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Understanding species persistence for defining conservation actions: A management landscape for jaguars in the Atlantic Forest



Carlos De Angelo^{a,*}, Agustín Paviolo^a, Thorsten Wiegand^b, Rajapandian Kanagaraj^b, Mario S. Di Bitetti^a

^a National Research Council (CONICET), Instituto de Biología Subtropical, Facultad de Ciencias Forestales, Universidad Nacional de Misiones, Asociación Civil Centro de Investigaciones del Bosque Atlántico, Bertoní 85 N3370BFA, Puerto Iguazú, Misiones, Argentina

^b Department of Ecological Modelling, UFZ Helmholtz Centre for Environmental Research, P.O. Box 500136, DE-04301 Leipzig, Germany

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ABSTRACT

Habitat models constitute useful instruments for understanding species-habitat interactions and can constitute helpful conservation tools. The Upper Paraná Atlantic Forest (UPAF) of South America still holds the world's southernmost jaguar (*Panthera onca*) population. Our aims were: (i) to test several a priori hypotheses on the factors affecting jaguar persistence in this region, (ii) to map habitat suitability and identify areas with potentially conflicting habitat conditions, and (iii) to identify priority areas for management and improve the conservation initiatives for jaguars and the UPAF. Following an information-theoretic approach, we used presence records of jaguars and pseudo-absences in generalized linear models. We structured hypotheses into two groups which demand different management actions: land cover and human persecution. The best model of each group was used to develop a two-dimensional habitat model. Jaguar persistence was favoured by current and historical native forest cover, and hindered by human land uses. Protection favoured jaguar presence whereas human accessibility and high human population density had negative effects. The two-dimensional model suggests that <8% (20,670 km²) of the landscape represents potential core areas for jaguars (good land-cover characteristics and low human persecution) and 11.8% (32,563 km²) stands as potentially attractive sinks where good land-cover conditions conflict with high human persecution. Reduction of human persecution is urgently needed to increase the core areas for jaguars in this region, but improvement of land-cover conditions is important for sustaining the connectivity among jaguar populations that seem to be isolated in different areas of the UPAF.

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1. Introduction

Understanding the relationship between landscape change and species persistence is a major issue of interest in applied ecology because of its direct relationship with biodiversity conservation (Tilman et al., 1994). Habitat models or species distribution models (SDMs) constitute useful instruments for predicting species distribution and understanding the species-habitat interactions, but also they can be used as conservation tools for delineating management actions (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000). However, implementation of SDMs in biological conservation is not always a simple task and often demands specific approaches for transforming these models into useful management tools (Guisan and Thuiller, 2005). Naves et al. (2003), for example,

Abbreviation: AICc, Akaike's Information criterion corrected for small samples; GLM, generalized linear model; UPAF, Upper Paraná Atlantic Forest eco-region.

* Corresponding author. Tel.: +54 3757 423511; fax: +54 3757 422370.

E-mail address: biocda@gmail.com (C. De Angelo).

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proposed an approach for mapping habitat suitability for large carnivores that involves two separate models: a natural model targeting habitat suitability regarding reproduction and a human impact model targeting habitat suitability concerning survival. This approach allows detection of not only the conventional categories where conditions for reproduction and survival are positively correlated (i.e., matrix, sink or poor habitat, and source or good habitat), but also otherwise undetectable areas with good conditions for reproduction though with low survival (attractive sinks), and areas with poor conditions for reproduction but with high survival (refuges). These areas have important management implications, mainly because attractive-sink areas may constitute ecological traps with large effects on populations' survival (Delibes et al., 2001).

The Upper Paraná Atlantic Forest (UPAF) of Argentina, Brazil and Paraguay, is the largest eco-region of the South American Atlantic Forest, and it constitutes one of the world's most endangered eco-regions (Mittermeier et al., 2005; Ribeiro et al., 2009). The main conservation initiative developed for the UPAF is the

Biodiversity Vision (Di Bitetti et al., 2003), a tri-national conservation strategy designed to sustain a viable population of jaguars (*Panthera onca*), considering this species as an umbrella for the vast biodiversity that the UPAF hosts (Miller and Rabinowitz, 2002). However, only scarce information existed about jaguars in the UPAF when this conservation plan was developed, and one of Biodiversity Vision's aims was the study and monitoring of jaguars and the use of this information for validating this biodiversity conservation strategy (Di Bitetti et al., 2003). Additionally, jaguars are among the most threatened species in the Atlantic Forest and the UPAF hosts two Jaguar Conservation Units (JCU) where jaguar experts encouraged research and conservation actions for this species (Sanderson et al., 2002b). Considering these demands of knowledge about jaguars in the UPAF, different research initiatives were developed that emphasized the urgent need of a deeper evaluation of the remaining habitat for jaguars in this region to delineate actions at an eco-regional scale (Cullen et al., 2005; De Angelo et al., 2011a,b; Paviolo et al., 2008).

In this study we compiled the previous information obtained about jaguars in the UPAF and used this information to: (i) test several a priori hypotheses on the factors influencing jaguar habitat suitability, (ii) map habitat suitability for jaguars and identify areas with potentially conflicting habitat conditions such as attractive sinks, and (iii) detect priority areas for implementing specific management actions and improving the conservation plans developed for jaguars and the UPAF.

2. Material and methods

2.1. Study area

The UPAF is a subtropical and semi-deciduous forest (annual precipitation range: 1000–2200 mm; mean temperature range: 16–22 °C), and it constitutes a highly degraded and fragmented region, where less than 8% of the forest remains (Di Bitetti et al., 2003). The history and dynamics of human settlement, land-use change, and fragmentation processes are heterogeneous along the UPAF (De Angelo, 2009; Izquierdo et al., 2008; Jacobsen, 2003). In the Brazilian UPAF, most of the forest was replaced around the middle of the last century (Ribeiro et al., 2009), while the Paraguayan UPAF has a more recent but accelerated process of forest destruction (Huang et al., 2007). The Argentinean UPAF has a long history of human settlement and forest exploitation but with much lower rates of forest replacement (Izquierdo et al., 2008).

We selected an area of 276,843 km² at the border shared by Brazil, Paraguay and Argentina, which includes most of the remnants of the UPAF (Fig. 1). This area encloses all the area surveyed by De Angelo et al. (2011b) in their monitoring of jaguar presence and is the same area used by De Angelo et al. (2011a) in their habitat suitability analysis for pumas and jaguars using a presence-only technique.

2.2. Species data

We utilized the presence records of jaguars collected by participatory monitoring between 2002 and 2008 (De Angelo et al., 2011b). We obtained records from different sources (tracks, scats, camera traps, radio-tracked animals, etc.), that were carefully selected and accurately identified for avoiding false positives. Jaguar tracks were identified using a discriminant model developed for recognizing jaguar tracks (De Angelo et al., 2010), and scats were identified through specific molecular markers developed for differentiating jaguar and puma (*Puma concolor*) faecal samples (Haag et al., 2009).

In total we obtained 974 jaguar records (De Angelo et al., 2011b). To reduce potential pseudo-replication biases caused by the unsystematic data collection, we superimposed a grid of 144-km² cells (the size estimated for a female jaguar home range; D. Sana, unpublished data; A. Paviolo, unpublished data; Cullen et al., 2005; Paviolo, 2010) and randomly selected one observation if more than one record occurred in a cell (Kanagaraj et al., 2011). This resulted in a total of 106 presence records to be used in our analysis. To test if our results were influenced by this particular selection of records, we created 10 further subsets of 106 records following the same procedure. This allowed us to explore whether the selected presence records were representative and whether models constructed with alternative sets of presence records agreed (see below Sections 2.3 and 2.4).

To obtain a binomial response variable we followed the approach developed by Engler et al. (2004), and we generated randomly the same number of pseudo-absences as presences (Liu et al., 2005). To this end, we followed several rules to ensure that pseudo-absences were located inside surveyed areas but not in areas that were known to be suitable areas for jaguars (Appendix A and Fig. A1). We also generated 10 further sets of pseudo-absences for model validation (see below Section 2.4).

2.3. Biological hypotheses and environmental variables

SDMs that predict average habitat suitability based on a single function may overlook areas where habitat conditions related to key factors with different management requirements are conflicting (Kanagaraj et al., 2011; Naves et al., 2003; Nielsen et al., 2006). For example, it is well known that deaths of large carnivores are mainly caused by humans, but nutritional condition determines reproductive rate (Naves et al., 2003; Woodroffe and Ginsberg, 1998). If key factors that determine reproduction and survival are not positively correlated, a single function SDM will overlook attractive sinks (good conditions for reproduction but low survival) and refuges (poor conditions for reproduction but with high survival). Thus, using a model based on two SDMs that describe habitat suitability from the perspective of different key factors that affect either survival or reproduction, allows for a more subtle and management relevant assessment of habitat suitability.

Indeed, we can identify such two management-relevant key factors for the jaguar in the UPAF. First, landscape conditions related with land cover and physical environment are important determinants of jaguar habitat suitability at a regional scale (e.g. forest cover, presence of water, or different human land uses; see Table 1). The main management actions associated with these conditions are related to policies of forest restoration and territorial or land-use planning (e.g. defining which human land uses will be promoted in certain regions, designing corridors, protecting river basins) (e.g. in Fernández et al., 2006; Muntiferi et al., 2006; Wikramanayake et al., 2004). Second, the presence or absence of this species is also determined by direct human persecution of jaguars and their prey (see Table 2). The most important management actions needed to improve habitat conditions in relation with these threats are different from those mentioned before: the priority actions would be protection, law enforcement, and actions for reducing jaguar mortality (e.g. for reducing poaching activity and other sources of jaguar mortality as road kills) (e.g. in Nielsen et al., 2004; Woodroffe and Ginsberg, 1998). By analyzing habitat suitability with respect to these two dimensions we can identify critical areas that need to be prioritized for the different management actions. We therefore tested several a priori hypotheses on factors that determine jaguar habitat suitability regarding the two main key factors: land-cover and physical environment [L], and human persecution [H] (Tables 1 and 2 respectively). We then

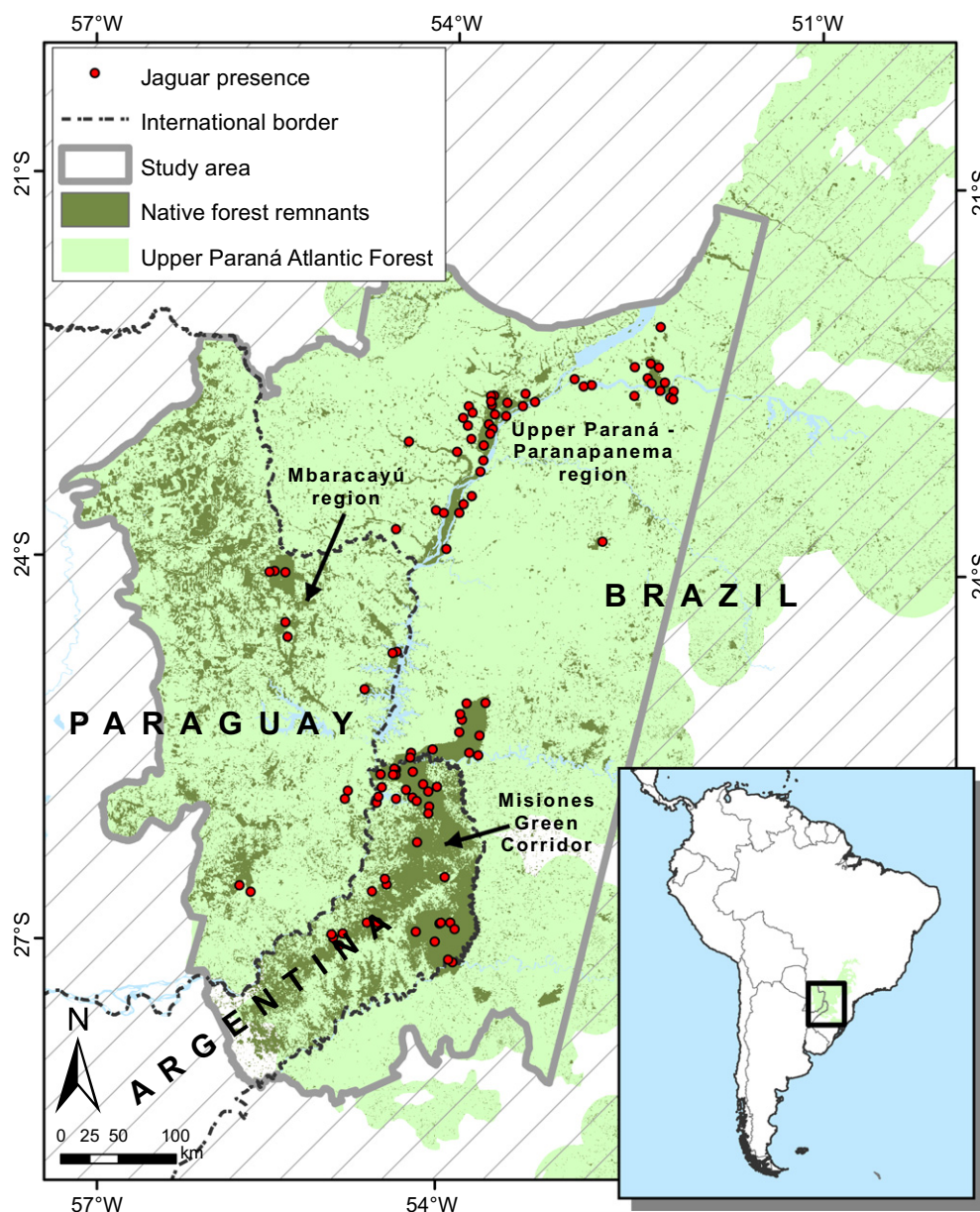


Fig. 1. Portion of the Upper Paraná Atlantic Forest eco-region selected for jaguar habitat suitability analysis. The right corner inset details the location of the study area in South America. Forest remnants include native forest and marshlands and they correspond to estimates for the year 2004 done by De Angelo (2009). Dots represent the 106 presence records of jaguars used in our analysis.

used the most parsimonious SDMs of these groups as the two dimensions for categorizing the habitat for jaguars (Fig. 2).

