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Cats under cover: Habitat models indicate a high dependency on woodlands by Atlantic Forest felids

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Abstract

Four Neotropical small and medium felids—the ocelot, jaguarundi, margay, and southern tiger cat—have overlapping geographic distributions in the endangered Atlantic Forest. Local studies show that these felids avoid areas with high human impact, but the three smaller ones use human-modified areas more frequently than do ocelots. To understand how landscape changes affect the habitat distribution of these four felids in the Atlantic Forest of Argentina, we used maximum entropy models to analyze the effect of environmental and anthropogenic factors. We estimated niche breadth and overlap among these felids. The conversion of the native forest to land uses without trees was the most important variable that determined the habitat distribution of the four species. For all four species, the optimal habitat covered about 1/3 of the study area and corresponds mainly to the native forest areas. Nearly 50% of these areas had some level of protection. The niche width was higher for the small felids than for ocelots. Niche overlap was high for all species pairs, but higher among the small felids and lower for each of these with the ocelot. The four felids were negatively affected by native forest loss, with ocelots being more sensitive than the smaller felids. The conversion of unprotected forest areas to other types of land uses would imply a greater habitat loss for these felids. The protection of current remnants of Atlantic Forest in Argentina is important for the long-term conservation of the four felids.

Abstract in Spanish is available with online material.

KEYWORDS

habitat-suitability maps, *Herpailurus yagouaroundi*, human impacts, landscape changes, *Leopardus guttulus*, *Leopardus pardalis*, *Leopardus wiedii*, MaxEnt

1 | INTRODUCTION

Landscape transformation by humans constitutes the most important threat to wildlife, generating population reductions and local extinctions due to habitat loss (Jetz, Wilcove & Dobson, 2007).

The accelerated habitat loss and fragmentation increase the need to understand their effects on animal populations. Mammalian carnivores are especially sensitive to landscape changes due to their relatively large home ranges, dependence on prey availability, low densities, and direct persecution by humans (Cardillo et al., 2004; Crooks, 2002). Knowing the ecological and geographical distribution

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of these species, and particularly how they respond to landscape transformations, has implications in ecology and conservation, among other disciplines, since they allow to evaluate the species conservation status and to understand the causes of species' decline or persistence in a spatially explicit framework (Ferraz, Ferraz, Paula, Beisiegel & Breitenmoser, 2012; Rushton, Ormerod & Kerby, 2004; Sunquist & Sunquist, 2001).

Four Neotropical small and medium felids—the ocelot (*Leopardus pardalis*), the jaguarundi (*Herpailurus yagouaroundi*), the margay (*Leopardus wiedii*), and the southern tiger cat (*Leopardus guttulus*)—constitute a guild of carnivores with overlapping geographic distributions in the endangered Atlantic Forest ecoregion (de Oliveira et al., 2016; Macdonald & Loveridge, 2010; Trigo et al., 2013). Local-scale studies of habitat use show that these four felids avoid areas with high human impact, but the three smaller ones use human-modified areas more frequently than do ocelots (Di Bitetti, De Angelo, Di Blanco & Paviolo, 2010; Kasper, Schneider & Oliveira, 2016; Rinaldi, Rodriguez, Carvalho & Passos, 2015). The last pattern could result from interference competition exerted by the ocelot on the smaller felids (the "pardalis" effect; de Oliveira et al., 2010; Cruz et al., 2018), whereby ocelots may occur in better conserved areas while the small felids are restricted totally or partially to suboptimal habitats (de Oliveira & Pereira, 2013; de Oliveira et al., 2010; Di Bitetti et al., 2010). In the Atlantic Forest of Argentina, the probability of habitat use by ocelots is negatively affected by habitat changes and anthropic pressures and the probability of habitat use by southern tiger cats is negatively affected by ocelot occupancy probability (Cruz et al., 2018). However, it is unknown how these relationships that affect the distribution and habitat use of these species at local scales may affect them at larger spatial scales and, particularly, to what degree they use the highly disturbed areas of the Atlantic Forest.

The habitat-suitability or species distribution models attempt to predict the distribution of a species by combining presence data of a species with environmental and anthropogenic landscape information (Elith et al., 2006). These models estimate the functional response of the species to each variable and the contribution of each variable to explaining the species' presence (Elith et al., 2006; Fourcade, Engler, Rodder & Secondi, 2014; Phillips, Anderson & Schapire, 2006). Using this information, the models estimate the suitability of the study areas for a species and can predict the potential presence of the species at sites that have not been surveyed, serving as a very useful tool to evaluate and elaborate conservation and management actions, for example, identifying valuable areas for the conservation of a species (Chefaoui, Hortal & Lobo, 2005; De Angelo, Paviolo & Di Bitetti, 2011; Ferraz et al., 2012).

