

Differential impact of landscape transformation on pumas (*Puma concolor*) and jaguars (*Panthera onca*) in the Upper Paraná Atlantic Forest

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ABSTRACT

Aim Jaguars and pumas, being similar in size and behaviour, are the largest felids of the Neotropics. However, pumas appear to be more resistant to human impacts. Our objective was to compare the response of both species with human impacts at a regional scale in a highly modified region where both species had continuous distribution in the past.

Location The Upper Parana Atlantic Forest (UPAF).

Methods Pumas and jaguars presence-only data were used in an Ecological Niche Factor Analysis (ENFA). From the total number of records, we resampled 95 records of each species 10 times to characterize and compare their habitat requirements, built habitat-suitability maps and examined interspecific differences in niche parameters related to present landscape characteristics.

Results Both species showed high dependence on native forest and habitat protection, and low tolerance to anthropogenic environments. However, jaguars showed higher differences between their optimal habitat and the available landscape (mean \pm SD; marginality $M = 2.290 \pm 0.072$) and lower tolerance to deviations from their optimal habitat (tolerance $T = 0.596 \pm 0.013$) than pumas ($M = 1.358 \pm 0.067$, $P < 0.001$; $T = 0.742 \pm 0.022$, $P < 0.001$). Although their niches highly overlapped (Pianka's $O = 0.746 \pm 0.069$), pumas' higher tolerance resulted in a larger area covered by suitable patches of habitat with higher connectivity. All jaguar-suitable areas were also suitable for pumas; however, $44 \pm 8\%$ of puma-suitable areas were unsuitable or marginal for jaguars.

Main conclusions Pumas showed more tolerance than jaguars to human impacts at a regional scale in the UPAF, a pattern also observed at local and continental scales. Although the proximate factors responsible for the differential response of pumas to human-altered environments seem to be similar at all spatial scales (e.g. broader trophic niche than jaguars), the resultant spatial configuration of suitable habitat at a regional scale might be another important factor determining puma persistence and higher jaguar demands on conservation efforts.

Keywords

Conservation biogeography, Ecological Niche Factor Analysis, habitat suitability, niche breadth, response to human pressures, tolerance.

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INTRODUCTION

Habitat loss and fragmentation, overexploitation and spread of invasive species are interrelated impacts associated with landscape transformation by humans and constitute the most important threats to biodiversity (Pimm & Raven, 2000; Jetz

et al., 2007). Species responses to habitat conditions and human pressures result from complex interactions and can be manifested in different ways and at different spatial scales (Gehring & Swihart, 2003; Storch & Gaston, 2004; Urban, 2005). For instance, species response to habitat conditions can be examined at distributional, regional or local scales

(Johnson, 1980; Wiens, 1989; Gehring & Swihart, 2003; Ciarniello *et al.*, 2007). For example, at a global scale, broad-range species would be less threatened because of the larger amount of available habitat and their natural tolerance to a wider range of biotic and abiotic conditions (Pimm & Raven, 2000; Swihart *et al.*, 2003; Jetz *et al.*, 2007). At a local population scale, species with higher intrinsic population growth rate are often less sensitive to direct human persecution (Purvis *et al.*, 2000; Cardillo *et al.*, 2004). Therefore, the analysis and comparison of species responses to human impacts at different spatial scales are important not only to evaluate their conservation status but also to understand the causes of species' decline or persistence (Sunquist & Sunquist, 2001; Ciarniello *et al.*, 2007; Liu *et al.*, 2009).

Large carnivores are area-demanding species as a result of their inherently low population densities and large territories (Woodroffe & Ginsberg, 1998; Cardillo *et al.*, 2004), enhancing the need of understanding their response to human pressures at large scales (Boyd *et al.*, 2008). Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are the largest felids of the American Continent (Sunquist & Sunquist, 2002). Being large predators, they not only require large territories and a good prey base but also are subject to direct human persecution; all of these factors make these species of particular conservation concern (Weber & Rabinowitz, 1996; Crooks, 2002). Pumas and jaguars are similar in size and behaviour, and they were once sympatric along most of the Neotropics (Currier, 1983; Seymour, 1989; Sunquist & Sunquist, 2002; Fig. 1a). Both species have suffered a reduction of their ranges in the last centuries, but jaguar has disappeared in many areas where pumas still persist (Sanderson *et al.*, 2002; Sunquist & Sunquist, 2002; Fig. 1b). This continental scale pattern suggests that pumas are more

resistant to human pressures and habitat modification than jaguars. Local scale studies of habitat use show that both species avoid areas with high human impact, but pumas use human-modified areas more frequently than jaguars (Silveira, 2004; Cullen, 2006). Additionally, the puma usually presents a broader trophic niche and the ability to consume smaller prey than jaguars (Scognamillo *et al.*, 2003; Azevedo, 2008), which may be a significant advantage for pumas in human-altered landscapes (Novack *et al.*, 2005; Haines, 2006). Despite this local-level evidence, no studies have described and compared the response of both felids with human impacts at a regional scale, even though important processes occur at this scale (e.g. metapopulation dynamics; Wiens, 1989; Hanski, 1998).

Pumas and jaguars have historically been sympatric along the Atlantic Forest of South America (Cabrera, 1929, 1934; Sunquist & Sunquist, 2002; Haines, 2006). The Atlantic Forest originally was a continuous mass of forest that occupied eastern and southern Brazil, eastern Paraguay and the Misiones Province in Argentina (de Gusmão Câmara, 2003), and it is considered a hotspot for biodiversity and Neotropical carnivore conservation (Mittermeier *et al.*, 2005; Loyola *et al.*, 2008). However, the Atlantic Forest is currently one of the planet's most endangered forests on account of its being highly fragmented, with only 7%–16% of its original cover remaining (Fig. 1c; Mittermeier *et al.*, 2005; Ribeiro *et al.*, 2009). Both jaguar and puma populations have been locally decimated in the Atlantic Forest (Cullen *et al.*, 2005; Paviolo *et al.*, 2008, 2009a; Mazzolli, 2009), but populations of both species still persist in this region (Leite *et al.*, 2002; De Angelo *et al.*, in press). Because these species were exposed to the same levels of anthropogenic landscape transformation in the Atlantic Forest, the study of the resultant pattern of remaining populations