To describe the landscape characteristics and human pressures that represent the different hypotheses we used a total of $9 + 4 \times 10 = 49$ variables with a spatial resolution of 330×330 m (Appendix B; Table B1). The first nine variables described the average conditions within each cell and included topography (i.e., elevation and slope), human accessibility, distance to rivers, roads and towns, protection category, rural population density and the mean human population density during the last 40 years (Table B1). To capture the jaguar perception of the different landscape elements we also used 4×10 neighborhood variables to describe for example the frequency of cells occupied by native forest within four different neighborhood radii (1, 4, 7, and 10 km) around the focal cell (Kanagaraj et al., 2011; Naves et al., 2003). We constructed neighborhood variables from the categories 'current native forest', 'intensive agriculture', 'extensive pastures', 'pine plantations', 'small farms', 'rivers', 'roads', and 'towns'. Additionally, we added

four neighborhood variables describing the historical condition of the forest in 1973 (*forest73_r*) (Table B1). The local connectivity for radii of 1 km (*connect_r1*) was discarded because of its redundancy with *forest_r1*.

To assess whether the 106 presence records selected for the analysis were a representative sample of the total 974 records available or not, we compared the distribution profile of these records for each independent variable with the distribution profile of the other 10 subsets of presence records. We observed no significant differences for any of the 48 variables (Appendix B; Table B2), indicating that the subset selected for the analysis was representative of the variables used.

2.4. Model selection and evaluation

We combined the selected presences and pseudo-absences as a binary response variable in generalized linear models (GLMs) with logit-link function (McCullagh and Nelder, 1989). We also

Table 1

Description of the general and the main particular hypotheses evaluated in relation to the land-cover and physical environment as determinants of jaguar presence in the Upper Paraná Atlantic Forest. Variables used for each hypothesis are in brackets (definitions in Table B1).

General hypotheses and justification	Particular hypotheses
Native forest (F): jaguar presence is directly conditioned by the presence and characteristics of the native forests. Cullen (2006) described this relationship in jaguar habitat selection in the northern UPAF. Previous studies on carnivores also showed that the amount and connectivity of native forest have been important predictors (Conde et al., 2010; Naves et al., 2003; Rodríguez-Soto et al., 2011; Schadt et al., 2002). The fast and varied dynamics of UPAF fragmentation means that the historical process of forest loss might also be involved as predictor of jaguar persistence as occurred with other species in the Atlantic Forest (Metzger et al., 2009) and in other areas (e.g. Brooks et al., 1999)	(F1) The amount of forest (forest_r) favors the presence of jaguars. (F2) The local connectivity of forest (connect_r) favors the presence of jaguars. (F3) Both, amount and connectivity of forest are important for jaguar presence. (F4) The historical presence of forest (forest73_r) determines the presence of jaguars. (F5) Combined effects of current and past forest characteristics are important
Physical Environment (PE): physical and geographical characteristics of the landscape are important predictors of jaguar presence. Jaguars are positively associated with water courses (Crawshaw and Quigley, 1991; Cullen, 2006; Hatten et al., 2005; Somma, 2006), and they were related with higher elevations and slopes in Mexican hills in Tamaulipas (Ortega-Huerta and Medley, 1999) but in general with lower elevations along Mexico (Rodríguez-Soto et al., 2011)	(PE1) The presence of rivers (rivers_d and rivers_r) is important for jaguar presence. (PE2) Elevation is an important predictor of jaguar presence (elevation). (PE3) Jaguars are present mainly in higher slopes (slope). (PE4) Combined effects of environment characteristics are important
Human land uses (U): human land uses have negative effects on jaguar presence at this scale due mainly to changes in land cover, but also lower prey availability (e.g. intensive agriculture), and higher human presence (e.g. pastures and farms) not only in the modified areas but also in the surroundings. Land use characteristics have been important predictors of jaguars (Conde et al., 2010) and many other carnivores' presence (Kanagaraj et al., 2011; Revilla et al., 2004).	(U1) Each land use has a particular negative impact (farms_r, int_agr_r, pastures_r and plant_r) at this scale mostly due to differences in cover, but also in prey and human presence. U2) Combined characteristics of different land uses are important
Land-cover and physical environment combined (L): Jaguar presence is determined by the characteristics of native forest, physical environment and/or human land uses	L = (1) F + PE + U. (2) F + PE. (3) F + U. (4) PE + U

Table 2

Description of the general and the main particular hypotheses evaluated in relation to the human persecution of jaguars and their prey as determinants of jaguar presence in the Upper Paraná Atlantic Forest. Variables used for each hypothesis are in brackets (definitions in Table B1).

General hypotheses and justification	Particular hypotheses
Protection and human access (PA): Jaguar presence is determined by habitat protection and it is negatively affected by the access of humans. Both, protection and human access, are directly related with poaching pressure on jaguars and their prey, but also with other direct impacts on jaguars (e.g. traffic killings) and forest (e.g. logging). Recent works demonstrated a direct relationship between protection and jaguar density in the UPAF (Paviolo et al., 2008), and the same pattern was observed with its main prey species where not only protection levels but also human access were important prey abundance predictors (Di Bitetti et al., 2008; Paviolo et al., 2009). Many authors have described negative association of large carnivores with human access (Conde et al., 2010; Kerley et al., 2002; Nielsen et al., 2004) and the positive effects of protected areas (e.g. Woodroffe and Ginsberg, 1998).	(PA1) Jaguar presence is favoured by protection (protect_cat). (PA2) Human access (access_cost, road_d, road_r, towns_d and towns_r) negatively affects jaguar presence. (PA3) Protection and human access are important predictors of jaguar presence and there is an interaction between them because jaguars often use access ways inside protected areas (protect_cat × access_cost)
Rural population (RP): Rural population density is negatively related with jaguar presence. Human density is a good predictor of human impacts (Sanderson et al., 2002a) and it is associated with carnivores' extinction risk (Cardillo et al., 2004). Altrichter et al. (2006) enhanced the importance of the history of human settlements in the existence of jaguars in Argentinean Chaco	(RP1) Jaguars occur in areas with low rural population density (population_2000). (RP2) Jaguars are present in areas historically low populated (population_hist)
Human persecution combined (H): Jaguar presence is determined by the combined effects of protection, human access and rural population density	H = PA + RP

compared linear, quadratic, and cubic GLM functions to test possible non-linear adjustments for each predictor variable (Guisan and Zimmermann, 2000). Our primary objective was to compare the support received by several a priori hypotheses on the factors that determine jaguar presence and absence in the UPAF. We therefore followed an information theoretic approach for model selection (Burnham and Anderson, 2002). This method has the additional advantage that biological knowledge is used in the process of variable selection through developing models following a priori hypotheses, ensuring biological interpretation of the resultant models. Also this approach allows one to assess the relative levels of support for the competing hypotheses and to draw inferences from the whole set of competing models (Burnham and Anderson, 2002; Johnson and Ommland, 2004).

To organize model selection, we grouped the hypotheses hierarchically, starting with the two main groups: land-cover and phys-

ical environment (L) and human persecution (H) (Tables 1 and 2 respectively). Each group contained a set of general hypotheses disaggregated into particular hypotheses. The particular hypotheses were described by GLMs through different combinations of variables. In the case that more than one variable representing a given hypothesis were highly correlated ($r > 0.7$), we conducted variable reduction (details in Appendix C1).

We used the Akaike Information Criterion corrected for small samples (AIC_c) for model selection, because it allows a comparison of the models in their relative fit to the data while penalizing model complexity (Johnson and Ommland, 2004). We selected the model with the lowest AIC_c for representing each particular hypothesis (Tables 1 and 2). We then compared the models selected for the particular hypotheses within each general hypothesis using the same criterion. Finally, we compared the general hypotheses in each main group and selected one final model for

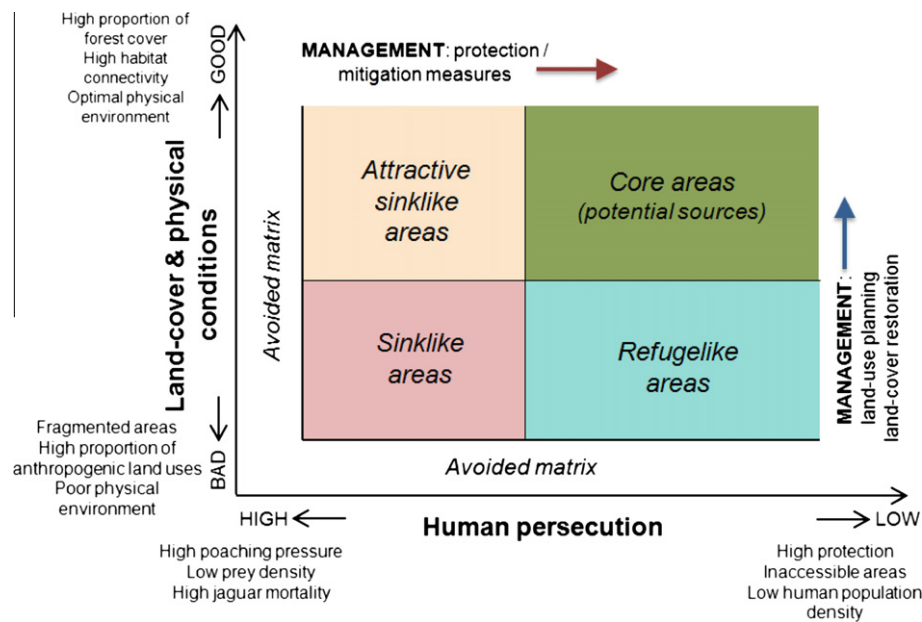


Fig. 2. Two-dimensional habitat categorization based on Naves et al. (2003), but using a different definition of habitat dimensions according to the available information for jaguars in the Upper Paraná Atlantic Forest (see Tables 1 and 2) and the landscape management alternatives for improving the habitat. The 'management arrows' indicate the direction of habitat improvement that would occur if this actions are implemented.

the land-cover and physical environment group and one model for the human persecution group. We also developed a global model combining the two final models (Burnham and Anderson, 2002).

We evaluated the final and the global models by the area under the receiver operating characteristic curve (AUC; Guisan and Zimmermann, 2000), the percentage of correctly predicted presences and pseudo-absences, and the continuous Boyce index (Hirzel et al., 2006). In order to evaluate potential overfitting, we conducted a cross validation (Fernández et al., 2003; Kanagaraj et al., 2011). To test if the particular selection of records and pseudo-absences influenced our results, we also estimated the prediction ability of the models based on the 10 alternative sets of presence and pseudo-absences (details in Appendix C2).

We mapped the final models with a 330-m resolution to obtain the relative probability of jaguar presence within the study area and transformed the maps into categories of habitat quality following Naves et al. (2003) and Hirzel et al. (2006) (Appendix C2).

2.5. Two-dimensional habitat categorization

We used the selected models of the land-cover and physical environment group and the human persecution group for categorizing the habitat for jaguars in a two dimensional way (Fig. 2). Because we modeled these dimensions only with presence data (neither actual reproduction nor mortality data), we termed potential sources as core areas, and sinks and attractive sinks as sinklike and attractive sinklike areas (Kanagaraj et al., 2011).

To validate our categorization particularly in relation to sinklike and attractive sinklike areas, we used independent records of killed or removed jaguars ($n = 30$) that occurred between 1998 and 2008 in the Argentinean part of the study area (De Angelo, 2009; Paviolo, 2010). Using a chi-square test, we compared the proportion of dead and removed animals that occurred in matrix habitat, sinks (i.e., sinklike and attractive sinklike areas), and core areas, with the expected value according to the surface available of each category in this area.

2.6. Validating and improving conservation plans

We used the two-dimensional habitat categorization to validate the different conservation initiatives for jaguars and the study area.

We overlaid our jaguar habitat model with the Biodiversity Vision conservation landscape (Di Bitetti et al., 2003) to observe the agreements and disagreements between both management maps. Based on the information available in 1999, Sanderson et al. (2002b) defined Jaguar Conservation Units as areas that can be considered as able to preserve a large enough (at least 50 breeding individuals) population of resident jaguars to be potentially self-sustaining over the next 100 years. Alternatively, they included areas containing fewer jaguars but with adequate habitat and a stable, diverse prey base, such that jaguar populations in the area could increase if threats were alleviated. Using these criteria and the new information available about jaguars in the UPAF, we updated and re-defined the JCUs in this region based on our two-dimensional habitat model.

To exemplify how our models can be used in adaptive management for prioritizing actions in these different conservation strategies (Sanderson et al., 2002c), we followed the least-cost corridors approach of Rabinowitz and Zeller (2010) to identify areas for alternative corridors connecting not only JCUs but also all core areas where the presence of jaguars was confirmed in the UPAF. For this analysis we used our global model as a permeability matrix and the Corridor tool of ArcGIS to find the least cost area between pairs of core areas with jaguars and revised JCUs (only the 0.1% of the grid cell values were extracted, see details of the method in Rabinowitz and Zeller, 2010).

3. Results

3.1. Determinants of jaguar presence

Land-cover conditions were important predictors of jaguar presence in the UPAF (Tables 3 and C1). The occurrence of this species was positively related not only with the local amount of forest and the proximity of forested areas (local connectivity), but also with the presence of forest in the past. These three characteristics constituted the best supported model for describing the native forest hypothesis (F). Among the physical environment hypotheses (PE), only the frequency of rivers was supported by the data indicating that jaguars were found more frequently in areas

Table 3
Selection of models for predicting jaguar presence in the UPAF according to the main groups of hypotheses. Only selected models from particular hypotheses and their combinations are shown (see Tables C1 and C2). The comparison among the final models is shown in bold type.