Previous studies have used habitat-suitability models to predict the distribution of small and medium Neotropical felids using climatic and topographic information as a proxy for habitat characteristics (Cuyckens, 2013; Espinosa et al., 2017; Martínez-Calderas et al., 2015, 2016). However, for studies conducted at regional or more bounded scales, where climatic variability is minimal, other factors may became more relevant for predicting and understanding current species distributions (Elith & Leathwick,

2009; Scheldeman & van Zonneveld, 2011), especially when focusing on human-modified landscapes and species affected by human persecution like the carnivores in the Atlantic Forest (De Angelo, Paviolo & Di Bitetti, 2011).

In Argentina, the Atlantic Forest has lost almost half of its original extension (Izquierdo, De Angelo & Aide, 2008; Zuleta et al., 2016). The remaining forests have different degrees of anthropic impacts, with several small and very degraded forest fragments and some large expanses of relatively well-preserved forests (e.g., Iguazú National Park and Urugua-í Provincial Park). Deforestation is mainly due to the conversion of the native forest to large-scale pine and eucalyptus monoculture plantations, and to small- and medium-scale agriculture and livestock farming (Chebez & Hilgert, 2003). In order to understand how these landscape changes affect the four sympatric felids, we aimed to estimate habitat distribution for the medium and small felids of the Atlantic Forest of Argentina and to analyze what environmental and anthropogenic factors determine the distribution of the four felids and compare the relative effect among species. We hypothesized that the ocelot is more sensitive to human impacts than the three small felids, expecting it to have a lower range of habitat suitability and niche amplitude, restricted to areas of low anthropogenic impact, while the small felids have a wider range of tolerance to human impacts. We also evaluated niche overlap, expecting higher overlap among the three smaller felids and lower overlap between each of them and the ocelot.