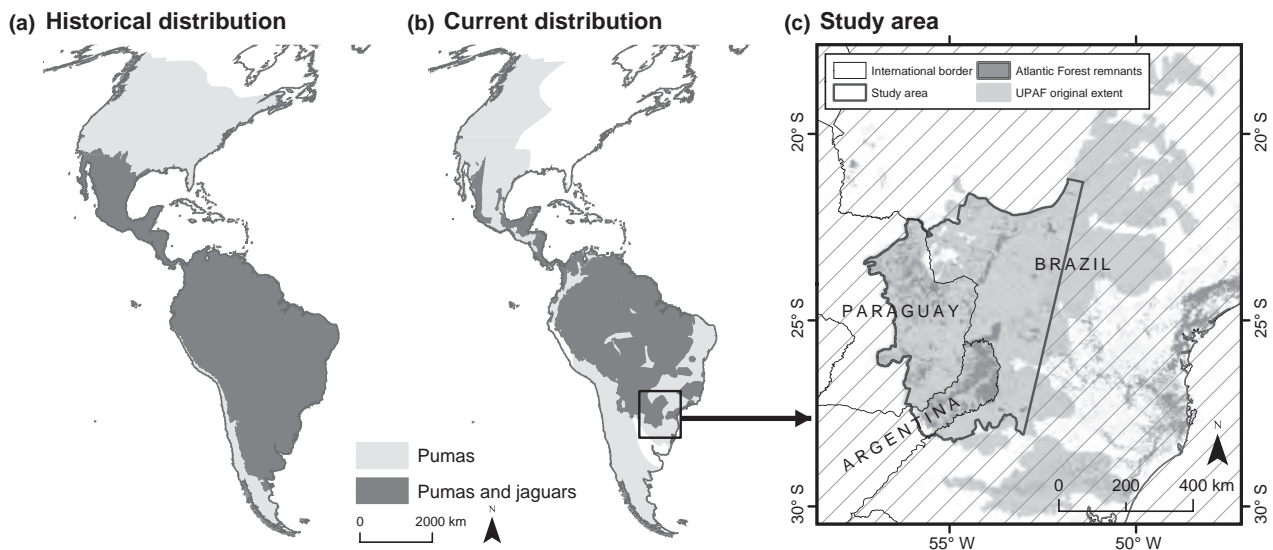


Figure 1 Historical (a) and current (b) continental distribution of pumas and jaguars, showing the sympatric areas for both species (dark grey) and exclusive for pumas (light grey; world-Mollweide projection; modified from: Sanderson *et al.*, 2002; Sunquist & Sunquist, 2002; Zeller, 2007). The inset (c) describes the location of the study area that includes the most important forest remnants of the Upper Paraná Atlantic Forest Eco-region (UPAF; Di Bitetti *et al.*, 2003; De Angelo, 2009).

may clarify the processes behind both species' responses. Additionally, this information is important for both the conservation of these species and the ecological integrity of the Atlantic Forest (Sanderson *et al.*, 2002; Di Bitetti *et al.*, 2003; Rabinowitz & Zeller, 2010).

The Ecological Niche Factor Analysis (ENFA; Hirzel *et al.*, 2002) is a novel analytical tool that uses ecogeographical layers (e.g. land cover, elevation) to characterize the multidimensional space where a species occurs and compares it with the existing conditions in the study area. This multidimensional space is created through orthogonal factors with direct interpretation in relation to the species' ecological niche. As in other species distribution models, this information is used to construct habitat-suitability models that are translated to the geographical space, thus obtaining habitat-suitability maps. Two main advantages of ENFA in relation to other methods (e.g. generalized linear models) are that it demands only presence records (no absences needed; Hirzel *et al.*, 2002) and that its results allow a direct comparison among multiple species that inhabit the same region by interpreting the parameters from the ecological niche perspective (e.g. their relative specialization level; Chefaoui *et al.*, 2005; Acevedo *et al.*, 2007; Sattler *et al.*, 2007; Durant *et al.*, 2010).

In this work, we used ENFA with the aim of evaluating the impact of anthropogenic landscape transformation and other human pressures on the persistence of pumas and jaguars in the Upper Paraná Atlantic Forest (UPAF), the largest of the eco-regions that make up the Atlantic Forest (Fig. 1c). Based on the pattern observed at continental and local scales, we hypothesized that pumas are more tolerant than jaguars to human impacts at a regional scale in the UPAF, which will be reflected in the niche parameters and in the amount and characteristics of the remaining suitable areas for each species in this region.

METHODS

Study area

The UPAF (Fig. 1c) is a semi-deciduous subtropical forest, with a mean annual precipitation that ranges from 1000 to 2200 mm and mean annual temperatures between 16 and 22 °C (Di Bitetti *et al.*, 2003), with a marked seasonality in day length, temperature and primary productivity (Di Bitetti, 2009). The topography of the UPAF ranges from flat areas with deep soils near the main rivers (Paraná, Uruguay, Paranapanema and Iguazú rivers; 150–250 m a.s.l.) to a relatively flat plateau (550–800 m a.s.l.; Di Bitetti *et al.*, 2003). We selected as study area a fraction of 276,843 km² (Fig. 1c), the limits of which coincide with the historical distribution of the UPAF, with the exception of the east and north-east limits that were demarked until the end of the 223th row and 75th path of the Landsat satellite images (Figs 1c & 2). We chose this region because it contains the largest amount of native forest remnants and constitutes the core area of regional conservation initiatives (Fig. 2; Di Bitetti *et al.*, 2003). Additionally,

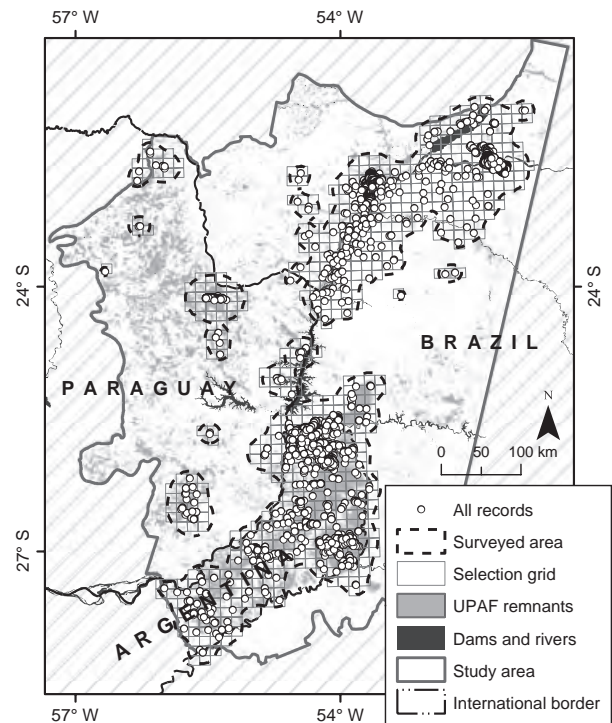


Figure 2 Distribution of all the records obtained by De Angelo *et al.* (in press) along the study area. These records include the 626 records of pumas and the 974 records of jaguars, which were used to determine the surveyed area (bold dashed line). The selection grid overlaid on this surveyed area was used for generating the random points, and for filtering and randomly selecting the data sets. See details in the Appendix S1 and Fig. S1 in Supporting Information.

more complete geographical and species data were available. The native forest, which historically covered the complete study area, is now distributed among several fragments that occupy only 18% of this region (Fig. 1c), separated by a heterogeneous matrix of human land uses (Huang *et al.*, 2007; Izquierdo *et al.*, 2008; De Angelo, 2009; Ribeiro *et al.*, 2009).

Presence data of pumas and jaguars

We used presence-only data collected through a participatory monitoring of these felids between 2002 and 2008 in the UPAF (see Appendix S1 in Supporting Information and De Angelo *et al.*, in press). The original 626 records of puma and 974 jaguar records were filtered to reduce potential bias and spatial interdependencies caused by opportunistic data collection (e.g. > 1 record from the same individual). For this purpose, we overlaid a grid with a 12 × 12 km cell size equivalent to a jaguar female home-range (144 km²; Fig. 2; D. Sana, unpublished data; Cullen *et al.*, 2005; Paviolo, 2010). We randomly selected a single point from each cell that contained more than one record (Sattler *et al.*, 2007; Kanagaraj *et al.*, 2011). We repeated this random selection process as a resampling method to obtain 10 different subsets of records for pumas and 10

subsets for jaguars with 95 points each. Additionally, we used the same resampling method for selecting 10 different subsets of random points generated along the surveyed area that were used as control data sets for further analysis (see details and justification in Appendix S1 and Fig. S1).