Hypotheses	Variables in the final model (+ or – effect)	χ^2	df	<i>p</i>	D_{adj}^2	AIC _c	ΔAIC_c	<i>w_i</i> (%)
Null model	Intersection	0	–	–	–	296	119	0.0
Land cover & physical (L)							6	3.9
Forest (F)	forest_r1(+), connect_r7(+), forest73_r7(+), forest73_r7 ² (–), forest73_r7 ³ (+)	121	5	<0.001	0.39	186	3	10.8
Physical Environment (PE)	rivers_r4(+)	11	1	0.001	0.03	287	104	0.0
Land uses (U)	int_agr_r1(–), farms_r4 (–), pastures_r4 (–)	108	3	<0.001	0.37	193	10	0.3
F + PE	forest_r1(+),connect_r7(+), forest73_r7(+), forest73_r7 ² (–), forest73_r7 ³ (+), rivers_r4(+)	125	6	<0.001	0.41	184	1	30.6
PE + U	rivers_r4(+), agri_r1(–), farms_r4(–), pastures_r4(–)	110	4	<0.001	0.36	195	12	0.1
F + U	forest_r1(+), connect_r7(+), forest73_r7(+), forest73_r7 ² (–), forest73_r7 ³ (+), int_agr_r1, (–) farms_r4(–),pastures_r4(–)	130	8	<0.001	0.42	183	0	41.3
F + PE + U	forest_r1(+), connect_r7(+),forest73_r7(+), forest73_r7 ² (–), forest73_r7 ³ (+), rivers_r4(+), int_agr_r1(–), farms_r4(–), pastures_r4(–)	130	9	<0.001	0.42	185	2	16.8
Human persecution (H)							39	0.0
Protection and human access (PA)	protect_cat × access_cost (+), protect_cat1 × access_cost (+), protect_cat2 × access_cost (+)	77	3	<0.001	0.25	226	11	0.5
Population density (RP)	population_hist (–)	22	1	<0.001	0.07	276	61	0.0
PA + RP	protect_cat0 × access_cost (+), protect_cat1 × access_cost (+), protect_cat2 × access_cost (+), population_hist (–)	87	4	<0.001	0.29	215	0	99.5
Global L + H	forest_r1(+),forest73_r7(+), forest73_r7 ² (–), forest73_r7 ³ (+), int_agr_r1, (–) farms_r4(–),pastures_r4(–), protect_cat0 × access_cost (+), protect_cat1 × access_cost (+), protect_cat2 × access_cost (+), population_hist (–)	141	11	<0.001	0.45	176	0	96.1

Notes: Variable abbreviations are from Table B1; χ^2 is the Wald's chi-square statistic; D_{adj}^2 is adjusted explained deviance; AIC_c is bias-corrected Akaike's Information Criterion; ΔAIC_c is (AIC_c)I–(AIC_c)min; *w_i* is the AIC_c weights expressed in percentages; (+) or (–) indicates the direction of the effect of the variable for predicting jaguar presence; * indicates interaction between variables; _r indicates the variable calculated for 1-, 4-, 7- or 10-km radius.

surrounded by rivers. All human land uses showed negative relationship with jaguar presence, but the combination of local frequency of intensive agriculture (1-km radius) with the frequency of farms and pastures in the surroundings (4-km radius) yielded the best model of the general human land use hypothesis (U).

When combining the best models of the three general hypotheses related to land-cover and physical environment, we found that the three models that contained the native forest hypothesis (i.e., F + PE, F + U, F + PE + U) received similar support from the data (i.e., $\Delta AIC_c < 2$; Tables 1 and 3). The model with the lowest AIC_c was the combination of native forest and human land use (i.e., F + U, hereafter the land-cover model), but it should be noticed that the difference in AIC_c between the native forest hypothesis (F) and the best combined model was only three (Table 3). The best model correctly classified 83.5% of the presences and pseudo-absences and yielded an AUC of 0.905, thus indicating good discrimination ability (Table C4).

In the human persecution group, all particular hypotheses yielded significant models but we did not find an overarching hypothesis such as native forest in the land-cover conditions group. Instead, the best model was obtained by the combination of the two general hypotheses (Tables 2 and 3, and C2). As expected, protected areas were positively related with jaguar presence while the frequency and proximity to roads and towns showed a negative effect. Human accessibility was selected for representing the direct effect of human presence on jaguars' occurrence. We found a higher support for the model that incorporated the interaction between protection and human access, showing that the influence of human accessibility changes according to the protection level (Table C2). Jaguars occurred in areas with low densities of rural population but both models (present and the last 30-year average) showed similar support (Table C2). Although the best human persecution model received less support than the best land-cover model (AIC_c of 215 vs. 183) it correctly classified 78% of the presences and pseudo-absences, and yielded AUC of 0.84, indicating good discrimination ability (Table C4).

The final models of each group were combined into one global model (details in Tables 3 and C3). In spite of its higher complexity, this model was selected as the most parsimonious model (lowest AIC_c), indicating that both groups of hypotheses (land-cover and human persecution) were important for predicting jaguar presence in this region. Cross validation showed that these models did not over-fit the data, and a similar validation success was obtained with the 10 alternative sets of presences and pseudo-absences (Table C4).

3.2. Two-dimensional habitat categorization

The final models of the land-cover and physical environment and human persecution groups defined our two-dimensional model (Figs. 3 and D1). The different categories of suitable habitat (i.e., low, medium and high suitability from Fig. C1) were used for increasing the resolution inside each habitat category of our two-dimensional model. This resulted in detailed maps of priority management actions for jaguars along the UPAF (marginal areas: Figs. D2 and D3; core areas: Figs. D4 and D5).

Core areas (suitable conditions predicted by both models) represented only 7.5% of the study area, and most of the region was covered by matrix (Fig. 3 and Table 4). The highest surface of core areas was located in Paraguay (42%), but the largest and more continuous core areas were located in the north part of the Argentinean region, including the Iguazu National Park in Brazil (Fig. 3). Sinklike and attractive sinklike areas occupied >25% of the study area. Attractive sinklike areas were more common surrounding the core areas in Argentina and Paraguay (Fig. 3 and Table 4).

Potential refuges were scarce along the study area and only present in few regions of Brazil and Paraguay (Fig. 3 and Table 4).

Analyzing the location of dead and removed jaguars in the Green Corridor showed that a higher proportion of animals were killed in sinklike and attractive sinklike areas than expected by the available area of these habitat categories (Fig. E1; Pearson's chi-squared test: $\chi^2 = 0.007$; $df = 2$; $p < 0.01$). Moreover, the relatively highest mortality of jaguars occurred in the attractive sinklike areas with the best land-cover conditions, supporting our hypothesis that these areas are ecological traps (Fig. E1).

3.3. Validating and improving conservation plans

We used the two-dimensional model for validating the conservation landscape designed by the Biodiversity Vision (Di Bitetti et al., 2003). We found that they detected most of the core areas that we described for jaguars (Table F1). However, 17% of Biodiversity Vision's core areas were attractive sinklike areas for jaguars and need protection. Additionally, our model detected two large areas in Brazil (Ivinhema State Park and Ilha Grande National Park) that could be incorporated as core areas (Fig. 3). More than 50% of the areas classified by the Biodiversity Vision as 'potential core areas' and as 'forested areas that need assessment' were classified by our model as core areas (Table F1). However, most of the areas classified by the Biodiversity Vision as 'high potential of becoming core areas' were classified by our model as attractive sinklike areas, which need more protection to constitute core areas. More than 30% of the 'corridors' were also classified as attractive sinklike areas and >20% as matrix, showing that many of these corridors may not be functional for jaguars (Table F1), demanding high efforts in protection and restoration to become so.

Based on our results we revised the existing Jaguar Conservation Units (JCU; Fig. 4; Sanderson et al., 2002b) and defined JCU as core areas with known reproductive populations (from Cullen et al., 2005; De Angelo, 2009; De Angelo et al., 2011b; McBride, 2009; Paviolo, 2010). We also included the surrounding core areas that were directly connected to or closer than 23 km from the reproductive populations (23 km was the maximum distance of a presence record to a core area). This procedure suggests a redefinition of the shape of the Misiones Green Corridor JCU, and the repositioning of the Upper Paraná – Paranapenama JCU according to the core areas. Our models suggest the incorporation of the Mbaracayú Biosphere Reserve and the surrounding areas as a third JCU in Paraguayan UPAF. The least-cost corridors proposed by Rabinowitz and Zeller (2010) were observed across many of the core areas of our model, showing the potential importance of the core areas as stepping stones in a regional and continental conservation strategy (Fig. 4). Their corridors also confirm the important role of the Mbaracayú area for regional and global connectivity among jaguar populations.

The least-cost areas that we detected across the core areas in our models offer other alternatives for connecting the JCUs in this region and exposed the important role of the core areas outside the JCU for an eco-regional jaguar conservation strategy (Fig. 4). Observing in more detail the habitat conditions in between the core areas (in the examples shown in Fig. 4), it is possible to use the two-dimensional model to prioritize the most urgent management actions needed for enlarging or connecting the core areas (e.g. the different strategies needed in the potential corridors in eastern Paraguay in Fig. 4C, and the need of increasing protection in the Green Corridor in Fig. 4D). However, in some areas like most of the Brazilian UPAF (Fig. 4B) and southern Paraguay (Fig. 3), the efforts needed for implementing corridors among core areas are higher and more challenging, demanding both protection and land-cover improvement for transforming the matrix into suitable

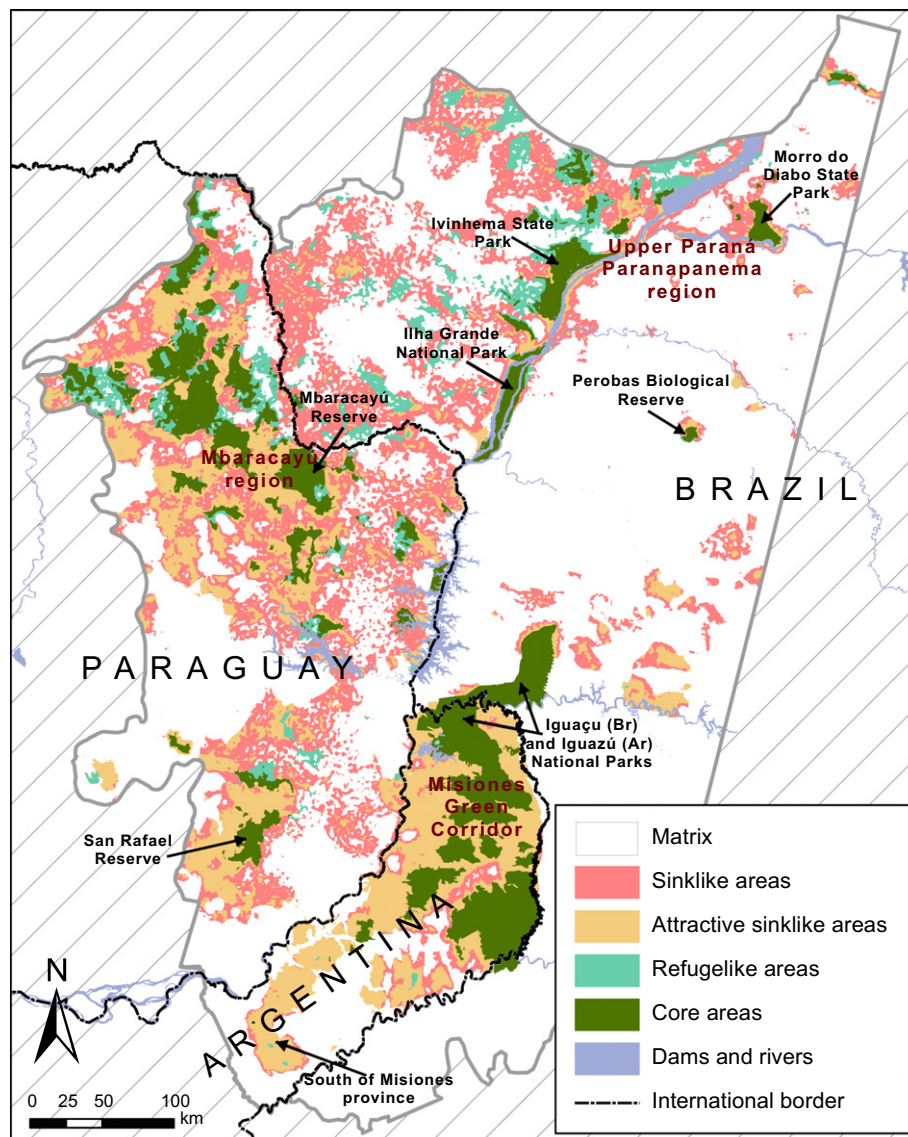


Fig. 3. Two-dimensional habitat model for predicting jaguar presence in the Upper Paraná Atlantic Forest and establishing priority management actions: protection/mitigation actions in the attractive sinklike areas and restoration or land-use planning in the refuge like areas (see details in Figs. D1–D5).

Table 4

Distribution of the different suitability and management habitat categories for jaguars along the three countries that share the Upper Paraná Atlantic Forest. These categories resulted from the two-dimensional combination of the main land-cover and human-persecution models. The percentages were calculated for each country (columns).

Habitat categories	Argentina (m ²)	Brazil (km ²)	Paraguay (km ²)	Total (km ²)
Lakes/cities	509 (1.7%)	4598 (2.9%)	1469 (1.7%)	6576 (2.4%)
Avoided matrix	8495 (28.4%)	120,551 (75.4%)	37,047 (42.5%)	166,092 (60.0%)
Sinklike	2040 (6.8%)	19,413 (12.1%)	20,280 (23.3%)	41,733 (15.1%)
Refugelike	85 (0.3%)	5381 (3.4%)	3743 (4.3%)	9209 (3.3%)
Attractive sinklike	11,534 (38.6%)	5065 (3.2%)	15,965 (18.3%)	32,563 (11.8%)
Core areas	7253 (24.2%)	4813 (3.0%)	8604 (9.9%)	20,670 (7.5%)
Total	29,916 (100%)	159,819 (100%)	87,108 (100%)	276,843 (100%)