2 | METHODS

2.1 | Study area

We conducted this study in the province of Misiones, Argentina (Figure 1; 54.2585° W, 25.9312° S). The area contains the world's largest continuous fragment of Upper Parana Atlantic Forest, a semi-deciduous subtropical forest. The remaining forest—shared by Argentina Paraguay and Brazil—is distributed among several fragments that occupy only 7% of the original extent of this ecoregion (Di Bitetti, Placci & Dietz, 2003). However, the area still contains the complete regional native mammal assemblage (Giraudo & Abramson, 2000). Misiones Province (29,801 km^2) still retains 55%–60% of the original native forest (Zuleta et al., 2016), although a large proportion corresponds to highly degraded forests due to intense logging and it is fragmented by forest plantations (pine and eucalyptus), agriculture (maize, tobacco, yerba mate, tea), and cattle ranching (Chebez & Hilgert, 2003; Placci, 2000). In the southernmost portion of Misiones Province, there are typical formations of the Southern Cone Mesopotamian savanna ecoregion, dominated by grasslands interspersed with native forests. These natural grasslands are very difficult to distinguish from those of anthropic origin resulting from forest conversion, since most of them are used for cattle ranching and both occupy <1% of the provincial surface. Since the limits of both ecoregions are not easily demarcated, we included the whole Misiones Province as our study area instead of only the portion exclusively belonging to the Atlantic Forest.
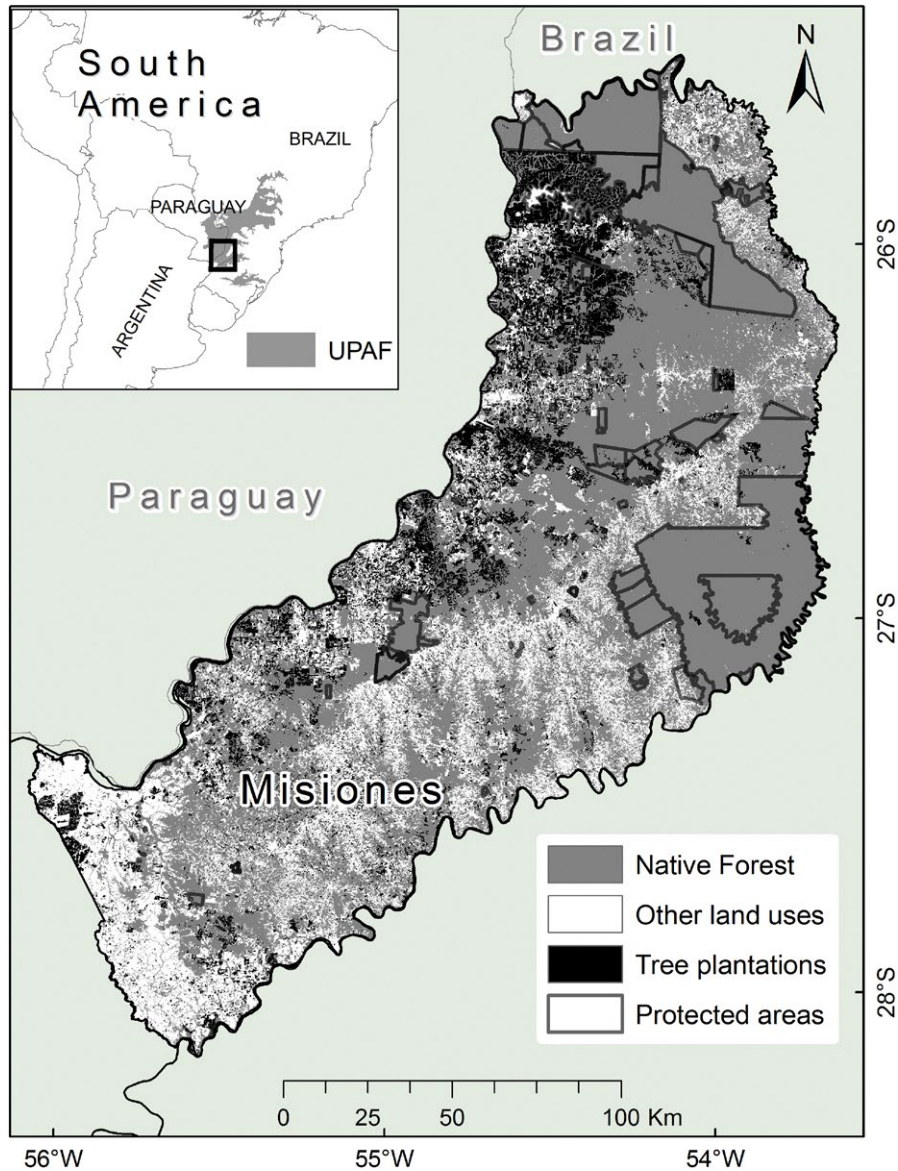
FIGURE 1 The study area, Misiones Province, Argentina. The area contains the largest remnants of the Upper Paraná Atlantic Forest (UPAF) and several protected areas

2.2 | Presence data of small and medium felids

We used presence-only data for the four felids collected throughout most of Misiones Province between 2003 and 2015. These data were obtained through the following sampling methods: camera trap records from the authors' own and colleagues' systematic and non-systematic surveys (Di Bitetti, Paviolo, De Angelo & Di Blanco, 2008; Iezzi, Cruz, Varela, De Angelo & Di Bitetti, 2018; Paviolo, De Angelo, Di Blanco & Di Bitetti, 2008; Paviolo, Di Blanco, De Angelo & Di Bitetti, 2009; Paviolo et al., 2016), roadkills, reliable sightings (i.e., animals seen by experts or a photograph allowing identification by experts), and feces identified by DNA analyses (Cruz, 2017). The feces were collected through the authors' own and colleagues' fieldwork and by a participatory monitoring network (De Angelo, Paviolo, Rode et al., 2011). We discarded doubtful records or those

that were not correctly georeferenced. We collected a total of 848 records: 489 of ocelots, 110 of jaguarundis, 57 of margays, and 192 of southern tiger cats.