Landscape variables

We characterized the study region using 29 variables related to direct human pressures and landscape characteristics and composition through the processing of the UPAF-GIS database compiled by Di Bitetti *et al.* (2003) and De Angelo (2009). A land-use map was constructed from a mosaic of Landsat-5 TM satellite images from 2004. Each image was classified indepen-

dently through 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; Izquierdo *et al.*, 2008; De Angelo, 2009). We resampled each land-use map to 330-m cell size for generating the mosaic of the study area, which obtained 87% of accuracy in an independent validation procedure (De Angelo, 2009). We used ENVI software Version 4.2 (Research Systems, Inc. 2005, USA).

All variables were resampled to 330-m cells and coregistered with the land-use map, removing lakes and urban areas (Hirzel & Le Lay, 2008). As ENFA utilizes only numerical variables, categorical maps were transformed into quantitative variables using different approaches (Table 1). The neighbourhood

Table 1 Description of the 23 variables used in the Ecological Niche Factor Analysis developed for pumas and jaguars in the Upper Paraná Atlantic Forest (*).

Name	Description
Cost of access†	Accessibility cost for humans measured as the hours needed to access the focal cell from the nearest town or city (see Appendix S2 and Table S1 in Supporting Information; Farrow & Nelson, 2001; Nelson, 2008).
Elevation	Elevation above sea level of the focal cell obtained from the Shuttle Radar Topography Mission Elevation Data Set of the US Geological Survey (original resolution of 88 m; http://seamless.usgs.gov).
Forest (r4)†‡ and Forest (r7)†‡	Frequency of cells occupied by native forest in a <i>circle</i> of 4- (r4) and 7-km (r7) radius around the focal cell.
Intensive agriculture (r4)†‡ and Intensive agriculture (r7)†‡	Frequency of cells occupied by intensive agriculture in a circle of 4- (r4) and 7-km (r7) radius around the focal cell.
Landscape heterogeneity (r4) and Landscape heterogeneity (r7)	Landscape heterogeneity index of the focal cell calculated in a circle of 4- (r4) and 7-km (r7) radius. This index is based on the Shannon–Wiener diversity index of habitat type diversity, and it is implemented in the Circular Analyst function of BIOMAPPER (Hirzel <i>et al.</i> , 2008). In the UPAF, high heterogeneity values represent strongly anthropogenic landscapes (with several human land uses in small surfaces).
Local connectivity (r4)†‡ and Local connectivity (r7)†‡	Frequency of cells occupied by native forest in a <i>ring</i> of 4- (r4) and 7-km (r7) radius and 1-km wide (3 cells) around the focal cell. This represents an index of local connectivity of forest around the focal cell (Schadt <i>et al.</i> , 2002; Naves <i>et al.</i> , 2003; Wiegand & Moloney, 2004).
Pastures (r4)†‡ and Pastures (r7)†‡	Frequency of cells occupied by extensive pastures in a circle of 4- (r4) and 7-km (r7) radius around the focal cell.
Pine plantations (r7)§‡	Frequency of cells occupied by pine plantations in a circle of 7-km (r7) radius around the focal cell.
Protection (r7)‡	Mean value of relative protection in the cells inside a circle of 7-km (r7) radius around the focal cell. Six categories of protection were defined: the oldest and best protected national park (value = 100), other national parks and national reserves (value = 80), provincial/state parks (value = 60), private reserves (value = 40), multiple use reserves (value = 20) and not implemented reserves (value = 10).
River distance¶¶	Straight line distance to the closest river.
River frequency (r4)†‡ and River frequency (r7)†‡	Frequency of cells occupied by rivers in a circle of 4- (r4) and 7-km (r7) radius around the focal cell.
Rural population	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; Carroll & Miquelle, 2006; De Angelo, 2009).
Slope	Terrain slope expressed in percentages, calculated from elevation maps.
Small farms (r4)†‡ and Small farms (r7)†‡	Frequency of cells occupied by small farms in a circle of 4- (r4) and 7-km (r7) radius around the focal cell.
Town distance¶¶	Straight line distance to the closest town or city.
Town frequency (r7)†‡	Frequency of cells occupied by urbanized areas in a circle of 7-km (r7) radius around the focal cell.

*Six variables were not included in the analysis: pine plantation frequency in a 4-km radius, distance to roads, frequency of roads (in a 4- and a 7-km radius), mean protection in a 4-km radius and frequency of towns (in a 4-km radius).

†Original variable Box–Cox transformed using BIOMAPPER (Hirzel *et al.*, 2008).

‡Calculated using ‘Neighbourhood statistics’ of Spatial Analyst for ARCMAP 9.1 and ‘Circular Analyst’ of BIOMAPPER (Hirzel *et al.*, 2008).

§Original variable square-root transformed using BIOMAPPER (Hirzel *et al.*, 2008).

¶¶Calculated using Spatial Analyst for ARCMAP 9.1 (ESRI Inc. 2004).

analysis is one of the commonest methods, where each cell of the landscape is characterized by the conditions in the neighbour cells (e.g. frequency of a specific land use; Hirzel *et al.*, 2002). Because the perception of the landscape by large carnivores is often related to their home-range size (Schadt *et al.*, 2002; Naves *et al.*, 2003; Kanagaraj *et al.*, 2011), we included two neighbourhood scales related to the approximate home-range size of females of both species: circles of 50 (puma) and 150 km² (jaguar) with radius of 4 and 7 km, respectively (Table 1). Variables related with human infrastructure (roads and towns) were also summarized in one continuous variable through a human accessibility cost analysis (Farrow & Nelson, 2001; see details in Appendix S2 and Table S1).

We prepared the variables (i.e. maps) for using in BIOMAPPER software, and we verified their consistency and usability with BIOMAPPER verification tools (Hirzel *et al.*, 2008). We eliminated those potentially conflictive maps (e.g. constant or nearly boolean maps; Hirzel *et al.*, 2002), and 23 of the original 29 variables were retained for the final analysis (Table 1). The same 23 variables were included in the analysis of both species to ensure comparable results (Hirzel *et al.*, 2002). Finally, we used Box–Cox or square-root transformation for variables' normalization as suggested by Hirzel *et al.* (2002) (Table 1).

Ecological Niche Factor Analysis

We combined the different subsets of 95 records (10 subsets of pumas, 10 of jaguars and 10 of random points) with the landscape variables in 30 independent ENFAs (Hirzel *et al.*, 2002). ENFA uses a multivariate factorial approach to compare the environmental conditions at locations where a species is detected with the available conditions throughout the study area. The first factor extracted by ENFA maximizes the marginality of the species, which is a measure of the discrepancy between the species distribution average and the global distribution average of each variable. The other uncorrelated factors maximize species specialization, defined as the ratio between the standard deviation of variable values in the complete study area, and the standard deviation only in species occurrences. The coefficients obtained for the variables in each factor show their relative contribution to the species marginality (factor 1) and specialization (other factors). The global marginality index takes into account the marginality in all the variables and gives a summary of how much the species range differs from the available conditions. Similarly, specialization is summarized in a global specialization index that is transformed into a tolerance index for better interpretation. The tolerance is the inverse value of the global specialization and represents a measurement of the focal species selectiveness within the available conditions in the area determined by the variables.