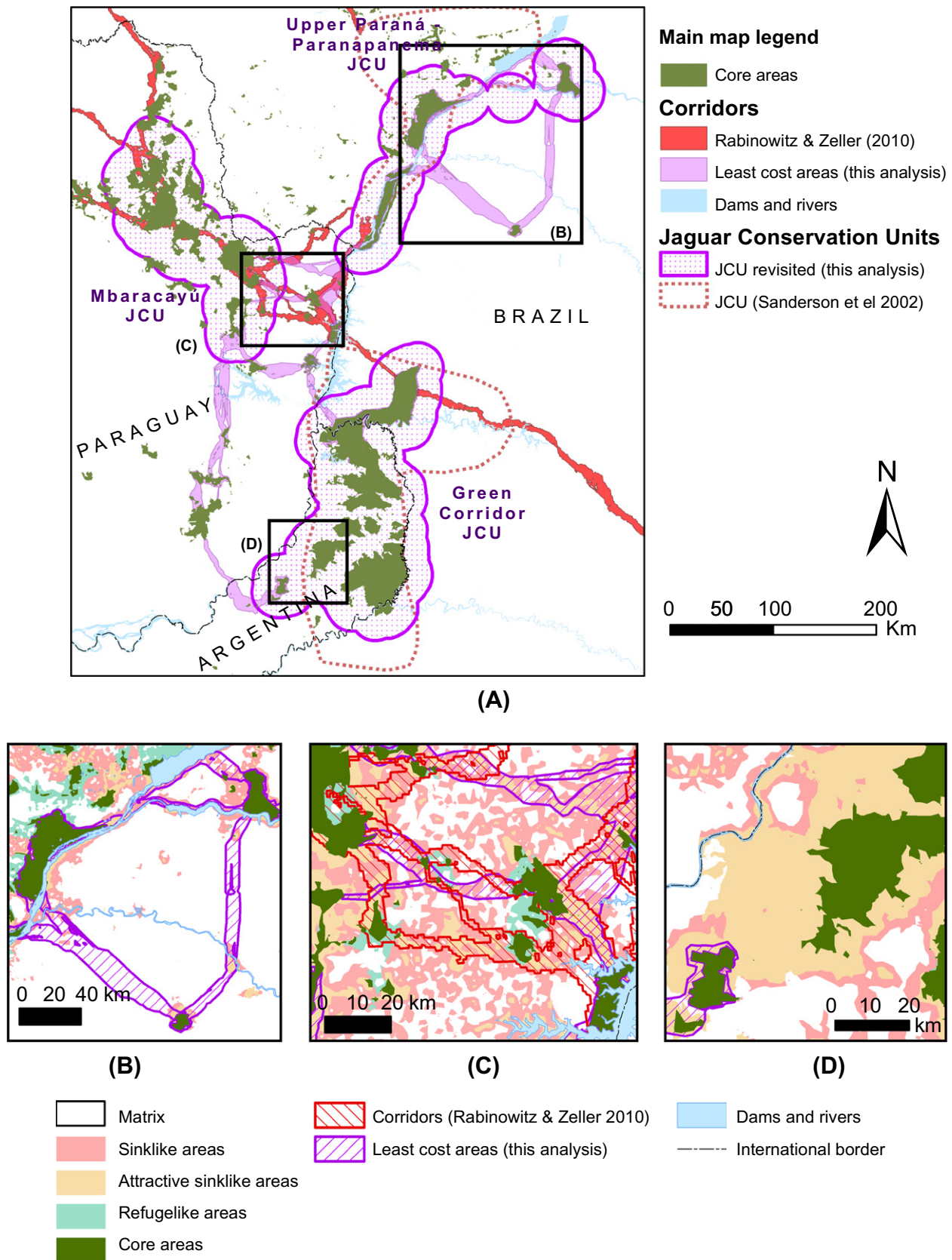


Fig. 4. Proposed redefinition of the Jaguar Conservation Units (JCUs revisited) and areas for evaluating corridors (least cost areas) for jaguar conservation in the Upper Paraná Atlantic Forest (A). Dashed lines indicate the original JCUs described by Sanderson et al. (2002b) and in red (dark gray) the corridors proposed by Rabinowitz and Zeller (2010) for connecting JCUs along the continent. The insets show examples of different areas of the JCUs and corridors, where the different habitat categories of the two-dimensional model may help to prioritize management actions: in attractive sinklike areas to increase protection is a priority, in refugelike areas land-cover restoration is the most important action; and in sinklike areas and matrix, both actions are necessary to create a corridor. (B) Possible areas for designing corridors among Morro do Diabo State Park, Ivinhema State Park and Perobas Reserve in Brazil; (C) possible corridors between Mbaracajú JCU and the core areas of the Paraná river in Paraguay; and (D) attractive sinklike areas separating core areas of the central and southern parts of the Green Corridor JCU in Argentina (see details in Figs. D1–D5).

habitat (see details in the priority actions recommended for different regions in [Appendix D](#)).

4. Discussion

4.1. Jaguar responses to habitat transformation

The Upper Paraná Atlantic Forest constituted a vast area covered by forest 200 years ago, where jaguars presumably had a continuous distribution ([De Angelo et al., 2011a](#)). Our results showed that jaguars were seriously affected by forest loss ([Fig. 3](#)), but their response was complex and affected not only by forest conditions but also by other factors related to landscape transformation and more direct human impacts ([Table 3](#)). A global model including both, land-cover conditions and human-persecution variables, received the highest support of our data, demonstrating the importance of considering these diverse aspects for jaguar conservation at a regional scale.

Not surprisingly, native forest cover and local forest connectivity are important for sustaining jaguars in the UPAF ([Tables 3 and C1](#)). Similar results were found in other regions of jaguar distribution ([Hatten et al., 2005](#); [Ortega-Huerta and Medley, 1999](#); [Somma, 2006](#)). However, a significant advance in our understanding of jaguar ecology is the importance of past forest conditions for predicting current jaguar presence ([Tables 3 and C1](#)). [Tilman et al. \(1994\)](#) found that habitat loss and fragmentation not only have immediate effects on biodiversity but also produce a series of time-delayed extinctions (i.e., the extinction debt). Clearly, such effects may be more common in species with long generations, such as large carnivores, where a few individuals can survive in isolated fragments for 10 years or more before the species becomes locally extinct. However, landscape or forest history is rarely included in habitat suitability models ([Guisan and Zimmermann, 2000](#)) and, to the best of our knowledge, it has not been considered previously for jaguars or other large carnivores' habitat models.

Considering past forest conditions allowed us to understand why jaguars were found in small and isolated fragments in eastern Paraguay while no jaguars persist in the relatively larger forest fragments of southern Misiones in Argentina ([Fig. 3](#)) ([De Angelo et al., 2011b](#)). Most of the jaguars found in the small fragments of eastern Paraguay may be survivors of recent deforestation but probably do not constitute viable subpopulations. Southern Misiones was the most developed area of this province 30 years ago, but many of these areas were abandoned and the forest has partially recovered ([Izquierdo et al., 2008](#)). However, the ecological characteristics of these secondary forests are probably different ([Metzger et al., 2009](#)) and may not sustain jaguars, or jaguars could not recolonize these areas because high human pressures are still persist ([Figs. 3 and D3](#)).

The physical characteristics of the landscape had a relatively low importance in predicting jaguar presence ([Tables 3 and C1](#)), probably due to the wide range of ecological conditions that jaguars can tolerate. In fact, jaguars had a continuous distribution along this area in the past ([Sanderson et al., 2002b](#)). Human land uses were more important than physical environment in predicting jaguar presence ([Table 3](#)). The local (1-km) effect of intensive agriculture is possibly associated with the severe transformation of the landscape (complete removal of forest) but with relatively low human presence reducing its impact in the neighborhood. Farms and pastures are also related with a reduction of the forest-cover but they had a larger impact in the surroundings (4-km radius; [Table C1](#)); a fact that can be associated with higher human presence producing more disturbances in the neighboring forested areas. Presence of cattle can also be important to explain the impact of these land uses due to the potential jaguar-cattle conflict

([Rosas-Rosas et al., 2010](#)). However, our regional scale analysis did not include detailed information about cattle abundance and management, and therefore our conclusions regarding this issue are limited.

Jaguars persist more frequently in inaccessible or protected areas with historically low human density ([Tables 3 and C2](#)). The variable accessibility (*access_cost*) was a useful way of representing direct human pressure, with better support than simpler measurements such as distance to roads or towns ([Table C2](#)). The access of humans to wild areas is associated with many different direct impacts, like poaching ([Kerley et al., 2002](#); [Nielsen et al., 2004](#)) and forest exploitation ([Chomitz and Gray, 1996](#)). Additionally, access ways can become an important threat to wild populations through road kills ([Kerley et al., 2002](#); [Kramer Schadt et al., 2004](#)). Protection reduces poaching pressure directly, but it can also be important in reducing other direct human impacts such as forest exploitation and transit of humans ([Bruner et al., 2001](#)). Large carnivores often use trails and roads for their movement in wild areas ([Kerley et al., 2002](#); [Noss et al., 1996](#)) and this behavior was also described for jaguars in the UPAF ([Cullen, 2006](#); [Paviolo, 2010](#)). This may explain why the effect of access is lower inside protected areas ([Tables 3, C2 and C3](#)), where jaguars may use the access ways more often than in unprotected areas.

Our one-dimensional habitat models are useful for assessing the distribution of the remaining potential habitat for jaguars and predicting unsurveyed areas where jaguars could be present ([Fig. C1](#)). On the other hand, our two-dimensional approach allowed for a more subtle assessment of multidimensional habitat suitability, to detect areas where different management relevant key factors were conflicting and to prioritize management actions ([Figs. 3 and 4, D1–D5](#)) ([Naves et al., 2003](#)). However, our models have some limitations. First, because they were explicitly constructed for a regional analysis, we could not include some important issues of local jaguar habitat selection (e.g. influence of different types of forest, a wider range in protection categories, or the relative impact of different cattle management; [Azevedo and Murray, 2007](#); [Conde et al., 2010](#); [Cullen, 2006](#)). Second, an analysis at finer scales or with other objectives would require different hypotheses for the two main dimensions. For example, one could include additional human land-uses (e.g. pastures with different management of cattle or diverse human activities in the small farms) in the jaguar persecution group to consider the potential jaguar-ranchers conflict. Finally, although our models showed a good performance and we could validate the sinklike areas, it is important to recognize that we used only presence records for model construction, instead of reproduction ([Naves et al., 2003](#)), mortality ([Nielsen et al., 2006](#)), or prey data ([Kanagaraj et al., 2011](#)). Collecting such data would be important for future habitat modeling of this species.

4.2. Recommendations for jaguar conservation

The population of jaguars of the UPAF now constitutes a highly spatially structured population ([Elmhagen and Angerbjörn, 2001](#)), divided into several core areas, many of them completely isolated by matrix or surrounded by attractive sinklike areas ([Figs. 3 and 4](#); [Table 4](#)). Less than 10% of the study area constitutes suitable habitat for jaguars and the internal structure of these areas indicates that many of them are probably under high pressure mainly due to human persecution ([Figs. C1 and D5](#)).

The Brazilian core areas are completely isolated by avoided matrix ([Figs. 3 and 4](#)); consequently, high efforts of active management are needed for restoring the connectivity among them and reducing the harmful effect of their isolation ([Haag et al., 2010](#)). Although some restoration initiatives exist along the Parana river, higher efforts are needed to ensure structural connectivity among

the core areas, as well as survival of migrant individuals (Cullen, 2006) (Fig. 4).

In Paraguay only a few core areas are effectively protected and many of them are recently fragmented areas with an extinction debt (Figs. 3 and D5) (De Angelo et al., 2011b). Although the core areas of Paraguay showed higher connectivity through marginal habitat than the Brazilian areas, many of these marginal areas are sinklike or attractive sinklike areas with high potential of being ecological traps for jaguars (Figs. 3 and 4 and D3). Even though several areas still hold jaguars and there is a potential for connectivity among them, jaguars in Paraguay are threatened by land-cover transformation and direct human persecution, and only few areas are known to have potential source populations (Fig. 4).

In the Green Corridor shared by Argentina and Brazil, most of the landscape constitutes attractive sinklike areas where jaguars may occur because the landscape offers good structural conditions (i.e., forest), but with a high risk of being killed by poachers or ranchers (Figs. 3 and 4 and D3). Extremely high mortality rates have been detected for jaguars in the surroundings of the Iguazú and Iguacu National Parks in Argentina and Brazil respectively (Crawshaw, 2002; Crawshaw et al., 2004; Paviolo et al., 2008). This high mortality, extended along the large proportion of the Green Corridor with attractive sinklike areas, can explain the recent population crash suffered by jaguars in this region (Paviolo et al., 2008) and the absence of jaguars in the forest fragments of the southern part of Misiones Province (De Angelo et al., 2011b) (Figs. 3 and 4). Reducing direct jaguar persecution and poaching of its prey are the most urgent actions needed to regionally preserve this species in the Green Corridor. Our model helps to identify areas where these actions will have the highest impact in reducing jaguar mortality and maintaining connectivity (e.g. see Fig. 4C and areas categorized as AS3-M in Fig. D3). For this reason, this model was used to construct the Conservation Landscape in the Action Plan for Jaguar Conservation in the Green Corridor (Schiaffino et al., 2011), approved by the National Parks Administration of Argentina in 2012.

5. Conclusions

Our modeling approach allowed us to understand that habitat destruction for jaguars implicates not only forest loss but also many different anthropogenic interventions on the landscape, including those that occurred in the past. Additionally, this approach was useful for validating and improving conservation strategies for this species and the Atlantic Forest landscape, and serves as input for an adaptive management conservation plan for both (Sanderson et al., 2002c). To include management criteria for selecting different dimensions for habitat modeling represents a novel approach for modeling the distribution of endangered species, and it has the main advantage of maintaining a direct link to landscape management and species conservation options.

Using the density estimates of jaguars along the UPAF, we calculated a mean density of 1 ind/100 km² (Cullen, 2006; Paviolo, 2010; Paviolo et al., 2008). Extrapolating this value to the total surface covered by core areas in our study area (around 20,000 km²) the total population of jaguars is about 200 adult individuals in the whole eco-region (Di Bitetti et al., 2006). These individuals are distributed along different patches, many of them isolated from the others (Figs. 3 and 4). This reinforces the need of diminishing direct threats and habitat loss in each of these patches, increasing the size of the core areas through reducing human persecution (Fig. 3), and maintaining or restoring connectivity among them via land-use planning and land-cover restoration (Fig. 4). A coordinated effort among the three countries would be essential to preserve the jaguars of the UPAF (Fig. 4), by maintaining a meta-population dynamic among the jaguar core areas not only of the

proposed JCU but including all the core areas of the eco-region (Di Bitetti et al., 2006).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.12.021>. These data include Google maps of the most important areas described in this article.

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Appendix. Supplementary data

Supplementary online data of De Angelo et al.: *Understanding species persistence for defining conservation actions: a management landscape for jaguars in the Atlantic Forest*

Appendix A. Rules for pseudo-absences generation.

Fig. A1. Distribution of pseudo-absences and rules for their generation.

Appendix B. Variables

B1. Variables used for describing the hypotheses and generating the models

Table B1. Description of variables.

Table B2. Tests for the selected records.

Appendix C. Models

C.1. Variable reduction procedure.

C.2. Models evaluation and habitat suitability categories.

Tables C1 and C2. Model selection for particular hypotheses.

Table C3. Description of the final models.

Fig. C1. One-dimensional habitat suitability maps of the final models.

Table C4. Evaluation of the final models.

Appendix D. Categories and sub-categories of habitat in the two-dimensional model.

Fig. D1. Presences and pseudo-absences distribution along the two dimensions of habitat.

Fig. D2. Presences and pseudo-absences distribution along the sub-categories of habitat inside the marginal habitats.

Fig. D3. Sub-categories of habitat inside the marginal habitats.

Fig. D4. Presences and pseudo-absences distribution along the sub-categories of habitats inside the core areas.

Fig. D5. Sub-categories of habitats inside the core areas.

Appendix E. Distribution of killed jaguars along the categories of habitat.

Fig. E1. Observed and expected proportion of killed jaguars in the categories of habitat

Appendix F. Validation of the Biodiversity Vision of the UPAF.

Table F1. Validation of the Biodiversity Vision of the UPAF.