In order to reduce potential biases and spatial interdependencies caused by opportunistic data collection (e.g., >1 record from the same individual; (Sattler, Bontadina, Hirzel & Arlettaz, 2007; Kanagaraj, Wiegand, Mohamed & Kramer-Schadt, 2013), we removed spatially clustered data from the analysis. For this purpose, we overlaid a grid with cell size equivalent to the home range of a female for each species using ArcGIS 10.1. These home ranges were obtained from radiotelemetry studies carried out in the Atlantic Forest region: 17.4 km² for the ocelot (Crawshaw, 1995), 19.6 km² for the jaguarundi (Crawshaw, 1995), 21.8 km² for the margay (Kasper et al., 2016), and 16.4 km² for the southern tiger cat (Kasper et al., 2016). We randomly selected a single

presence record from each cell that contained more than one record (Kanagaraj, Wiegand, Kramer-Schadt, Anwar & Goyal, 2011; Sattler et al., 2007). As a result of this filtering procedure, sample sizes were reduced to 127 presence records for ocelots, 59 for jaguarundis, 46 for margays, and 97 for southern tiger cats (Supporting Information Figure S1).

2.3 | Landscape variables

The study area was characterized using variables related to human pressures and landscape characteristics, each with a 30 × 30-m resolution. We used a land-use map constructed from a mosaic of Landsat-8 TM satellite images from 2013 and 2014 by Zuleta et al. (2016). This map contained the following land uses and covers: native forest, exotic tree plantations (e.g., pine and eucalyptus plantations), shrub crops (e.g., yerba mate, tea), herbaceous crops (e.g., tobacco, maize), mixed crops (e.g., small patches of shrubs and herbaceous plants), pastures, natural water bodies, artificial water bodies, wetlands, bare natural areas, and urban areas. The urban areas, natural water bodies, and artificial water bodies were considered not suitable sites for the felids, and therefore, they were excluded from the analysis. Although presence data were collected between 2003 and 2015, we selected a land-use map from 2014 for building our variables as it was the map that best describes the land uses occurring when most records were obtained. The older records correspond mostly to protected areas, a land use that has not changed during the study period.

From the land-use map, we generated four continuous variables: (a) the distance to potential source habitats (*distance to forest*), (b) the proportion of native forest (*% of forest*), (c) the proportion of *Pine* and *Eucalyptus* plantations (*% of tree plantations*), and (d) the proportion of productive lands excluding tree plantations (*% of land uses without trees*). The proportion of productive land uses without or with very few trees (herbaceous crops, mixed crops, shrub crops, pastures, wetlands, and bare natural areas) were grouped in a single variable (*% of land uses without trees*) because they were correlated (Spearman coefficients > 0.70) and due to the low number of presence records for the four felids in each of them. The variable *distance to forest* represents the Euclidean distance from each cell to the edge of the nearest large native forest fragment. These large native forest fragments were continuous native forest blocks that included only areas surrounded by more than 95% forest cover within a 2-km radius for each cell. This distance is positive for cells located outside the large forest fragments and negative for those within the large forest fragments. The percentage of native forest and productive land uses were also estimated within a 2-km radius. For calculating these variables, we used a neighborhood analysis, where each cell in the landscape is characterized by the conditions in the neighboring cells (Hirzel, Hausser, Chessel & Perrin, 2002). Because the scale of perception of the landscape by carnivores is often related to their home-range size (Kanagaraj et al., 2011; Naves, Revilla, Delibes & Wiegand, 2003; Schadt et al., 2002), we used a neighborhood scale related to the approximate home-range size of females of the four felids: a circle with radius of 2 km.

2.4 | Habitat-suitability models

We chose MaxEnt for running the species distribution models for the four felids. MaxEnt estimates the realized niche of the species and the probability of occurrence using a maximum entropy algorithm (Phillips et al., 2006). It does not use absence data but uses background locations to contrast those with presence data. These background locations are randomly selected from the entire study area. If the sampling effort for data collection is not homogeneously distributed throughout the study area, it may lead to imprecisions or biases in the results (Fourcade et al., 2014; Kramer-Schadt et al., 2013; Merow, Smith & Silander, 2013; Phillips et al., 2009). In order to reduce this bias, MaxEnt allows incorporating a "bias file," where background data are chosen with the same spatial bias as sampling effort. This approach has been found to improve habitat-suitability model performance (Kramer-Schadt et al., 2013; Phillips et al., 2009). The bias file should be an indicator of the sampling effort throughout the study area. In our study, we developed a bias file using the location of all camera traps (regardless of whether they registered any of the four felids or not), and the locations of all the feces collected (including other felid feces, such as jaguar and puma feces). With these data and the point density tool of ArcGIS, we developed a map with four sampling effort categories: null effort, low effort, medium effort, and high effort (Supporting Information Figure S2).