To summarize ENFA results, we calculated the mean and standard deviation for each parameter of the three analysed groups (pumas, jaguars and random). To observe which parameters were significantly different than random, we

applied an ANOVA and a Dunnett post hoc comparison using the random group as a control. Then, we compared pumas and jaguars parameters where they differ from random through Student's *t*-test for independent samples.

Factors generated by ENFA were used to construct habitat-suitability maps for pumas (10 maps) and jaguars (10 maps). We utilized 'MacArthur's broken-stick distribution' for selecting the number of factors to consider in the habitat-suitability modelling (Jackson, 1993; Hirzel *et al.*, 2002). The analysis was developed using BIOMAPPER 4.07.303 (Hirzel *et al.*, 2008) that contains four algorithms for habitat-suitability calculation (Braunisch *et al.*, 2008). We chose the 'median + extremum' algorithm for our analysis on account of the expected response of most of the selected variables, where the optimum of the species is expected to be around the highest or the lowest values of the variable (Braunisch *et al.*, 2008).

To evaluate the robustness and predictive power of each model, we applied a jack-knife cross-validation procedure implemented in BIOMAPPER using 10-fold. The cross-validation is used to construct a curve to observe the relationship between the mean predicted/expected ratio of independent points and the habitat-suitability values (Hirzel *et al.*, 2006). These curves were examined for final habitat-suitability maps reclassification in three categories of habitat quality: unsuitable (habitat suitability = 0 and predicted/expected ratio = 0; no records of species presence under this condition); marginal ($0 < \text{predicted/expected ratio} \leq 1$; the model predicts fewer presences than expected by chance) and suitable (predicted/expected ratio > 1 ; the model predicts more presences than expected by chance; Hirzel *et al.*, 2006; Sattler *et al.*, 2007). From the curve of each map, we calculated two Boyce indexes (Hirzel *et al.*, 2006), one for the continuous curve [B_{cont}] and another for the curve of the reclassified maps [$B_{(3)}$]. Boyce index is calculated by the mean Spearman rank correlation coefficient of the curve that varies from -1 to 1 , with 0 indicating a random model and 1 indicating a consistent model with high predictive power (Boyce *et al.*, 2002; Hirzel *et al.*, 2006). We determined only three categories of habitat quality with clearly defined thresholds because our main objective was to compare both species; therefore, we needed a simple and not biased map reclassification to obtain comparable maps. We estimated the mean \pm SD Boyce index for the 10 maps produced for each species. To obtain a final suitability map, we overlaid the maps of each species and computed the mode of each cell among the maps to assign a category to the cell on the final map (majority analysis).

Species comparisons

We examined interspecific differences in niche parameters related to landscape characteristics through the ENFA indexes for each species. Additionally, in a similar approach to that of Sattler *et al.* (2007), we used BIOMAPPER software tools for applying a discriminant analysis to estimate traditional niche breadth and overlap indexes (Hirzel *et al.*, 2008; Qi *et al.*, 2009; Simard *et al.*, 2009). BIOMAPPER uses the records of both

species to compute a discriminant factor that maximizes the separation between them along a linear combination of the ecogeographical variables. This factor is used as a summary of the resources used by each species in the calculation of traditional niche breadth (Levins' standardized index) and overlap indexes (Pianka's overlap index and Lloyd's asymmetric overlap index). Additionally, BIOMAPPER computes those indexes that demand estimates of resource availability (Hurlbert's niche breadth index and Rathke's asymmetric overlap index; Colwell & Futuyma, 1971; Hurlbert, 1978). Resource availability is estimated by applying the discriminant model to the complete study area (discriminant map; Hirzel *et al.*, 2008). We applied the discriminant analysis to all possible combinations among the 10 subsets of records of pumas and the 10 subsets of jaguars to obtain the mean \pm SD value of each index (100 comparisons). We evaluated the differences among these indexes of both species through paired *t*-test comparisons.

Finally, we compared the mean surface estimated for the three habitat categories from the 10 habitat-suitability maps developed for each species, and we overlaid pumas with jaguar maps to observe the differences in suitable areas. We described and compared the fragmentation and structural connectivity of the suitable patches of each species maps using FRAGSTATS 3.3 (McGarigal & Marks, 1995): number of patches, mean patch size, area-weighted mean patch size, the Euclidean nearest neighbour distance and the effective mesh size (Jaeger, 2000; McGarigal, 2002).

RESULTS

The relative contribution of landscape variables to ENFA marginality factor was similar for pumas and jaguars (Table 2). Both species preferred areas with high levels of protection and with high native forest cover in the surroundings (4 km), but avoided areas surrounded mainly by small farms and pastures.

Table 2 Average contribution of landscape variables in the marginality and specialization for pumas ($n = 10$ subsets) and jaguars ($n = 10$ subsets). In the marginality factor, negative or positive coefficients indicate that the species is found in areas with lower (–) or higher (+) values than the average value in the study area. In specialization factors, the higher the absolute value, the more restricted the range of the focal species on the corresponding variable in relation to the available range in the study area (low tolerance; Hirzel *et al.*, 2002).