Appendix A. Details on the rules for pseudo-absences generation

To obtain a binomial response variable we generated pseudo-absences randomly within the study area, but following several rules (Fig. A1). First, the probability of occurrence of pseudo-absences was weighted by a habitat suitability index based on the presence-only habitat suitability map developed for jaguars in the UPAF by De Angelo et al. (2011a). This resulted in a higher proportion of pseudo-absences located in unsuitable areas compared with suitable areas (Chefaoui and Lobo 2008; Engler et al. 2004; Hengl et al. 2009; Titeux 2006). Second, pseudo-absences were generated only in areas identified in previous analysis as unsuitable or marginal habitats for jaguars (De Angelo et al. 2011a). This rule avoids location of pseudo-absences in areas expected to be suitable for jaguars (Chefaoui and Lobo 2008). Third, we generated pseudo-absences only inside the area surveyed by the participatory monitoring where presence data was collected (De Angelo et al. 2011b), ensuring that pseudo-absences occurred only in areas that were surveyed (Mateo et al. 2010; Phillips et al. 2009). This rule also prevents that pseudo-absences occur by chance only in remote areas that may show, due to their large geographical distance, habitat conditions that differ from what is jaguar habitat (VanDerWal et al. 2009). Finally, we generated the same number of pseudo-absences as presences (n=106; Engler et al. 2004; Kanagaraj et al. 2011; Liu et al. 2005) following the same rule used for stratifying presence records (no more than one pseudo-absence per each 12×12 -km grid cell; Kanagaraj et al. 2011). Additionally, we generated 10 further sets of pseudo-absences for model validation. For pseudo-absence generation we used the Sampling Tools of Hawth's Analysis Tools (Beyer 2004).

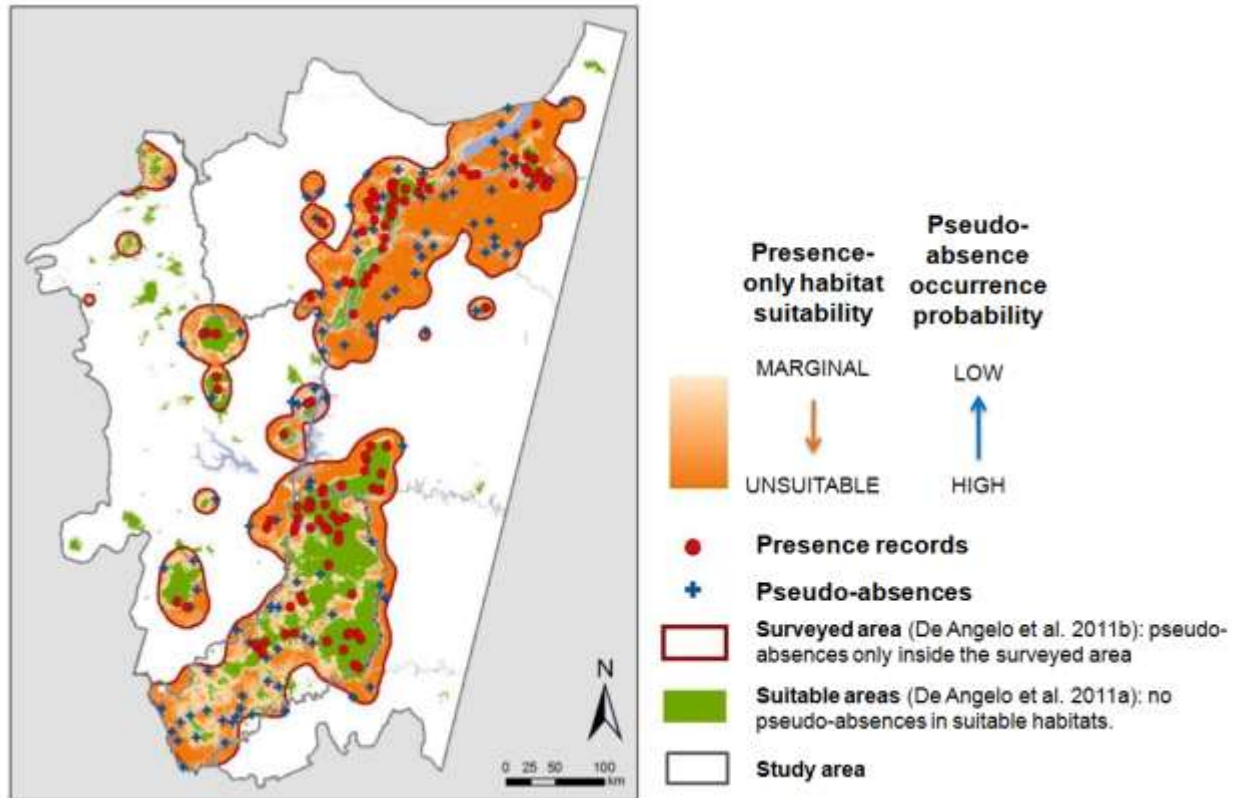


Fig. A1. Distribution of presence and pseudo-absences used for data analysis. This figure illustrates the rules used for pseudo-absence random generation.

Appendix B. Variables

B.1. Variables construction

To describe the land-cover and physical characteristics of the landscape, and the human persecution of jaguar and their prey, for representing the different hypotheses, we constructed a total of $9 + 4 \times 10 = 49$ variables with a spatial resolution of $330 \text{ m} \times 330 \text{ m}$ as it is described in the main text and in Table B1. The local connectivity for radii of 1 km (*connect_r1*) was discarded because it redundancy with *forest_r1*. The maps used as base map for variables construction were obtained from the UPAF-GIS database compiled by Di Bitetti et al. (2003) and De Angelo (2009). The land-use map for our analysis was developed by De Angelo (2009) using a mosaic of Landsat-5 TM satellite images from 2004 and a maximum likelihood supervised classification into seven land-uses categories (water, native forest and marshlands, pine plantation, intensive agriculture, small farms with mixed land uses, pastures, and urban areas). This analysis was based on the variables used by De Angelo et al. (2011a). All these analyses were developed with ENVI software Version 4.2 (Research Systems, Inc. 2005, USA), Spatial Analyst for ArcMap 9 (ESRI Inc. 2004) and Hawth's Analysis Tools (Beyer 2004).

Table B1. Description of independent variables used for describing land-cover and physical characteristics of the landscape, and the human persecution of jaguars and their prey in the Upper Paraná Atlantic Forest (see details in De Angelo 2009; and De Angelo et al. 2011a). Nine variables describe the average conditions within each cell while the other ten represent neighbourhood variables (r) that were calculated at four different neighbourhood scales of radius $r = 1, 4, 7$ and 10 km.

Name	Description
access_cost	Accessibility cost measured as the hours needed to access the focal cell from the nearest town or city (De Angelo et al. 2011a; Farrow and Nelson 2001).
connect_r	Frequency of cells occupied by native forest in a ring of radius r and 1-km wide (3 cells) around the focal cell. This represents an index of local connectivity of forest around the focal cell (Naves et al. 2003; Schadt et al. 2002; Wiegand and Moloney 2004).
Elevation	Elevation above sea level of the focal cell (from http://seamless.usgs.gov).
farms_r	Frequency of cells occupied by small farms in a circle of radius r around the focal cell.
forest_r	Frequency of cells occupied by native forest in a circle of radius r around the focal cell.
forest73_r	Frequency of cells occupied by native forest in 1973 in a circle of radius r around the focal cell.
int_agr_r	Frequency of cells occupied by intensive agriculture in a circle of radius r around the focal cell.
pastures_r	Frequency of cells occupied by extensive pastures in a circle radius r around the focal cell.
plantat_r	Frequency of cells occupied by pine plantations in a circle of radius r around the focal cell.
population_2000	Rural population density obtained from the most recent national census (Brazil 2000, Paraguay 2002 and Argentina 2001). This map was constructed using local census units (municipalities in Brazil, districts in Paraguay and Departments in Argentina), and translated to a 10-km grid of points that was used for interpolating rural population values along the entire area with a smoothed effect (Carroll and Miquelle 2006; De Angelo 2009)
population_hist	Mean historical rural population density. This map was constructed by the average of rural population density maps from 1970, 1980, 1990 and 2000 built by the same method as population_2000 (De Angelo 2009).
protect_cat	Categorical classification of relative protection levels: 0 = unprotected; 1 = intermediate protection (e.g. private and biosphere reserves); 2 = high protection (e.g. national and provincial parks).
rivers_d	Straight line distance to the closest river.
rivers_r	Frequency of cells occupied by rivers in a circle of radius r around the focal cell.
roads_d	Straight line distance to the closest road (including paved and dirt roads).
roads_r	Frequency of cells occupied by roads (including paved and dirt roads) in a circle of radius r around the focal cell.
slope	Terrain slope expressed in percentage.
towns_d	Straight line distance to the closest town or city.
towns_r	Frequency of cells occupied by towns or cities in a circle of radius r around the focal cell.

81 **Table B2.** Comparisons between the 106 presence records selected for the analysis and each of the other 10 random subsets of 106 records resampled from
82 the total 974 presence registers. For each subset, the statistic of the Mann-Whitney U test and the corresponding p value is reported for all the independent
83 variables used in the analysis. In the case of the categories of the protected areas, a Pearson's Chi square test was used. NA indicates that this variable was
84 not used in the analysis. None of the subsets showed significant differences for any of the variables.

	Subset 1		Subset 2		Subset 3		Subset 4		Subset 5		Subset 6		Subset 7		Subset 8		Subset 9		Subset 10	
Variable	U	p	U	p	U	p	U	p	U	p	U	p	U	p	U	p	U	p	U	p
<i>acces_cost</i>	5593	0.955	5554	0.887	5443	0.695	5802	0.682	5621	0.996	5492	0.778	5390	0.611	5667	0.914	5529	0.842	5557	0.891
<i>connect_r01</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>connect_r04</i>	5725	0.812	5700	0.856	5665	0.918	5908	0.517	5901	0.527	5535	0.853	5717	0.826	5757	0.756	5647	0.949	5705	0.847
<i>connect_r07</i>	5678	0.895	5605	0.977	5557	0.891	5734	0.797	5644	0.955	5629	0.982	5677	0.897	5666	0.916	5626	0.987	5607	0.981
<i>connect_r10</i>	5585	0.941	5563	0.903	5663	0.921	5698	0.859	5571	0.916	5673	0.904	5608	0.982	5678	0.895	5593	0.955	5613	0.991
<i>elevation</i>	5512	0.813	5604	0.976	5507	0.805	5614	0.994	5602	0.971	5457	0.718	5534	0.852	5585	0.942	5540	0.862	5576	0.926
<i>farms_r01</i>	5686	0.872	5846	0.584	5823	0.623	5680	0.884	5743	0.767	5656	0.930	5897	0.503	5480	0.743	5785	0.691	5750	0.753
<i>farms_r04</i>	5581	0.934	5606	0.979	5658	0.929	5404	0.632	5429	0.672	5722	0.816	5635	0.970	5413	0.646	5665	0.917	5575	0.923
<i>farms_r07</i>	5560	0.898	5608	0.982	5670	0.908	5405	0.633	5577	0.927	5686	0.881	5617	0.998	5538	0.859	5700	0.856	5642	0.959
<i>farms_r10</i>	5563	0.903	5624	0.990	5639	0.964	5399	0.624	5555	0.888	5683	0.885	5605	0.977	5562	0.901	5635	0.971	5594	0.957
<i>forest_r01</i>	5466	0.728	5517	0.818	5595	0.958	5644	0.954	5634	0.972	5504	0.795	5349	0.540	5673	0.901	5454	0.709	5542	0.863
<i>forest_r04</i>	5535	0.853	5643	0.956	5575	0.923	5783	0.713	5708	0.841	5471	0.743	5616	0.996	5716	0.828	5591	0.952	5631	0.979
<i>forest_r07</i>	5664	0.919	5637	0.968	5589	0.949	5822	0.649	5732	0.800	5538	0.858	5646	0.952	5733	0.799	5644	0.954	5660	0.927
<i>forest_r10</i>	5645	0.954	5607	0.981	5583	0.938	5770	0.734	5667	0.914	5551	0.882	5640	0.962	5698	0.859	5601	0.971	5639	0.964
<i>forest73_r01</i>	5684	0.883	5545	0.871	5371	0.579	5634	0.972	5629	0.982	5405	0.633	5496	0.784	5658	0.907	5585	0.941	5615	0.996
<i>forest73_r04</i>	5602	0.971	5604	0.976	5527	0.839	5796	0.690	5633	0.975	5552	0.882	5707	0.843	5717	0.826	5717	0.826	5590	0.951
<i>forest73_07</i>	5686	0.881	5656	0.933	5581	0.935	5838	0.623	5650	0.945	5618	1.000	5676	0.898	5702	0.853	5735	0.794	5619	1.000
<i>forest73_10</i>	5692	0.870	5655	0.935	5577	0.927	5779	0.720	5640	0.962	5569	0.913	5632	0.976	5631	0.979	5670	0.908	5605	0.977
<i>int_agr_r01</i>	5573	0.901	5334	0.438	5464	0.669	5495	0.732	5586	0.928	5643	0.946	5600	0.961	5488	0.718	5451	0.643	5394	0.537
<i>int_agr_r04</i>	5625	0.989	5386	0.601	5611	0.987	5543	0.865	5490	0.774	5734	0.795	5586	0.943	5536	0.854	5501	0.792	5474	0.746
<i>int_agr_r07</i>	5466	0.734	5361	0.565	5599	0.967	5503	0.798	5469	0.738	5675	0.900	5526	0.837	5584	0.940	5546	0.873	5505	0.801
<i>int_agr_r10</i>	5559	0.896	5459	0.722	5658	0.930	5523	0.832	5622	0.994	5607	0.981	5519	0.825	5561	0.898	5597	0.962	5591	0.952
<i>pastures_r01</i>	5646	0.930	5749	0.673	5760	0.647	5549	0.829	5707	0.776	5617	0.997	5773	0.617	5680	0.845	5728	0.725	5653	0.912
<i>pastures_r04</i>	5597	0.962	5716	0.822	5799	0.677	5513	0.810	5562	0.897	5759	0.746	5628	0.983	5571	0.915	5750	0.761	5725	0.806
<i>pastures_r07</i>	5561	0.898	5649	0.945	5741	0.783	5371	0.579	5546	0.872	5657	0.931	5496	0.784	5447	0.701	5637	0.967	5570	0.914