Correlations among the four variables showed that *distance to forest*, *% of forest*, and *% of tree plantations* were highly correlated to each other (Supporting Information Table S1), and therefore, we decided to not combine them in a single model. Using the possible combinations of the uncorrelated variables, we ran models using three combinations of variables for each felid with Maxent 3.3.3k (Phillips & Dudík, 2008): (a) models including *% of land uses without trees* and *% of tree plantations*, (b) models including *% of land uses without trees* and *% of forest*, and (c) models including *% of land uses without trees* and *distance to forest*. In order to analyze the potential interaction between the variables, for each combination of variables, we run models with and without the product feature (i.e., using the linear and quadratic format (LQ) and the linear quadratic and product format (LQP; Merow et al., 2013). To evaluate the fit of each model and to select the best model for each species, we used the Akaike information criterion adjusted to the sample size (AICc; Burnham & Anderson, 2002; Warren & Seifert, 2011; Merow et al., 2013), using the program ENMTools 1.4 .4 (Warren, Glor & Turelli, 2010). Once selected the best model for each species, we re-ran 10 replicates of these models with cross-validation and we set them with a convergence threshold = 1.0E-5, maximum iterations = 500, regularization multiplier = 1, and 10,000 background points (Merow et al., 2013). The resulting models of MaxEnt are maps with continuous cell values ranging from 0 (least suitable habitat cells) to 1 (most suitable habitat cells). These values can be interpreted as the probability of presence of optimal habitat conditions for the species (Veloz, 2009).

For conservation or management purposes, it is useful to obtain maps with defined habitat-suitability categories (Liu, Berry, Dawson & Pearson, 2005) since these allow, for example, to make

easier comparisons of habitat suitability among species or areas within a study region or to know the amount of certain environments available for a specie within a habitat-suitability category. In order to separate habitat from non-habitat areas, we used the minimum training presence criteria. This threshold identifies the minimum area that contains all presence data (Liu et al., 2005). To classify habitat areas into optimal and marginal habitats, we used the maximum training sensitivity plus specificity threshold that maximizes the sum of the sensitivity (true predicted presences) and specificity (true predicted absences). This threshold criterion has been described as the most objective and adequate criterion to identify optimal habitats when only presence data are available (Jiménez-Valverde & Lobo, 2007; Liu, Newell & White, 2016; Liu, White, Newell & Pearson, 2013; Liu et al., 2005). With the resulting maps, we estimated the area of optimal habitat available for each felid, the percentage of the different land uses within the optimal habitat for each species, and the percentage of the optimal areas that has some level of protection (e.g., public and private protected areas).

2.5 | Niche species comparisons

We estimated niche parameters for the four felids from the resulting habitat-suitability models using the ENMTools 1.4.4 program (Nakazato, Warren & Moyle, 2010; Warren et al., 2010). The niche amplitude was estimated using Levin's inverse concentration index (Levins, 1968). This index ranges from 0, the lowest niche amplitude possible, to 1, the maximum possible (Mandle et al., 2010). We also estimated the niche overlap index among felids, using the "I" index based on the Hellinger index (Warren, Glor & Turelli, 2008). The "I" index ranges from 0 (no niche overlap) to 1 (total niche overlap). These indices ("Levins" and "I") are based on the continuous habitat-suitability model values. From the ten replicates of each model selected by AICc, we estimated the average value of these indices and their confidence intervals (Warren, Wright, Seifert, Shaffer & Franklin, 2014).