Variables	Puma marginality		Jaguar marginality		Puma specialization‡		Jaguar specialization‡	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Cost of access	0.087 ^A	0.029	0.157 ^{***B}	0.007	3.496 ^C	0.380	4.780 ^{****D}	0.388
Elevation	–0.107	0.012	–0.074	0.003	4.861 ^{*C}	1.154	5.205 ^{**C}	0.615
Forest (r4)	0.311 ^{***A}	0.016	0.277 ^{**B}	0.006	10.593 ^{***C}	1.444	15.543 ^{****D}	1.424
Forest (r7)	0.271	0.013	0.280	0.004	16.314 ^{***C}	1.528	26.170 ^{****D}	2.005
Intensive agriculture (r4)	–0.237	0.016	–0.164	0.008	6.996	0.871	6.741	0.715
Intensive agriculture (r7)	–0.225	0.023	–0.159	0.008	8.033	0.983	8.319	1.128
Landscape heterogeneity (r4)	–0.176	0.021	–0.177	0.011	6.567 ^C	0.978	7.433 ^{****D}	0.474
Landscape heterogeneity (r7)	–0.170	0.021	–0.171	0.011	7.941 ^{**C}	1.226	11.383 ^{****D}	0.864
Local connectivity (r4)	0.240	0.014	0.265	0.004	7.599 ^C	1.334	17.389 ^{****D}	1.945
Local connectivity (r7)	0.198	0.017	0.263	0.005	6.638 ^C	0.733	15.424 ^{****D}	1.459
Pastures (r4)	–0.145 ^{*A}	0.014	–0.175 ^{**B}	0.006	7.685 ^C	1.475	9.634 ^{****D}	1.195
Pastures (r7)	–0.114 ^A	0.008	–0.170 ^{*B}	0.008	9.044 ^C	2.226	11.098 ^{****D}	1.749
Pine plantations (r7)	0.145	0.035	0.139	0.017	2.375 ^C	0.351	3.839 ^{****D}	0.237
Protection (r7)	0.484 ^{***A}	0.042	0.534 ^{***B}	0.015	3.087 ^{*C}	0.473	6.911 ^{****D}	0.563
River distance	–0.173 ^{***A}	0.023	–0.071 ^{*B}	0.010	4.709 ^{**C}	0.706	4.055	0.391
River frequency (r4)	0.202 ^{***A}	0.022	0.092 ^B	0.012	5.462 ^{***C}	0.656	4.918 ^{**C}	0.574
River frequency (r7)	0.231 ^{***A}	0.027	0.135 ^B	0.014	4.729 ^{***C}	0.507	5.478 ^{****D}	0.507
Rural population	–0.182	0.024	–0.150	0.010	3.311 ^C	0.397	5.056 ^{****D}	0.537
Slope	–0.045	0.019	–0.022	0.009	4.216	0.641	4.327	0.444
Small farms (r4)	–0.198 ^{***A}	0.020	–0.228 ^{***B}	0.005	7.020 ^C	1.202	12.786 ^{****D}	0.895
Small farms (r7)	–0.165 ^{**A}	0.016	–0.210 ^{***B}	0.006	9.018 ^{*C}	1.019	14.925 ^{****D}	1.666
Town distance	0.115 ^A	0.029	0.183 ^{***B}	0.008	4.209 ^C	0.358	5.936 ^{****D}	0.282
Town frequency (r7)	–0.100 ^{*A}	0.022	–0.113 ^{*A}	0.009	4.723 ^C	0.667	8.449 ^{****D}	1.659

‡Sum of absolute contribution in all factors of ENFA pondered by the Eigen values of each factor.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ from a Dunnett post hoc comparison using the random data set results as a control group. No asterisk means that the marginality or specialization value was not significantly different from the same parameter estimated by random points generated along the surveyed area.

^{A,B}Marginality and specialization (^{C,D}) values in the same row that do not share the same letter were significantly different between puma and jaguar in a *t*-test comparison ($P < 0.05$). This test was used only when pumas or jaguars demonstrated significantly higher marginality or specialization than the random data sets.

However, jaguars showed higher marginality than pumas in relation to the avoidance of these human land uses and in the preference of areas with some degree of protection. Additionally, jaguars occurred in areas more distant from towns and inaccessible to humans, while pumas did not show significant differences with random points in relation to these conditions. Both species preferred areas close to rivers, but pumas showed a significant association with rivers not observed in jaguars. The highest specialization of both species (Table 2) was associated with forest cover, showing that pumas and jaguars have low associations with areas lacking natural cover in this region. However, jaguars were more specialized than pumas in relation to forest cover and local connectivity. Jaguars were also less tolerant towards changes in most of the variables with the exception of distance to rivers, terrain slope and intensive agriculture. Pumas, instead, did not show significant specialization (i.e. no differences with random points) in relation to the frequency of human land uses, rural population density and presence of towns; all these variables were highly associated with human pressures.

Jaguars' global marginality was higher than that of pumas, but values were high for both species relative to the random subsets (Fig. 3; Table S2), showing that under present conditions, pumas and jaguars occupy uncommon areas. High global specialization also characterized both species, but pumas were more tolerant than jaguars (Fig. 3; Table S2). However, this pattern was not reflected in Levins' standardized niche breadth index that showed a slightly broader niche in jaguars than in pumas (Table 3), probably as a result of this index not taking into account the values available in the whole landscape. Nevertheless, jaguars had a higher niche breadth when estimated with Hurlbert's index, which considers the relative abundance of resources. Additionally, asymmetric overlap indexes showed more overlap between the jaguars' niche and that of the pumas than the reverse (Table 3), but their niches were highly overlapping as indicated by the Pianka's niche overlap index (mean \pm SD = 0.746 ± 0.069 ; where 1 indicates complete overlap).

Twenty habitat-suitability maps resulted from the analysis of pumas and jaguar subsets (Fig. S2). The factors used to compute the maps explained on average 88% of the information for pumas and 87% for jaguars, and the mean explained specialization was 75% for both species (Table S3). The continuous habitat-suitability models had intermediate predictive capacity [mean $B_{(\text{cont})} = 0.51$; SD = 0.08 for puma models and $B_{(\text{cont})} = 0.52$; SD = 0.09 for those for jaguars; Table S3]. But the evaluation values were much higher after reclassifying the maps in three categories of habitat [mean $B_{(3)} = 0.92$; SD = 0.05 for puma models and $B_{(3)} = 0.97$; SD = 0.02 for those for jaguars; Table S3].

The final habitat-suitability maps (Fig. 4) showed that the major proportion of the landscape was categorized as marginal habitat for pumas and presented unsuitable conditions for jaguars, and only a low proportion (< 15%) was classified as suitable for both large felids (Table 4). The lower tolerance of jaguars was reflected in a higher proportion of unsuitable areas