	Subset 1		Subset 2		Subset 3		Subset 4		Subset 5		Subset 6		Subset 7		Subset 8		Subset 9		Subset 10	
Variable	U	p	U	p	U	p	U	p	U	p	U	p	U	p	U	p	U	p	U	p
<i>pastures_r10</i>	5613	0.992	5673	0.903	5712	0.835	5502	0.796	5592	0.954	5684	0.883	5562	0.901	5575	0.923	5634	0.973	5640	0.962
<i>plantat_r01</i>	5673	0.771	5561	0.776	5561	0.776	5460	0.453	5510	0.599	5672	0.773	5618	1.000	5622	0.988	5618	1.000	5622	0.988
<i>plantat_r04</i>	5674	0.852	5608	0.973	5612	0.984	5601	0.955	5563	0.855	5663	0.882	5651	0.912	5505	0.712	5647	0.923	5518	0.743
<i>plantat_r07</i>	5646	0.935	5592	0.940	5653	0.919	5643	0.942	5631	0.970	5658	0.907	5656	0.911	5589	0.931	5727	0.742	5610	0.982
<i>plantat_r10</i>	5584	0.924	5570	0.892	5535	0.816	5568	0.887	5611	0.984	5572	0.897	5531	0.806	5562	0.875	5596	0.950	5573	0.900
<i>pop_2000</i>	5639	0.964	5623	0.992	5614	0.993	5574	0.922	5618	1.000	5633	0.975	5620	0.997	5579	0.930	5588	0.946	5642	0.958
<i>pop_hist</i>	5618	1.000	5615	0.996	5644	0.955	5614	0.994	5585	0.941	5674	0.901	5665	0.918	5637	0.968	5619	1.000	5697	0.861
<i>rivers_d</i>	5545	0.871	5582	0.937	5555	0.888	5625	0.988	5532	0.847	5480	0.758	5572	0.919	5531	0.846	5533	0.849	5525	0.835
<i>rivers_r01</i>	5732	0.772	5740	0.756	5721	0.793	5810	0.624	5818	0.608	5746	0.744	5921	0.435	5821	0.603	5753	0.734	5812	0.620
<i>rivers_r04</i>	5672	0.904	5709	0.838	5714	0.829	5582	0.936	5640	0.961	5762	0.746	5663	0.920	5734	0.794	5680	0.889	5597	0.962
<i>rivers_r07</i>	5703	0.850	5785	0.709	5681	0.890	5592	0.954	5666	0.915	5749	0.770	5750	0.768	5780	0.718	5641	0.960	5720	0.820
<i>rivers_r10</i>	5825	0.645	5826	0.642	5704	0.849	5673	0.903	5776	0.725	5735	0.795	5803	0.679	5837	0.625	5661	0.925	5785	0.710
<i>roads_d</i>	5590	0.951	5662	0.922	5522	0.831	5710	0.838	5659	0.928	5410	0.642	5510	0.810	5731	0.802	5530	0.844	5665	0.917
<i>roads_r01</i>	5601	0.956	5682	0.833	5551	0.829	5467	0.631	5611	0.982	5710	0.759	5707	0.768	5534	0.785	5715	0.748	5652	0.913
<i>roads_r04</i>	5638	0.962	5495	0.764	5717	0.807	5560	0.887	5607	0.979	5695	0.851	5600	0.966	5530	0.830	5699	0.843	5560	0.886
<i>roads_r07</i>	5722	0.815	5526	0.836	5890	0.537	5533	0.848	5637	0.967	5752	0.763	5758	0.752	5687	0.877	5619	1.000	5565	0.905
<i>roads_r10</i>	5709	0.839	5574	0.921	5746	0.775	5571	0.916	5681	0.888	5755	0.760	5686	0.881	5671	0.907	5605	0.978	5626	0.987
<i>slope</i>	5441	0.692	5535	0.853	5618	1.000	5606	0.979	5611	0.988	5540	0.861	5491	0.776	5585	0.941	5634	0.972	5592	0.954
<i>towns_d</i>	5538	0.858	5646	0.951	5665	0.918	5785	0.709	5578	0.930	5645	0.953	5522	0.831	5714	0.831	5795	0.693	5574	0.922
<i>towns_r01</i>	5618	1.000	5618	1.000	5618	1.000	5618	1.000	5618	1.000	5618	1.000	5618	1.000	5618	1.000	5618	1.000	5618	1.000
<i>towns_r04</i>	5670	0.808	5619	1.000	5721	0.618	5614	0.987	5618	1.000	5619	1.000	5618	1.000	5669	0.810	5518	0.660	5669	0.810
<i>towns_r07</i>	5690	0.826	5786	0.601	5684	0.841	5534	0.802	5728	0.735	5535	0.803	5557	0.856	5643	0.942	5438	0.593	5696	0.810
<i>towns_r10</i>	5618	1.000	5563	0.888	5554	0.868	5318	0.443	5588	0.938	5425	0.620	5560	0.880	5341	0.478	5363	0.514	5629	0.978
	<i>Chi-sq</i>	<i>p</i>	<i>Chi-sq</i>	<i>p</i>	<i>Chi-sq</i>	<i>p</i>	<i>Chi-sq</i>	<i>p</i>	<i>Chi-sq</i>	<i>p</i>	<i>Chi-sq</i>	<i>p</i>	<i>Chi-sq</i>	<i>p</i>	<i>Chi-sq</i>	<i>p</i>	<i>Chi-sq</i>	<i>p</i>	<i>Chi-sq</i>	<i>p</i>
<i>protect_cat</i>	0.115	0.944	0.467	0.792	0.066	0.967	0.312	0.856	0.000	1.000	0.066	0.967	0.022	0.989	0.062	0.970	0.340	0.844	0.095	0.954

Appendix C. Models

C.1. Variable reduction procedure

We selected the variables for representing each hypothesis using the available knowledge about the biology of jaguars (see details in the Table 1 and 2) (Burnham and Anderson 2002; Zuur et al. 2010; Zuur et al. 2009). To avoid problems with multicollinearity in the models and model selection process (Burnham and Anderson 2002; Zuur et al. 2010), we calculated Spearman's rank correlation coefficients among the variables. When two or more variables proposed for one hypothesis showed high collinearity ($r > 0.7$), we retained the variable that better reflects the hypothesis represented by this model. For those variables that we had not a biological criterion for their selection, we used a Mann-Whitney U test to observe the differences between presences and pseudo-absences, and we removed the variable that showed the lowest univariate difference from among high-correlated variables. The variable reduction procedure was applied also to combinations of models where a combination was only allowed if the variables were just weakly correlated (i.e., $r < 0.7$).

C.2. Models evaluation and habitat suitability categories

We evaluated the final and the global models by the area under the receiver operating characteristic curve (AUC; Guisan and Zimmermann 2000), and the percentage of correctly predicted presences (sensitivity) and pseudo-absences (specificity) using a 0.5 threshold based on the prevalence approach (Liu et al. 2005). Additionally, we included a presence-only evaluation method, the continuous Boyce index (Hirzel et al. 2006) using Biomapper software version 4.07.303 (Hirzel et al. 2008). In order to evaluate overfitting of models, we conducted a cross validation (Fernández et al. 2003; Kanagaraj et al. 2011). To this end we randomly partitioned the presence and pseudo-absence data into ten folds, and we used nine of them for model fitting and the remaining one for model evaluation. We repeated this

procedure 10 times and we observed the average sensitivity and specificity of each of the final models and the global model. Additionally, we used the 10 subsets of 106 presence records and the 10 sets of 106 pseudo-absences that were not used in the analysis (see the main text) for evaluating the prediction capacity of the models.

To transform the final and global models into habitat suitability maps, we used the logistic model equation (Burnham and Anderson 2002). We combined the maps representing each variable of the model with the Map Calculator of ArcGIS Spatial Analyst. The resultant maps that represent the relative probability of jaguar presence were transformed into categories of habitat quality following Naves et al. (2003) and Hirzel et al. (2006). Areas with values where $\leq 5\%$ of the presence records occurred were categorized as matrix (Naves et al. 2003). Marginal habitat was defined as the area with $>5\%$ of the presence records until the value from which more presence records occurred than expected by chance (Hirzel et al. 2006). Areas above this value were categorized as suitable habitat which was then subdivided into three suitability categories (low, medium and high suitability) using the changes in the slope of the curve of the continuous Boyce index as described by Hirzel et al. (2006).

Table C1. Evaluation of hypotheses and selection of models for the particular hypotheses representing land-cover and physical conditions of the landscape. Only the selected models for each particular hypothesis are shown; the best model is in bold type.

General hypotheses	Particular hypotheses	Variables in the final model (+ or - effect)	Wald's χ^2	df	<i>p</i>	D ² _{adj}	AIC _c	ΔAIC _c	w _r (%)
Null model	Null model	intersection	0.0	-	-	-	295.9		
Native forest (F)	F1) Amount of forest	forest_r7 (+)	97.1	1	<0.001	0.33	200.9	15.2	0.0
	F2) Local connectivity	connect_r7 (+)	77.9	1	<0.001	0.26	220.1	34.4	0.0
	F3) Amount and connectivity	forest_r1 (+), connect_r7 (+)	103.9	2	<0.001	0.35	196.2	10.5	0.5
	F4) Forest history	forest73_r7(+), forest73_r7 ² (-), forest73_r7 ³ (+)	67.3	3	<0.001	0.22	234.8	49.1	0.0
	F5) Combination	forest_r1(+), connect_r7(+), forest73_r7(+), forest73_r7² (-), forest73_r7³(+)	120.7	5	<0.001	0.39	185.6	0.0	99.4
Physical environment (PE)	PE1) Rivers	rivers_r4(+)	11.4	1	0.001	0.03	286.6	0.0	87.6
	PE2) Elevation	elevation (n.s.)	0.3	1	0.583	0.00	297.7	11.1	0.3
	PE3) Slope	slope (n.s.)	0.0	1	0.838	0.00	297.9	11.4	0.3
	PE4) Combinations	elevation (n.s.), slope (n.s.), rivers_r4 (+)	11.5	3	0.009	0.03	290.6	4.0	11.8
Human land uses (U)	U1a) Intensive agriculture	int_agr_r1(-)	19.4	1	<0.001	0.06	278.6	85.8	0.0
	U1a) Farms	farms_r4 (-)	71.0	1	<0.001	0.24	227.0	34.2	0.0
	U1a) Pastures	pastures_r4 (-)	30.4	1	<0.001	0.10	267.5	74.7	0.0
	U1a) Plantations	plant_r10 (-), plant_r10 ² (+)	18.1	2	<0.001	0.05	281.9	89.1	0.0
	U2) Combinations	int_agr_r1(-), farms_r4 (-), pastures_r4 (-)	108.3	3	<0.001	0.37	192.8	0.0	100.0

Notes: Variable abbreviations are from Table B1; D²_{adj} is adjusted explained deviance; AIC_c is bias-corrected Akaike's Information Criterion for fitted models; ΔAIC_c is (AIC_c)I – (AIC_c)min; w_r is the AIC_c weights expressed in percentages; (+) or (–) indicates the direction of the effect of the variable or the variable components for predicting jaguar presence, * indicates interaction between variables; superscripts numbers indicate quadratic or cubic adjustments; _r followed by 1,4,7 or 10 indicates the variable calculated for 1-, 4-, 7- or 10-km radius respectively.

Table C2. Evaluation of hypotheses and selection of models for the particular hypotheses representing human persecution of jaguars and their prey. Only the selected models for each particular hypothesis are shown; the best model is in bold type.

General hypotheses	Particular hypotheses	Variables in the final model (+ or - effect)	Wald's χ^2	df	<i>p</i>	D^2_{adj}	AIC_c	Δ_{AIC_c}	w_r (%)
Null model	Null model	intersection	0.0	-	-	-	295.9		
Protection and human access (PA)	PA1) Protection	protect_cat0 (+), protect_cat1 (+), protect_cat0 (+)	62.6	2	<0.001	0.21	237.4	11.9	33.2
	PA2) Access cost	access_cost (+)	37.9	1	<0.001	0.12	260.0	34.4	0.0
	PA3) Protection and access cost	protect_cat0 × access_cost (+), protect_cat1 × access_cost (+), protect_cat2 × access_cost (+)	76.5	3	<0.001	0.25	225.6	0.0	66.8
Population density (RP)	RP1) Present	population_2000 (-)	21.2	1	<0.001	0.07	276.8	0.5	44.1
	RP2) Historical average	population_hist (-)	21.7	1	<0.001	0.07	276.3	0.0	55.9

Notes: Variable abbreviations are from Table B1; D^2_{adj} is adjusted explained deviance; AIC_c is bias-corrected Akaike's Information Criterion for fitted models; Δ_{AIC_c} is $(AIC_c)I - (AIC_c)min$; w_r is the AIC_c weights expressed in percentages; (+) or (-) indicates the direction of the effect of the variable or the variable components for predicting jaguar presence, * indicates interaction between variables; $_r$ followed by 1,4,7 or 10 indicates the variable calculated for 1-, 4-, 7- or 10-km radius respectively.

Table C3. Variables and parameters for the final models of each main group of hypotheses (land cover and human persecution) and for the global model. Variable abbreviations are from Table B1, and the model selection process is detailed in Tables 3 and 4 in the manuscript. The maps representing each of these models in the study area are shown in Fig. C1.