3 | RESULTS

3.1 | Habitat-suitability models

The models containing the negative effects of the *distance to forest* and *% of land uses without trees* (Supporting Information Table S2) were
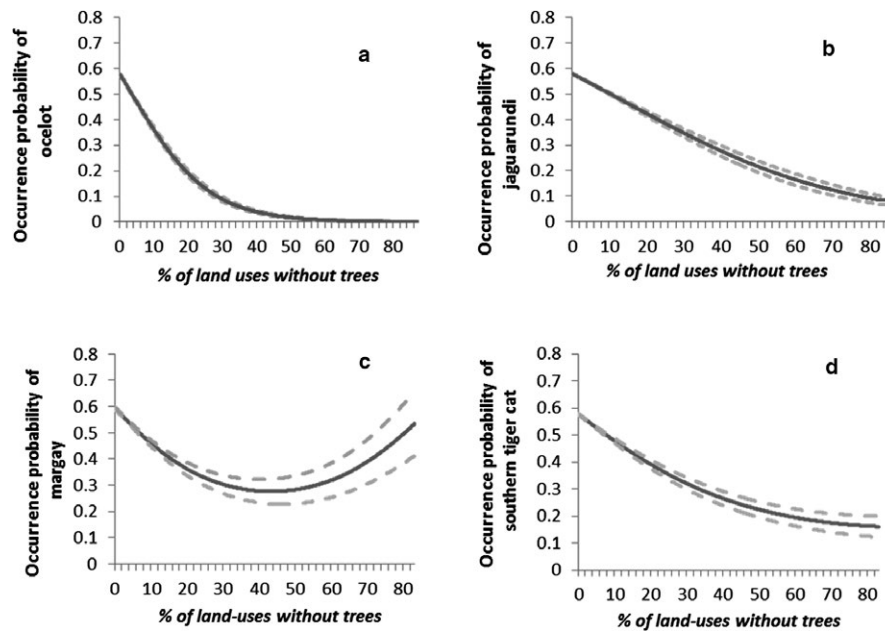
selected as the best combination of variables for each of the four felids given its lower AICc value. For the margay and the southern tiger cat, the best models included the linear and quadratic features (LQ), and for the ocelot and the jaguarundi, they also included the product feature (LQP), denoting some level of interaction between the variables for these two felids (Supporting Information Table S2).

For the four felids, the contribution of the two variables to the models was similar, with the *% of land uses without trees* showing the highest weight (Table 1). Though generally similar, each felid showed a slightly different probability response curve (Figures 2 and 3). The response curve of ocelots to *% of land uses without trees* decreases at a higher rate than the curves of the three small felids. For example, at 40% of land uses without trees, the probability of occurrence for ocelots was 0.03 (Figure 2a), while for jaguarundis, it was 0.26 (Figure 2b), for margays 0.28 (Figure 2c), and for southern tiger cat 0.26 (Figure 2d). Also, at 70% of land uses without trees, the probability of occurrence of ocelots is almost zero, whereas for small felids, it is well above 0.15 and it does not reach zero even in locations with almost 100% *of land uses without trees*. For margays, the graph of this relationship is U-shaped, with a minimum at 40% *of land uses without trees* and rising as the percentage of these land uses increases or decreases (Figure 2c). The four felids decrease their probabilities of occurrence as the *distance to forest* increases, although the ocelot showed again a higher response rate than the three small felids. The probability of occurrence for ocelots becomes lower than 0.1 at 15 km of *distance to forest* (Figure 3a), whereas for the jaguarundi, it happens at 22 km (Figure 3b), for the margay at 35 km (Figure 3c), and for the southern tiger cat, the probability of occurrence is approximately 0.3 at a distance of 25–30 km (Figure 3d). For the ocelot, the negative effect of the *distance to forest* is higher at sites with 11%–50% *of land uses without trees* than at sites with 0%–10% of these uses, and at areas with more than 50% *of land uses without trees*, the *distance to forest* seems to have no effect since the probability of occurrence is almost zero (Figure 4). For jaguarundis, the negative effect of the *distance to forest* seems to be more important at sites with 11%–90% *of land uses without trees* than at sites with 0%–10% (Figure 4).

Areas with the highest habitat suitability for the four felids corresponded with the largest native forest fragments of northern Misiones Province, formed mostly by contiguous protected areas (compare Supporting Information Figure S3 with Figure 1). To the south, the sites with suitable habitat quality were smaller and more isolated but they still overlap the forest remnants. For ocelots, this southern portion was dominated by areas of low habitat suitability, while for the smaller felids, there was a predominance of areas with intermediate and low habitat suitability values (Supporting Information Figure S3).

3.2 | Discrete habitat-suitability models

By applying the threshold criterion, we obtained categorical maps with three categories of habitat quality (Figure 5). About 30% of

TABLE 1 Contribution of the variables *distance to forest* and *% of land uses without trees* to the best model (model 3) for each of the four felids

Variables	Percent of contribution for			
	Ocelot	Jaguarundi	Margay	Southern tiger cat
Distance to forest	20.1	32.3	24.5	21.4
% of land uses without trees	79.9	67.7	75.5	78.6