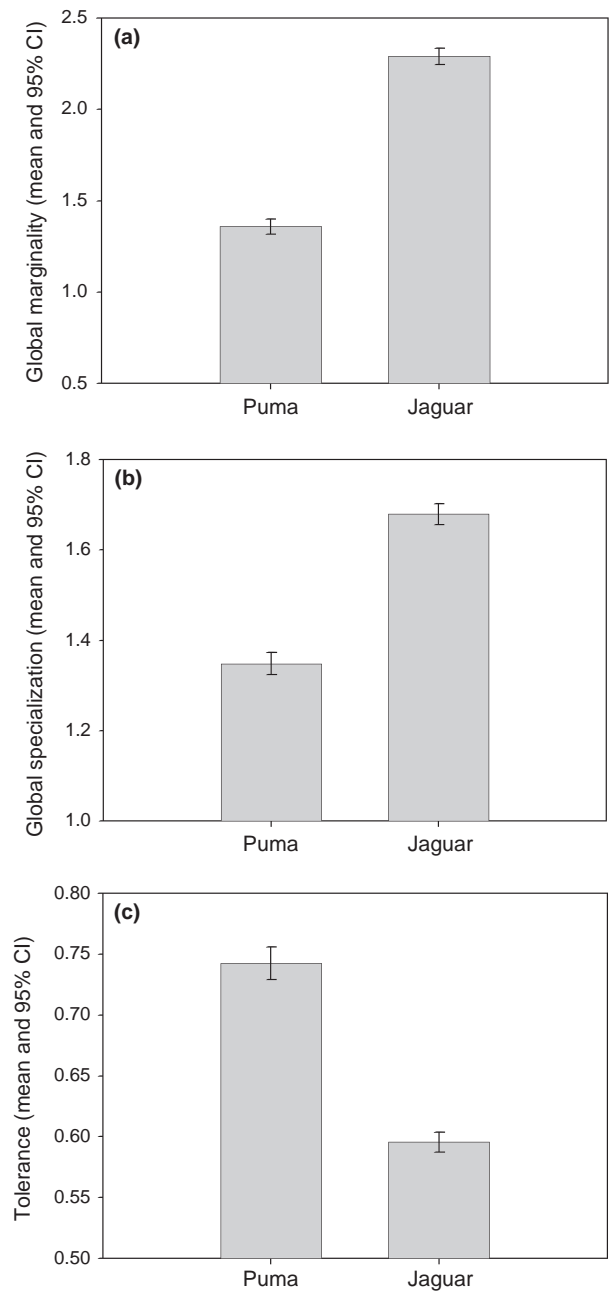


Figure 3 Average global marginality (a), specialization (b) and tolerance (c) estimated for pumas ($n = 10$) and jaguars ($n = 10$) in the human-modified landscape of the Upper Paraná Atlantic Forest. Marginality values close to 0 indicate that the species tends to live in average conditions throughout the study area, and values close to or higher than 1 indicate a tendency to live in extreme habitats in relation to typical conditions present in the study area (Hirzel *et al.*, 2002). Tolerance values close to 0 indicate a 'specialist' species tending to live in a very narrow range of conditions, while values close to 1 indicate species highly tolerant of variation in the landscape variables (Hirzel *et al.*, 2008). For both pumas and jaguars, marginality, specialization and tolerance values differ from those estimated with random points (control group) using a Dunnett comparison ($P < 0.001$). These parameters also showed significant differences between pumas and jaguars in a t -test comparison ($P < 0.001$).

Table 3 Average difference between the traditional niche breadth and asymmetric overlap indexes calculated for the 100 possible pair combinations of the 10 data sets of records of pumas with the 10 data sets of jaguars. These indexes were estimated summarizing the resource states (landscape conditions) along a discriminant factor created by the Discriminant Analysis tool of the BIOMAPPER software (Hirzel *et al.*, 2008). We compared the differences between pumas and jaguars through a paired *t*-test.

Species	Niche breadth		Lloyd's asymmetric overlap†		Rathke's asymmetric overlap‡	
	Levins' standardized index (B*)§	Hurlbert's index¶	Puma (Z21)	Jaguar (Z12)	Puma (Z21)	Jaguar (Z12)
Puma						
Mean	0.411	0.470	–	3.203	–	167.4
SD	0.045	0.106		0.580		47.7
Jaguar						
Mean	0.430	0.351	3.326	–	174.0	–
SD	0.070	0.167	0.595		50.3	
Difference						
Mean	–0.020**	0.118***		0.122***		6.60***
SD	0.066	0.099		0.048		3.67

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ from a paired *t*-test comparison ($n = 100$).

†Lloyd's asymmetric overlap index is a measure of directional niche overlap: Z12 represents the density of species 2 encountered, on average, by the species 1; Z21 is the reciprocal (Hurlbert, 1978).

‡Rathke's asymmetric overlap index is a modification of the Lloyd's index that takes into account the relative abundance of the resource states (Hurlbert, 1978).

§B* is calculated as the frequency of intraspecific encounter expected when all the resources are utilized equally divided by the frequency of intraspecific encounters expected on the basis of the observed distribution. A value of B* close to 0 means that the species is associated with a single resource state (minimum niche breadth) and a value of B* close to 1 means that the species does not discriminate among the resource states (maximum niche breadth; Colwell & Futuyma, 1971; Hurlbert, 1978).

¶Hurlbert's index is similar to B*, but it takes into account the relative abundance of the resource states: it yields 0 only if the species is specialized on the least abundant resource (Hurlbert, 1978).

and less of the study area covered by suitable patches (Fig. 4 and Fig. S2; Table 4 and Table S4). As suggested by their high niche overlap, all jaguar-suitable areas were also suitable for pumas (Fig. 4), but $44 \pm 8\%$ (mean \pm SD) of puma-suitable areas were unsuitable for jaguars. Although suitable areas for pumas were distributed across a larger number of smaller patches than for jaguars, which is usually associated with higher fragmentation, the area-weighted mean patch size was similar for both species (Table 4 and Table S4). This indicates that the larger patches of suitable habitat constitute a similar proportion of the landscape for both pumas and jaguars. However, jaguar-suitable habitat showed less structural connectivity than that of pumas, as their patches were more distant from each other, and the effective mesh size was smaller (Fig. 4; Table 4 and Table S4).

DISCUSSION

Pumas and jaguars responses to human impacts

Both pumas and jaguars have been seriously affected by habitat destruction in the UPAF, as indicated by the high global marginality and the low proportion of landscape with suitable conditions for these large predators (Tables 3 and 4, Fig. 4). Pumas and jaguars presented similar responses to habitat alteration (Table 2), and they showed high niche overlap

regarding their habitat preferences in this landscape (Table 3). However, our results support the hypothesis that pumas are more resistant or resilient to human pressures than jaguars at a regional scale. In the UPAF, where both species inhabited prior to human-induced habitat changes and where they jointly experienced same levels of landscape transformation, the puma persists in less marginal areas and demonstrated a higher association with anthropogenic change than jaguars (Fig. 3). This was reflected in the puma's broader niche (Table 3) and the greater connectivity of suitable habitat for this species (Fig. 4; Table 4).

This regional pattern can be compared with global patterns of ranges for pumas and jaguars. Pumas occurred throughout the geographic distribution of jaguars, while jaguars were absent from approximately 48% of the puma's range (Fig. 1a). Pumas and jaguars both suffered an important retraction in their ranges associated with human pressures (Fig. 1b; Sunquist & Sunquist, 2002). The puma lost at least 28% of its range (Sunquist & Sunquist, 2002), while jaguars have lost around 39% (Zeller, 2007). Both species disappeared from the humid pampas of Argentina, some areas of southern United States and the most disturbed areas of the Atlantic and Pacific coasts of South America. However, in most areas where jaguars have been extirpated, pumas still persist (Fig. 1b). At a regional scale in our study area, we found severe habitat reductions for both species, but a higher loss for jaguars (78% of habitat lost