Model	Parameter	β	Std. error	95% Confidence interval	
				Lower	Upper
Land cover	(intersection)	-3.311	1.898	-7.031	0.409
	forest_r1	4.2E-02	2.9E-02	-1.4E-02	9.8E-02
	connect_r7	3.6E-03	2.5E-03	-1.3E-03	8.6E-03
	forest73_r7	0.017	0.008	0.002	0.032
	forest73_r7 ²	-1.9E-05	1.1E-05	-4.0E-05	2.1E-06
	forest73_r7 ³	6.4E-09	4.5E-09	-2.3E-09	1.5E-08
	int_agr_r1	-0.062	0.041	-0.142	0.018
	farms_r4	-0.009	0.003	-0.014	-0.003
	past_r4	-0.005	0.004	-0.012	0.003
Human	population_hist	-0.093	0.018	-0.128	-0.058
persecution	protect_cat=0 \times access_cost	3.0E-04	9.2E-05	1.2E-04	4.9E-04
	protect_cat=1 \times access_cost	7.9E-04	2.9E-04	2.1E-04	1.4E-03
	protect_cat=2 \times access_cost	0.003	0.001	0.001	0.005
Global	protect_cat=0 \times access_cost	1.8E-04	1.8E-04	-1.7E-04	5.3E-04
	protect_cat=1 \times access_cost	1.2E-04	3.1E-04	-4.9E-04	7.2E-04
	protect_cat=2 \times access_cost	0.001	0.001	0.000	0.003
	population_hist	-0.076	0.032	-0.139	-0.014
	forest_r1	0.008	0.028	-0.047	0.063
	forest73_r7	0.011	0.004	0.002	0.020
	forest73_r7 ²	-1.3E-05	7.3E-06	-2.7E-05	1.3E-06
	forest73_r7 ³	4.5E-09	3.3E-09	-1.9E-09	1.1E-08
	int_agr_r1	-0.093	0.041	-0.173	-0.014
	farms_r4	-0.011	0.003	-0.016	-0.005
	past_r4	-0.009	0.003	-0.016	-0.002

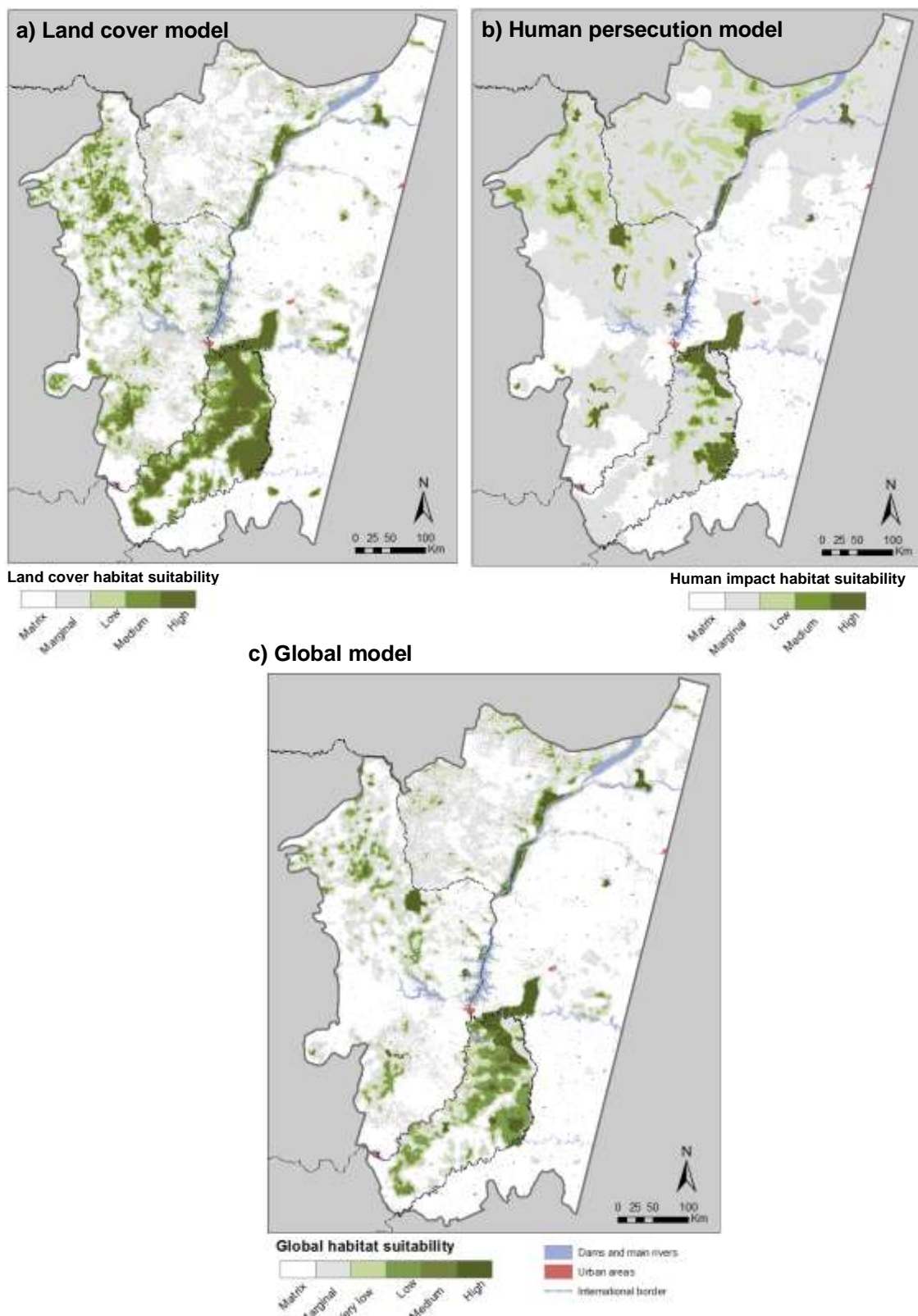


Fig. C1. One-dimensional habitat suitability maps of the final models: a) Land-cover model; b) Human persecution model; and c) Global model.

151 **Table C4.** Evaluation of the final models developed for predicting jaguar presence along the Upper Paraná Atlantic Forest. Boyce index calculated using
 152 Biomapper 4.07.303 (Hirzel et al. 2008; Hirzel et al. 2006). *AUC*: area under the receiver operating curve; *Sensitivity*: prediction of presences; *Specificity*:
 153 prediction of pseudo-absences; *General*: prediction capacity including both presences and pseudo-absences.
 154

Model	Presence only	Original presences and pseudo-absences				Cross validation ^a			Data or pseudo-absences resampling ^a		
	<i>Boyce</i>	<i>AUC</i>	<i>Sensitivity</i>	<i>Specificity</i>	<i>General</i>	<i>Sensitivity</i>	<i>Specificity</i>	<i>General</i>	<i>Sensitivity</i>	<i>Specificity</i>	<i>General</i>
Land-cover	0.998	0.905	85.0 %	82.0 %	83.5%	84.0 %	82.1 %	83.1 %	84.4 %	74.4 %	79.4%
Human persecution	0.998	0.841	74.0 %	82.0 %	78.0 %	71.7 %	77.4 %	74.6 %	60.8 %	91.3 %	76.1 %
Global	0.977	0.915	80.0 %	79.0 %	79.5 %	84.9 %	80.2 %	82.6 %	76.5 %	88.6 %	82.5 %

155 ^a Mean percentages after ten evaluations with different extracted folds or resampling sets or subsets.

Appendix D. Categories and sub-categories of habitat in the two-dimensional model.

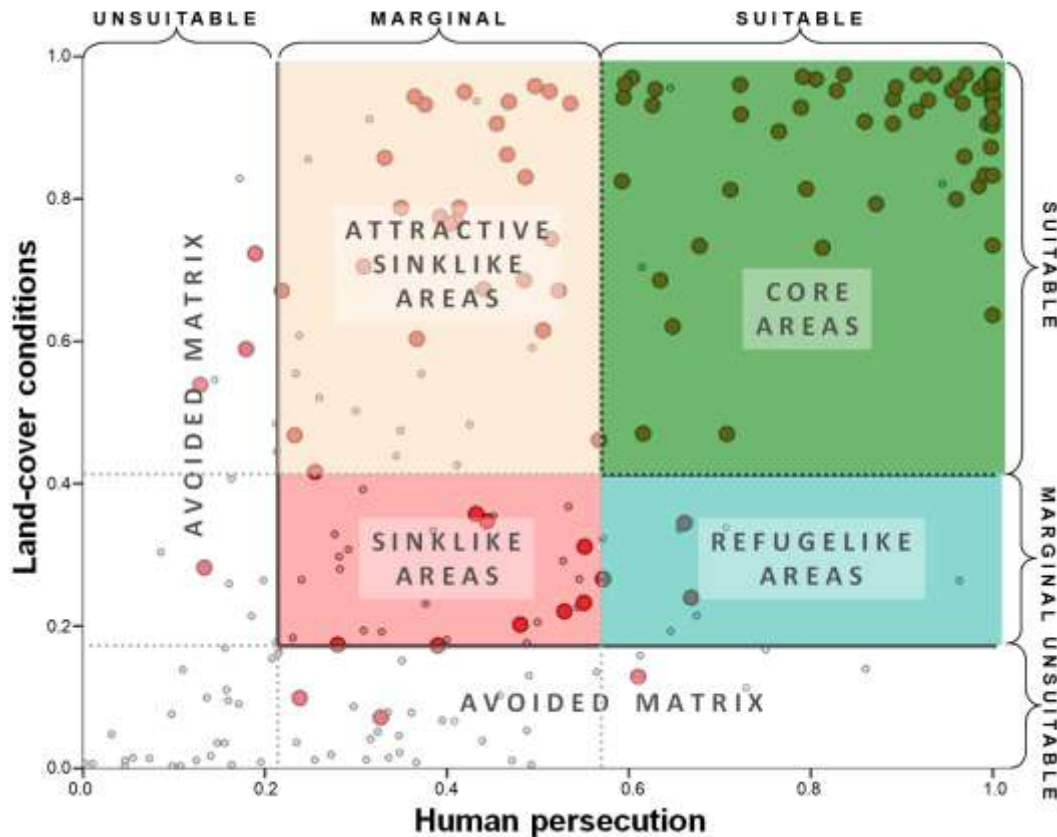


Fig. D1. Distribution of the presences (red large dots) and pseudo-absences (empty small dots) along the habitat categories of the two final models used for the two-dimensional categorization of habitat suitability for jaguars in the Upper Paraná Atlantic Forest. Most of the presence records occurred in or around the core areas, and the longest distance of a presence record from a core area was 23 km. However, areas classified as core areas included some small and isolated areas that may not be significant for the target species (Hirzel and Le Lay 2008). The Perobas Biological Reserve (Fig. 3) and surroundings in Brazil (74 km²) was the smallest isolated core area with confirmed jaguar presence. We therefore re-categorized as potential refuges the core areas that were smaller than 74 km² and located farther than 23 km from another core area.

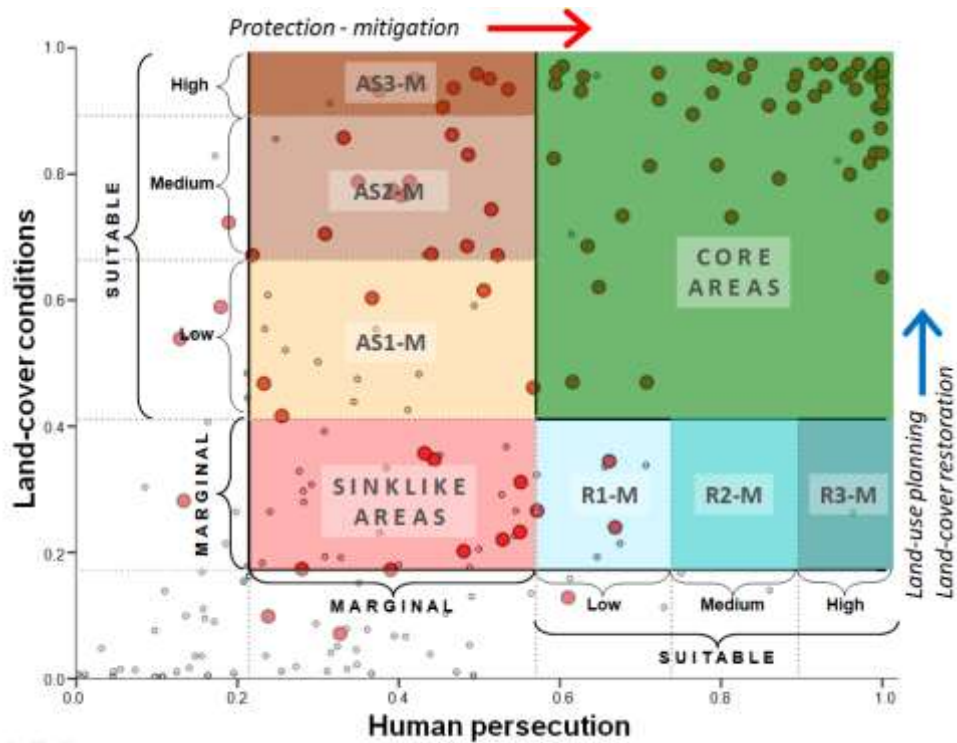


Fig. D2. Sub-categories of marginal habitats according to the different levels of suitability determined by the land-cover conditions and human persecution models. The graph shows the distribution of presences (red dots) and pseudo absences (small empty dots) along the habitat categories. The red and blue arrows indicate the priority management action needed for transforming the suboptimal areas (i.e. refugelike and attractive sinklike areas), into core areas. AS: attractive sinklike areas; R: refugelike areas; -M: located in marginal habitats.

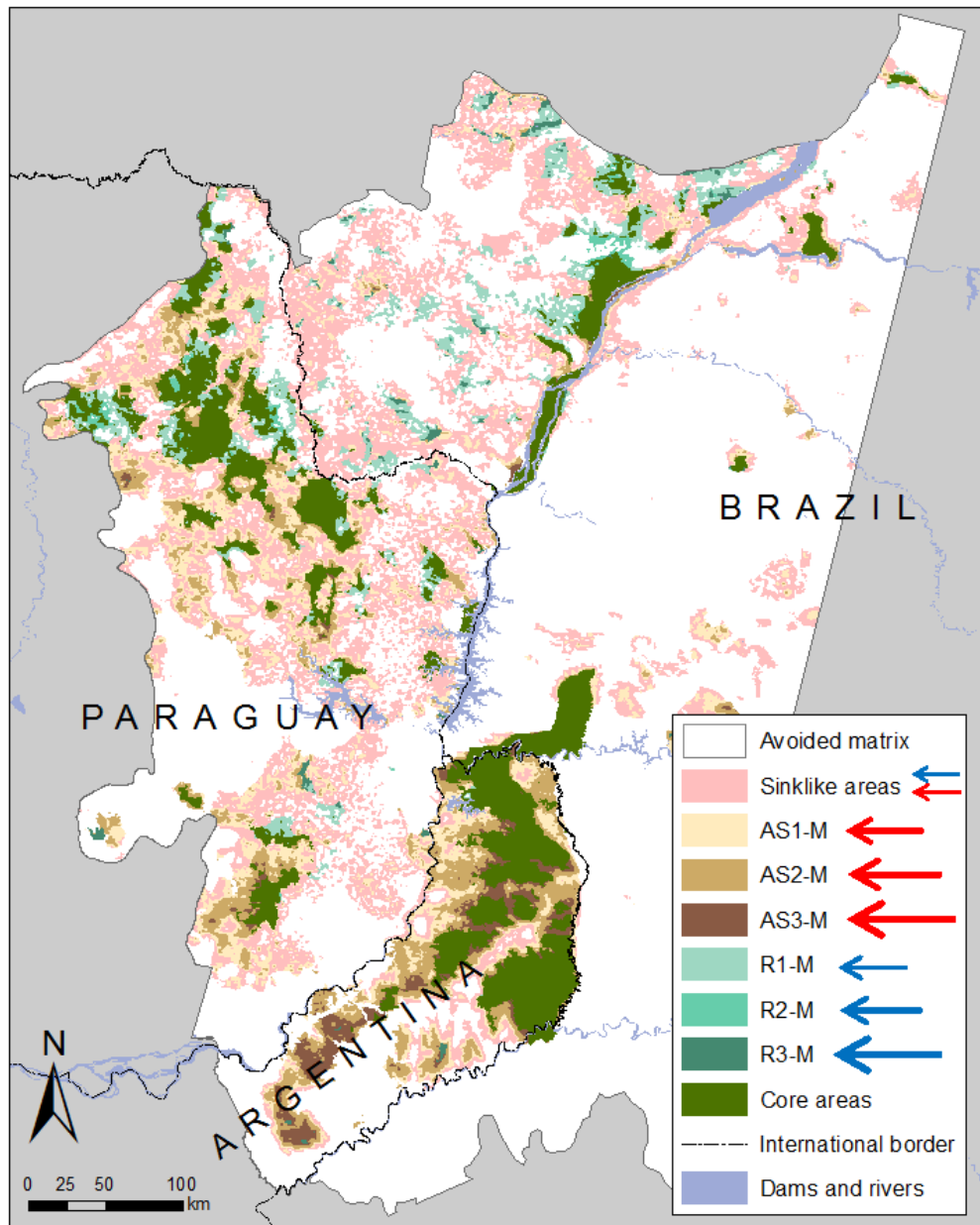


Fig. D3. Distribution of the sub-categories of marginal habitats determined by the different levels of suitability from the land-cover and human persecution models (see Fig. D2). The arrows in the legend indicate the main management actions needed for increasing the suitability of each habitat category (red: protection/mitigation; blue: territorial planning for land-cover recovery and restoration). Larger arrows indicate priority areas (better land-cover conditions or less human persecution) where management interventions will have a greater effect in transforming these areas into core areas. AS: attractive sinklike areas; R: refugelike areas; -M: located in marginal habitats.