FIGURE 2 Relationship between the occurrence probability for ocelot (a), jaguarundi (b), margay (c), and southern tiger cat (d) and the percentage of land uses without trees within a radius of 2 km
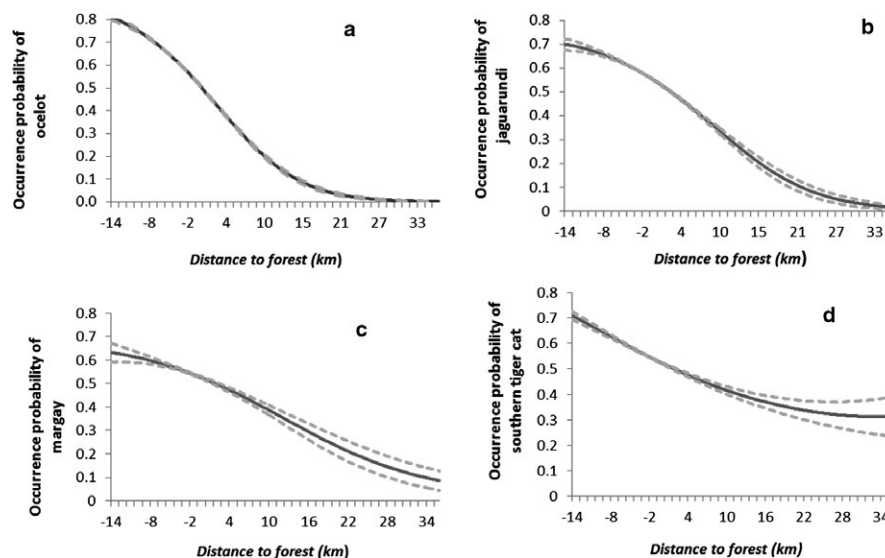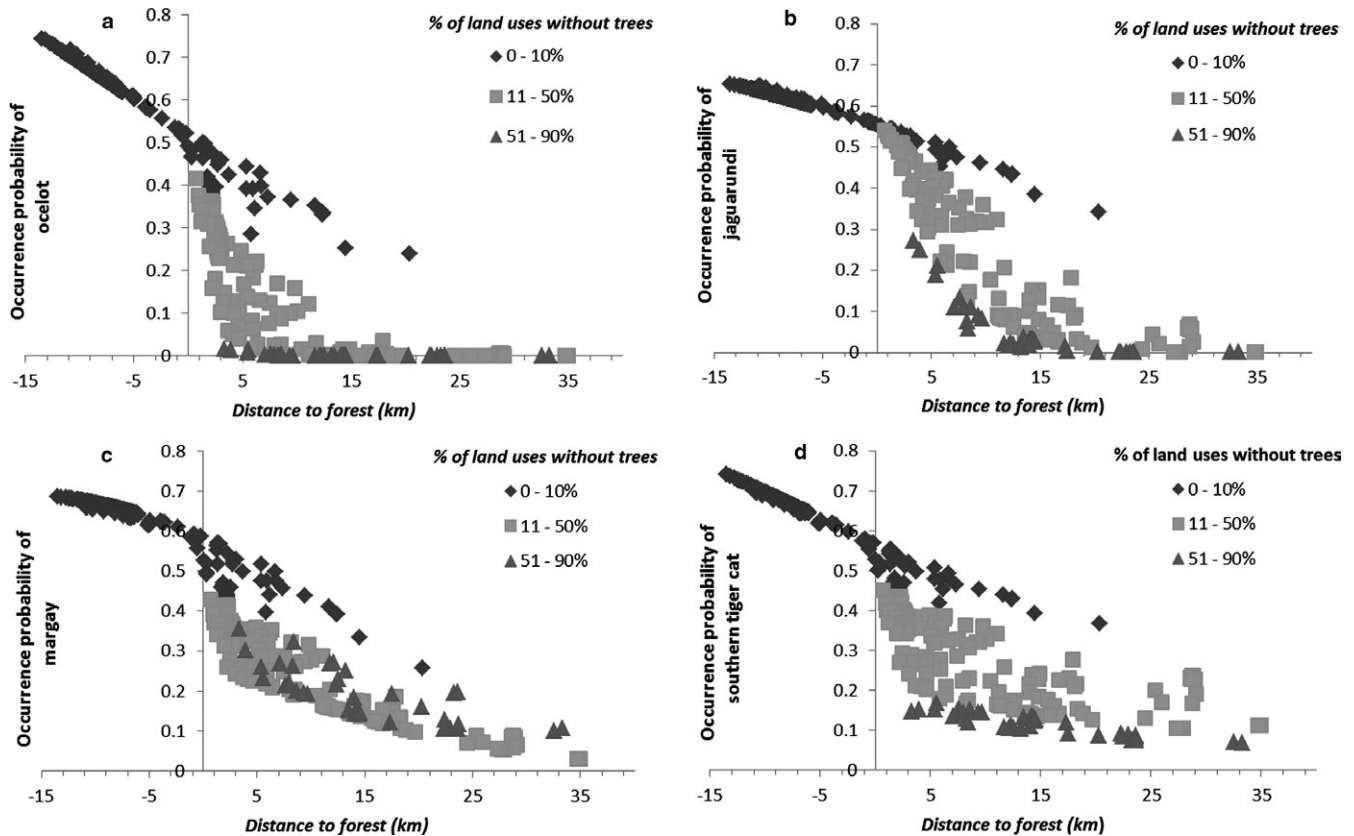