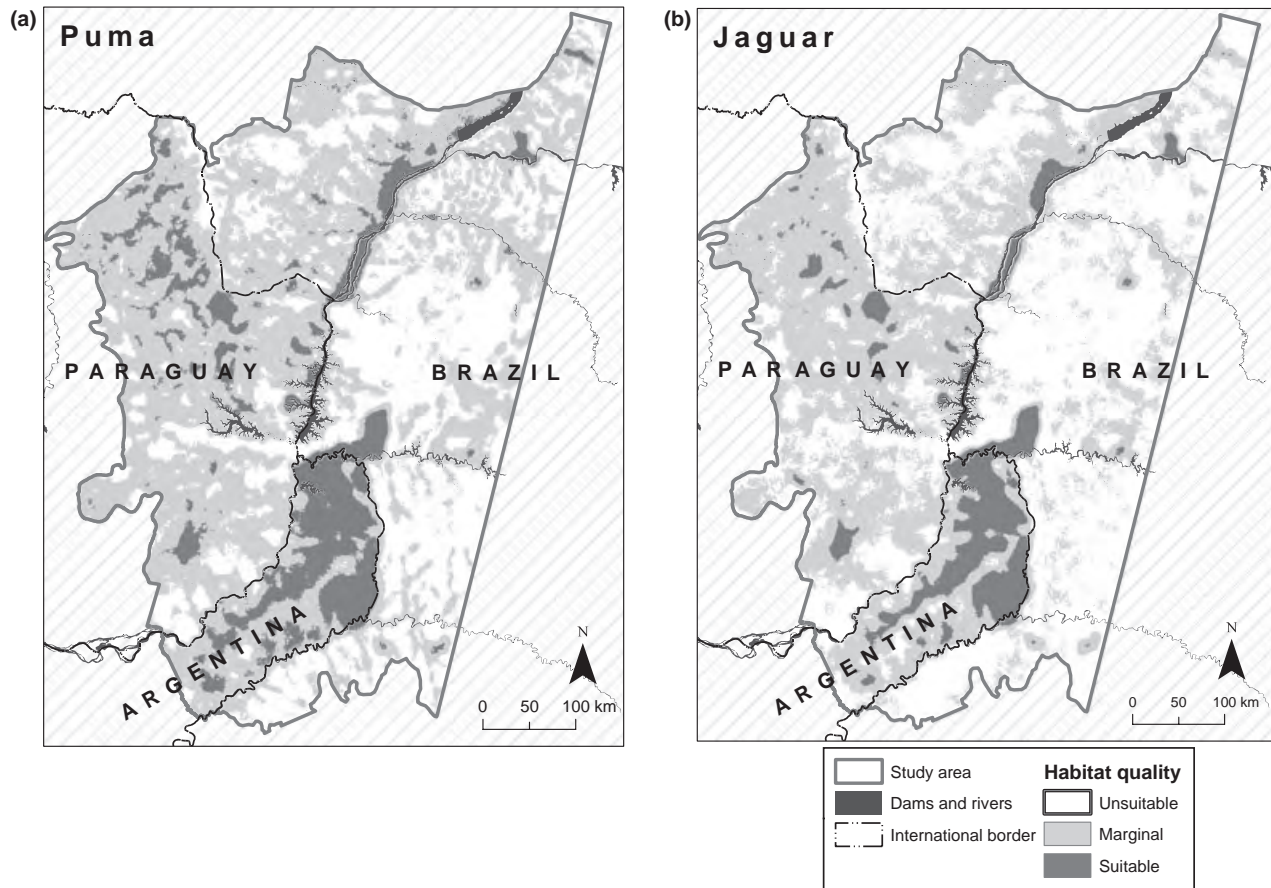


Figure 4 Final habitat-suitability maps of pumas (a) and jaguars (b) in the UPAF. Each cell of these maps was classified into one of the three categories (unsuitable, marginal and suitable) according to a majority analysis of the 10 suitability maps developed for each species applying ENFA with different data sets.

for pumas and 93% lost for jaguars; Fig. 2, Table 4). These differences described for pumas and jaguars in the Americas and in the UPAF are comparable with the relationship observed between leopards (*Panthera pardus*) and the other large felids of Asia and Africa (tigers, *Panthera tigris*, and lions, *Panthera leo*). Leopards, smaller and with a wider distribution, also survive in many areas where the other large cats have disappeared because of habitat alteration and human pressures (Seidensticker, 1976; Sunquist & Sunquist, 2002; Durant *et al.*, 2010).

Considering that most of the study area was covered by forest until the 1800s, we assumed the positive effect of native forest cover and local connectivity and the negative effect of most of the anthropogenic land uses observed in the marginality factor for both jaguars and pumas (Table 2). Similar patterns to those we obtained by ENFA were observed in studies of habitat selection at less extensive spatial scales (Crawshaw & Quigley, 1991; Dickson & Beier, 2002; Silveira, 2004; Kautz *et al.*, 2006). Specifically, in the northern portion of the UPAF, radio-collared jaguars selected native habitats and avoided disturbed areas, and pumas also avoided disturbed areas but used dry forests and extensive pastures more frequently than jaguars (D. Sana, unpublished data;

Cullen, 2006). In our analysis, the main difference between species occurred in the magnitude of the marginality and specialization factors, where jaguars showed higher marginality and specialization than pumas in most of the variables directly related with human alterations and pressures (Table 2).

Pumas and jaguars also were positively associated with rivers (Table 2). Jaguars, but not pumas, are frequently related with marshlands or flooded areas (Crawshaw & Quigley, 1991; Sunquist & Sunquist, 2002; Cullen, 2006). However, our results showed that pumas had a higher association with rivers than jaguars which may be related to the selection of riparian vegetation by pumas for movement and migration, as observed by Dickson *et al.* (2005) in southern California (USA). Small strips of riparian vegetation usually represent the last forest remnants in areas heavily impacted by humans in the UPAF; these seem to constitute inadequate areas for jaguars but are suitable enough for the movement of the more tolerant puma.

Although habitat models for both species had a good fit after reclassification, it is important to note that presence-only models could overestimate the amount of suitable habitat because they ignore absence information (Brotons *et al.*, 2004; Engler *et al.*, 2004; Chefaoui & Lobo, 2008) and because some of the presence records may not come from truly suitable areas

Table 4 Description of the habitat characteristics for pumas and jaguars in the UPAF. The total area covered by each habitat category was calculated by the average of the habitat-suitability maps created for pumas ($n = 10$) and jaguars ($n = 10$) (Fig. S2) and for the final maps (Fig. 4). Fragmentation indices were calculated only for the patches of suitable areas using FRAGSTATS 3.3 (McGarigal & Marks, 1995).

Species	Habitat quality (km ²)			Fragmentation indices for suitable patches				
	Unsuitable	Marginal	Suitable	No. of patches	Mean patch size (km ²)	Area-weighted mean patch size (km ²)*	Euclidean nearest neighbour distance (km)†	Effective mesh size (km ²)‡
Puma								
Mean	84,445 ^A	146,840 ^A	39,090 ^A	3541 ^A	11.2 ^A	7725 ^A	1111 ^A	1144 ^A
SD	32,225	23,635	6233	678	1.9	2008	64	489
Final	101,134 (37%)	141,984 (51%)	33,725 (12%)	2228	15.1	8030	1445	1060
Jaguar								
Mean	128,601 ^B	126,696 ^A	21,545 ^B	855 ^B	26.4 ^B	8140 ^A	1339 ^B	650 ^B
SD	28,572	28,125	1328	214	5.3	1072	97	100
Final	140,331 (51%)	116,058 (42%)	20,454 (7%)	487	42.0	8789	1214	701

^{A,B}Values in the same column that do not share the same letter were significantly different between puma and jaguar in a t -test comparison ($P < 0.05$).

*It is calculated using the area of the patches as relative weights for the weighted average calculation. It is interpreted as the average condition that an individual will find if it is dropped at random on the landscape (McGarigal, 2002).

†It represents the average minimum distance between patches of suitable habitat, and it is a basic measure of isolation (McGarigal, 2002).

‡It is a measure of the structural connectivity of the landscape calculated from the distribution function of the remaining patch sizes. It can be interpreted as the probability that two randomly chosen pixels in the landscape are situated in the same patch, then higher mesh size means higher structural connectivity (Jaeger, 2000).

