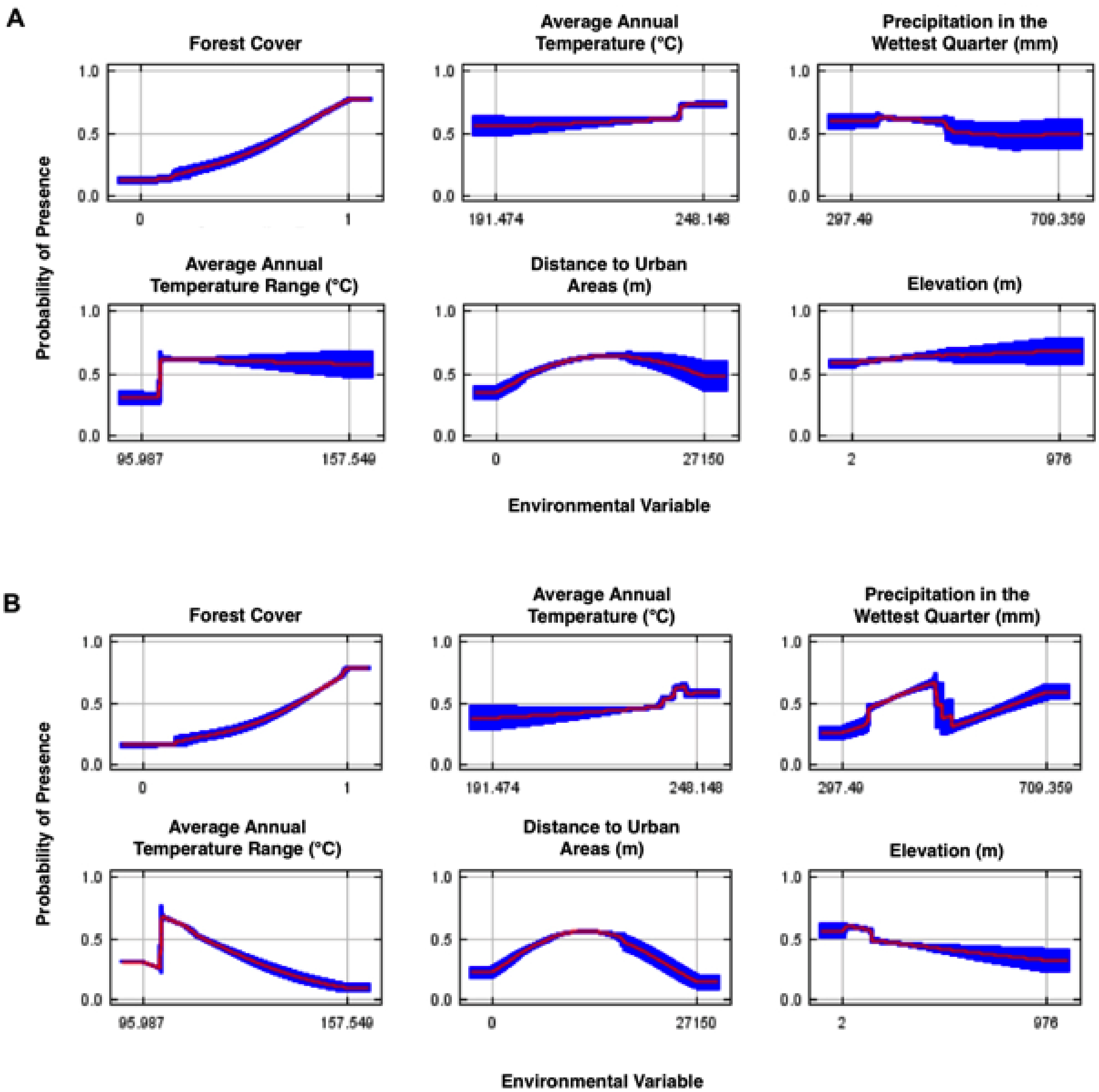

Fig. A4 Response curves for environmental variables in GHLT models. A) Marginal response curves for environmental variables based on full models B) Response curves for environmental variables based on a Maxent model built using only that variable.