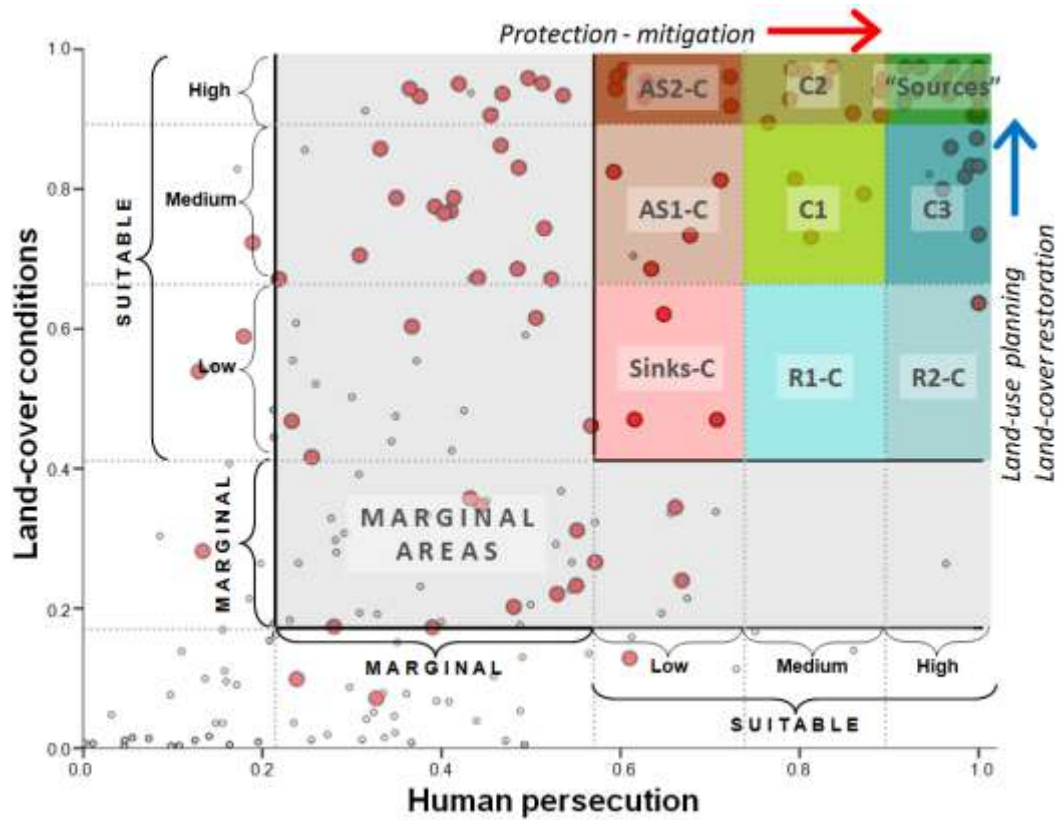


Fig. D4. Sub-categories of habitats inside the core areas determined by the different levels of suitability from the land-cover conditions and human persecution models. The graph shows the distribution of presences (red dots) and pseudo absences (small empty dots) along the habitat categories. The red and blue arrows indicate the priority management action needed for transforming the suboptimal areas (i.e. refugelike and attractive sinklike areas), into core areas. AS: attractive sinklike areas; R: refugelike areas; C: core area sub-category; -C: located in core areas.

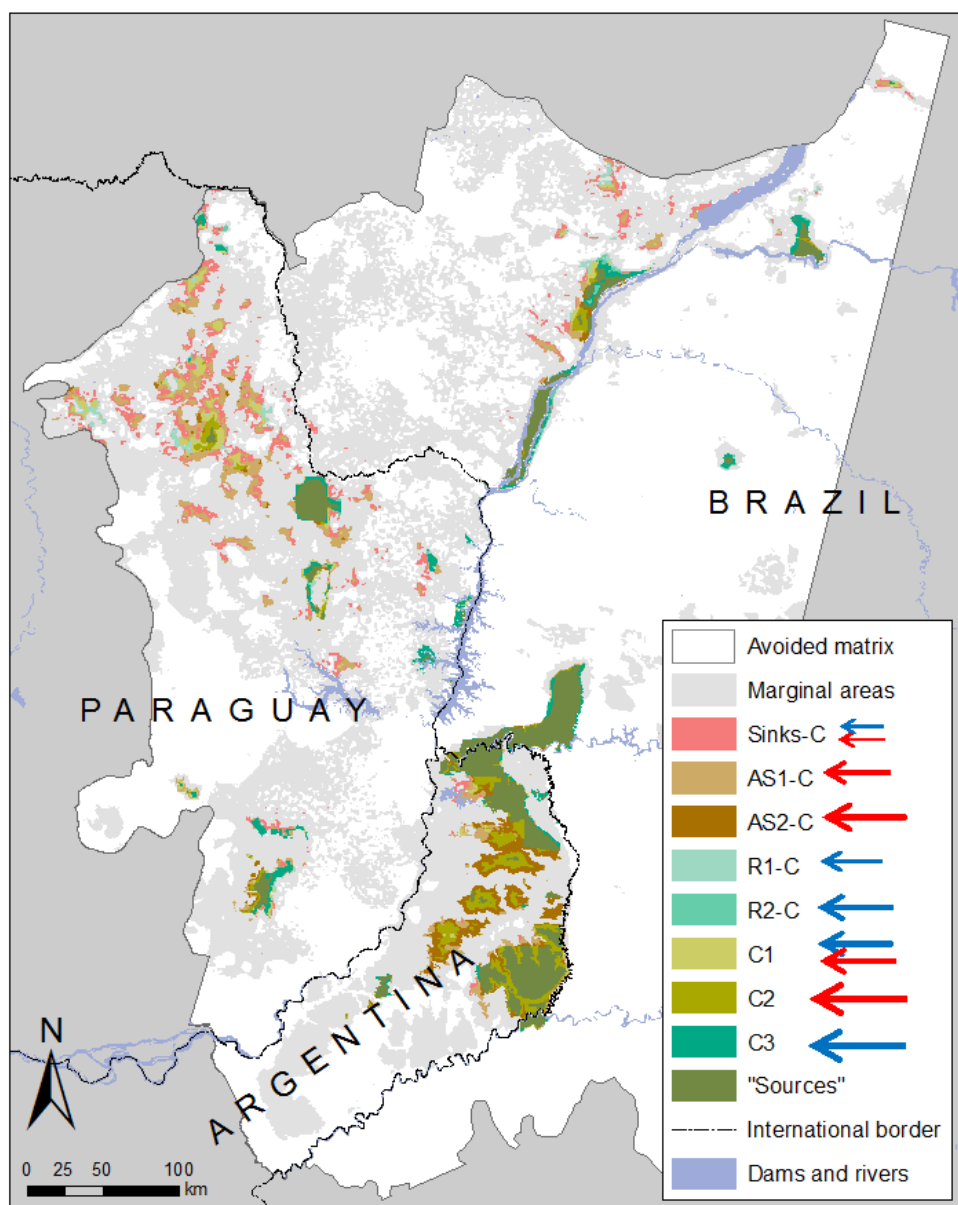


Fig. D5. Distribution of the sub-categories of habitats inside the core areas determined by the different levels of suitability from the land-cover and human persecution models (see Fig. D4). The arrows in the legend indicate the main management action needed for increasing the suitability of each habitat category (red: protection/mitigation; blue: territorial planning for land-cover recovery or restoration). Larger arrows indicate priority areas (better land-cover conditions or less human persecution) where management interventions will have a greater effect in transforming these areas into potential sources. AS: attractive sinklike areas; R: refugelike areas; C: core area sub-category; -C: located in core areas.

Appendix E. Distribution of killed jaguars along the categories of habitat.

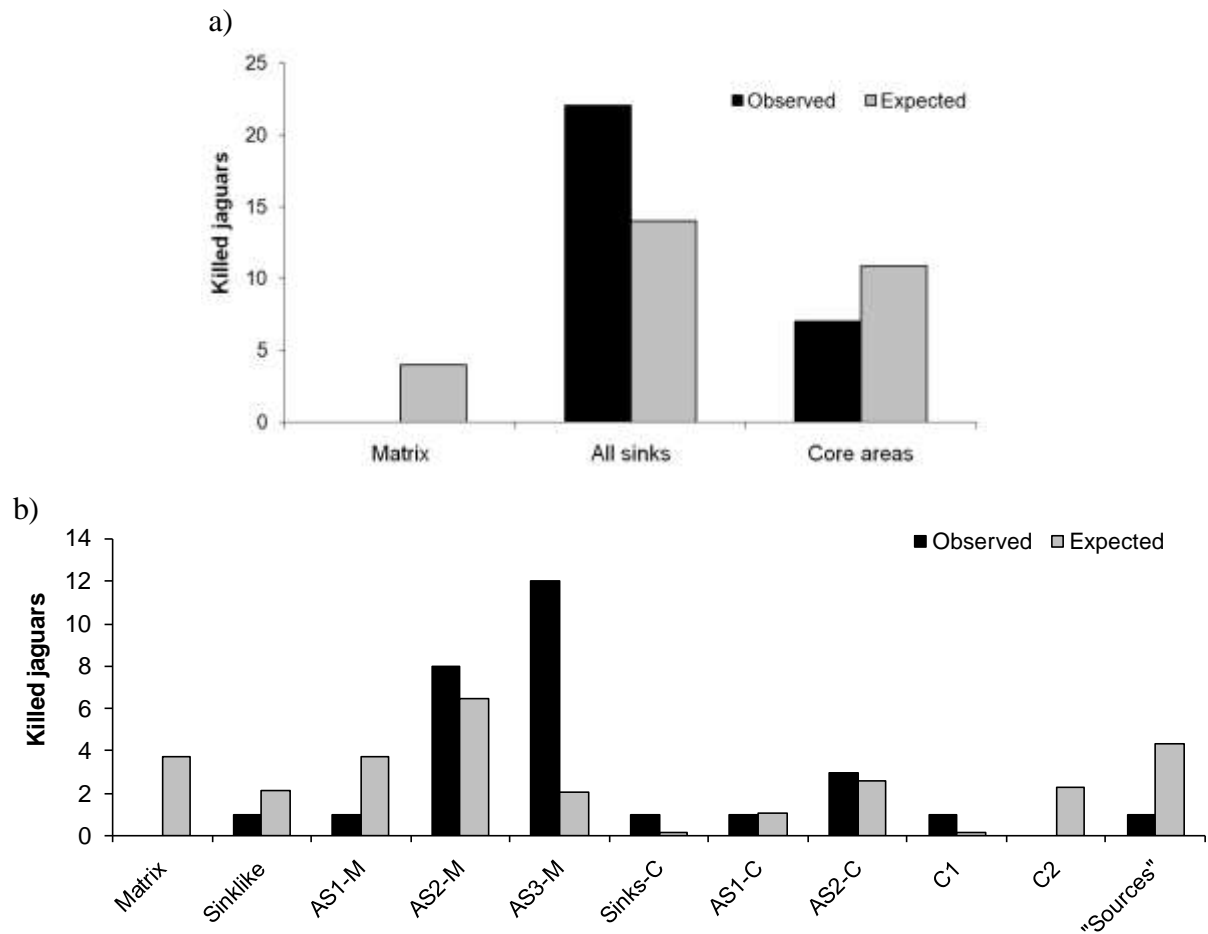


Fig. E1. Observed and expected proportion of killed and removed jaguars (n=30) that occurred in the different categories of habitat along the Green Corridor of Argentina plus a 23 km buffer area. In the upper graph (a) we joined both sinklike and attractive sinklike areas in one all-sinks category for the statistical analysis (no refugelike areas occurred in this region, see the results of the analysis in the main text). The bottom graph (b) shows a detailed distribution of the observed and expected frequency of killed and removed jaguars, where potential attractive-sinklike in marginal areas are (from worst to better land-cover conditions): AS1-M, AS2-M, AS3-M. Potential attractive sinklike areas in core areas are (from worst to better land-cover conditions): Sinks-C, AS1-C, AS2-C. See sub-categories in Figs. D2 and D4.

Appendix F. Validation of the Biodiversity Vision of the UPAF.

Table F1. Validation of the Biodiversity-Vision conservation landscape (Di Bitetti et al. 2003) through the two-dimensional model developed for jaguars in the Upper Paraná Atlantic Forest.

Biodiversity Vision categories	Jaguar model categories				
	Matrix (%)	Sink like (%)	Refuge like (%)	Attractive sinklike (%)	Core areas (%)
Core areas	3	1	0	17	79
High potential for became core area	3	3	0	66	28
Potential core area	6	6	9	28	51
Forested area that needs assessment	4	5	13	12	65
Satellite areas	9	3	23	40	25
Main corridors	21	17	2	43	16
Secondary corridors	28	16	8	30	18
Lateral expansions of corridors	23	19	4	40	14
Isolated areas	67	8	1	19	5
Potential corridors	65	18	1	11	4
Areas needing a corridor	87	10	0	3	0
Priority river basin	56	20	7	12	6

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