(e.g. records obtained from sink habitats; Pulliam, 2000; Naves *et al.*, 2003). For example, sex differences in habitat selection could result in counting as 'suitable areas' those that do not hold reproductive populations but only dispersing males (Boydston & López González, 2005; Conde *et al.*, 2010). These biases are probably present in our study for both species, which render our results optimistic in terms of the amount of suitable habitat available for jaguars and pumas in the UPAF. Despite this drawback, one of the main advantages of ENFA technique is the possibility of direct species comparison (Hirzel *et al.*, 2002; Acevedo *et al.*, 2007; Sattler *et al.*, 2007; Durant *et al.*, 2010; Pettorelli *et al.*, 2010), or, as in our case, to understand how ecologically similar species respond to anthropogenic transformations of the landscape. Using ENFA for species comparison has the requirement that the same variables be used for all species, which limits the setting of species-specific models. However, our results are important not only for species comparison but also as a preliminary step for developing further analysis focused exclusively on pumas or jaguars, and generating and testing species-specific hypotheses with more precise methods. For example, our habitat-suitability maps can be used for pseudo-absence generation and then utilized in generalized linear modelling for each species through the approach proposed by Engler *et al.* (2004) and followed by different authors (Chefaoui & Lobo, 2007; Acevedo & Cassinello, 2009; Kanagaraj *et al.*, 2011).

Why are pumas more tolerant than jaguars to human impacts?

Different mechanisms observed at local and global scales may help us understand the patterns observed at the regional scale

in the UPAF. Wide-ranging species are often generalist species, with broad habitat-use ecological niches (Lawton, 1993; Swihart *et al.*, 2003; Jetz *et al.*, 2008). This means that wide-ranging species not only occupy extensive areas, but also use more habitats within their distribution range than sympatric specialist species with narrower ranges (Swihart *et al.*, 2003; Jetz *et al.*, 2008). Pumas' historically wider range may reflect their higher capacity to exploit a more diverse array of habitats than jaguars (Iriarte *et al.*, 1990), including the 'new' habitats created by humans. As our study area is mostly covered by a human-modified landscape, the higher tolerance, broader niche and greater surface of suitable habitat that we described for pumas at regional scales in the UPAF support this explanation (Figs 3 & 4; Tables 3 and 4).

The proximity to range boundaries can be another large-scale explanation for species sensitivity to habitat loss and fragmentation because conditions for species survival are likely to decline in these areas reducing their population abundances and species tolerance to human alterations (Lawton, 1993; Swihart *et al.*, 2003, 2006). The puma still persists in the southernmost portion of their original range in South America (Sunquist & Sunquist, 2002). On the contrary, although the UPAF currently comprises the southern limit of the jaguar range (De Angelo *et al.*, in press), this limit is located about 1000–1500 km north of its historical distribution (Fig. 1). As the region where our study took place is not located on the boundary of the jaguar's original distribution, there is little support for this hypothesis.

Trophic niche breadth is also thought to be important for species resistance to human impacts (Swihart *et al.*, 2003). Pumas and jaguars are opportunistic predators, with broad trophic niches that extensively overlap where these species live

in sympatry (Iriarte *et al.*, 1990; de Oliveira, 2002). However, where both species live together, pumas are smaller than jaguars (Iriarte *et al.*, 1990); they usually exploit a broader trophic niche, often including smaller prey species (Polisar *et al.*, 2003; Scognamiglio *et al.*, 2003; Haines, 2006). Additionally, the higher energetic requirements of jaguars may determine their higher reliance on larger prey species (Novack *et al.*, 2005). Large ungulates are among the mammals most affected by habitat conversion and direct human pressures, and a reduction in the abundance of these species has been documented in different areas along pumas and jaguars ranges (Novack *et al.*, 2005), including the UPAF (Cullen *et al.*, 2000; Paviolo *et al.*, 2009b). The higher tolerance (i.e. lower specialization) of pumas to extensive pastures and little farms that we observed in the UPAF (Table 2) may be related to the availability of small- and medium-sized prey species in these land uses (Perovic, 2002).

Instead of these intrinsic biological traits, population and range reduction can result from the exposure to direct external anthropogenic threats, such as human persecution (Cardillo *et al.*, 2004). Large predators have been historically persecuted by humans (Inskip & Zimmermann, 2009; Karanth & Chellam, 2009). However, human biases towards large carnivores can result in different responses of similar species to anthropogenic landscapes. For example, in North America, wolves (*Canis lupus*) and brown bears (*Ursus arctos*) suffered stronger human persecution than pumas as a result of different human attitudes against them, even though pumas often caused more conflicts with humans and over cattle than the other species (Kellert *et al.*, 1996). Likewise, where pumas and jaguars coexist, jaguars are usually perceived as more dangerous to human safety and more harmful to the cattle (Conforti & Azevedo, 2003; Altrichter *et al.*, 2006; Paviolo *et al.*, 2009a). Furthermore, jaguars have historically been more hunted than pumas because of the higher commercial value of the pelts of the former species (Weber & Rabinowitz, 1996). For these reasons, jaguars might be more persecuted by humans than pumas in most of their distribution. This bias in human attitudes towards these species may explain the higher importance of protected areas for jaguars and the lesser tolerance of this species to the high populated areas, farms and pastures and areas more accessible to humans (Table 2).

These and other mechanisms may interact with each other to explain pumas' higher availability of suitable habitat in relation to jaguars. However, one of the more significant findings that emerge from our work is that these interactions may also result in mechanisms that are operating specifically at a regional scale. Besides the difference in the amount of suitable habitat available for pumas and jaguars, the spatial configuration of suitable habitat in the UPAF also differs (Fig. 4, Table 4). Suitable patches for jaguars have lower structural connectivity than for pumas, which may imply that jaguars experience more harmful effects on their metapopulation dynamics and long-term population and genetic viability (Hanski, 1998; Cullen *et al.*, 2005; Haag *et al.*, 2010).

The study and understanding of species responses to human impacts at different spatial scales is essential for the definition of species-specific management and conservation actions (Sunquist & Sunquist, 2001; Ciarniello *et al.*, 2007). For example, in the UPAF, not only urgent actions are needed for reducing local threats on jaguars (Paviolo *et al.*, 2008), but also regional scale measures are necessary to increase the amount and connectivity of suitable habitats, mainly through habitat protection and forest restoration (Table 2). As a crude approximation, the habitat-suitability maps we developed can direct the selection of specific areas (e.g. marginal habitats) to implement these conservation actions. Additionally, they may guide more detailed (fine-scale) analyses on the specific response of jaguars to anthropogenic landscapes that will provide a better understanding on how their jaguar population structure and viability is affected by the landscape transformation in the UPAF (see De Angelo, 2009).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Details on the species data acquisition and pre-processing.

Appendix S2 Description of the human accessibility cost analysis done for the creation of the cost of access variable (see Table 1).

Figure S1 Scheme describing data selection and pre-processing.

Figure S2 Habitat-suitability maps developed for all the data sets of pumas and jaguars.

Table S1 Table with the speeds and layers utilized for the accessibility cost analysis.

Table S2 Global indexes calculated by ENFA for all data sets.

Table S3 Characteristics of the habitat-suitability maps developed for each data set and evaluation indexes for these models.

Table S4 Description of habitat quality and fragmentation for the habitat-suitability maps of all data sets.

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BIOSKETCHES

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