Appendix 5: Response Curves for Wied's Marmoset Models

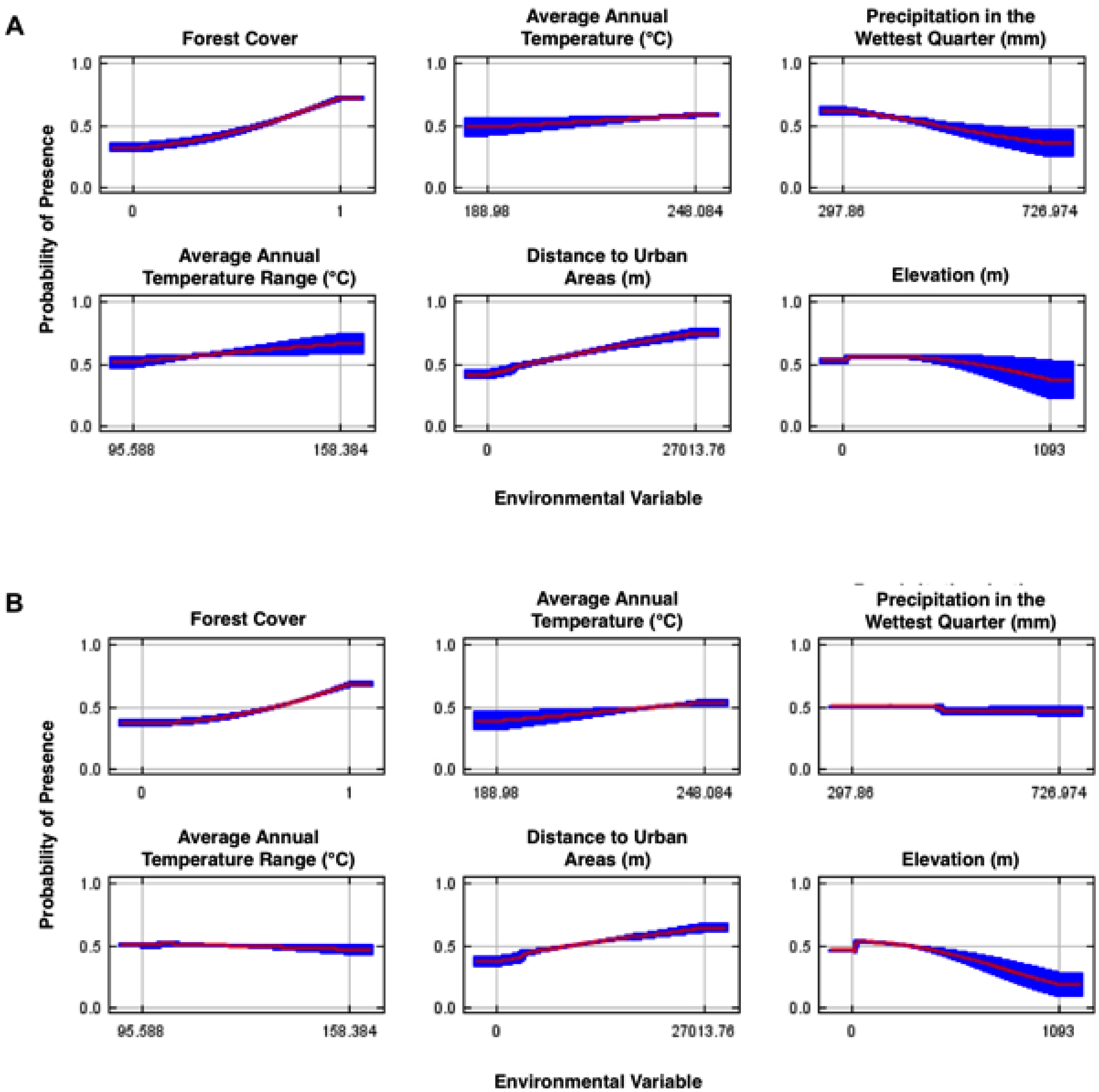

Fig. A5 Response curves for environmental variables in Wied's marmoset models. A) Marginal response curves for environmental variables based on full models. B) Response curves for environmental variables based on a Maxent model built using only that variable.

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