FIGURE 3 Relationship between the occurrence probability for ocelot (a), jaguarundi (b), margay (c), and southern tiger cat (d) and the distance to the edge of large native forest fragments

Misiones represented suitable habitat for the four felids, ranging from 27% for the margay to 36% for the jaguarundi (Table 2). The spatial distribution of these suitable habitats was similar for the four felids. About 90% of these optimal areas were located in native forests, nearly 9% were located in tree plantations (pines and eucalyptus), and about 1% were distributed among shrub crops, herbaceous crops, and mixed crops for the four felids. The tree plantations and the different crops identified as suitable habitat were all surrounded by native forest fragments and close to the large forest fragment. About 50% of the suitable areas presented some protection category (national park, provincial parks, public and private reserves).

The ocelot presented the greatest area of unsuitable habitat. The margay and the southern tiger cat presented a greater area of marginal habitat than suitable habitat, while the jaguarundi presented similar proportions for these habitat categories (Table 2). For ocelots, the tree plantations represented higher percentages of marginal and unsuitable habitat, whereas for jaguarundis, margays, and southern tiger cats, they represented higher percentages of marginal habitat. The mixed, shrub, and herbaceous crops represented higher

FIGURE 4 Relationship between the occurrence probability for ocelot (a), jaguarundi (b), margay (c), and southern tiger cat (d) and the distance to the edge of large native forest fragments for different percentages of land uses without trees within a radius of 2 km

percentages of unsuitable habitat for ocelots, but for jaguarundis and southern tiger cats, they represented mostly marginal or un-suitable habitat and for margays they represented mainly marginal habitat (Table 2).

3.3 | Niche species comparisons

The niche breadth was similar for the three small felids and higher for them than for the ocelot (Table 3). Niche overlap was high for all species, indicating similar habitat preferences. However, the over-lap was higher among the three smaller felids and slightly lower be-tween each of them and the ocelot (Table 3).

4 | DISCUSSION

In the Atlantic Forest of Argentina, the small and medium wild cat species have been negatively affected by forest loss, since their habitat suitability decreased with the distance to the continuous na-tive forest and in areas without tree cover. However, not all of these species responded to these variables with the same magnitude. The ocelot was the most affected by land uses associated with the lack of forest and by the distance to the native forest, showing a rapid drop in the probability of occurrence as the productive land uses

and the distance to the native forest increased, especially in areas with 10%–50% of lack of cover. These results support the hypothesis that the ocelot is more sensitive to human disturbance compared to the smaller felids (de Oliveira et al., 2010; Dematteo et al., 2014; Di Bitetti, Paviolo & De Angelo, 2006; Di Bitetti, Paviolo, De Angelo et al., 2008; Di Bitetti et al., 2010; Kasper et al., 2016; Rinaldi et al., 2015).

Ocelots can inhabit regions with low tree cover (brushlands in Mexico and the United States), so the greater sensitivity to tree cover loss may not be due exclusively to the loss of the forest structure itself but rather to other associated factors. The areas with the low-est tree cover in Misiones are those with the highest human activity (agriculture, livestock, and subsistence farms). In general, in these areas, there is less availability of medium and large prey which are important for the ocelot but not for the smaller felids (Cruz, 2017). In addition, these areas often present greater threats (presence of dogs, greater density of roads, etc.), which could also negatively af-fect this species.

The southern tiger cat and the jaguarundi, like the ocelot, showed a monotonic decrease in their probability of occurrence with an increase in land uses without trees. This can be expected for the southern tiger cat since it inhabits mostly forested areas of the Atlantic Forest. However, it was not expected for the jaguarundi since it also inhabits non-forested areas, such as scrublands and
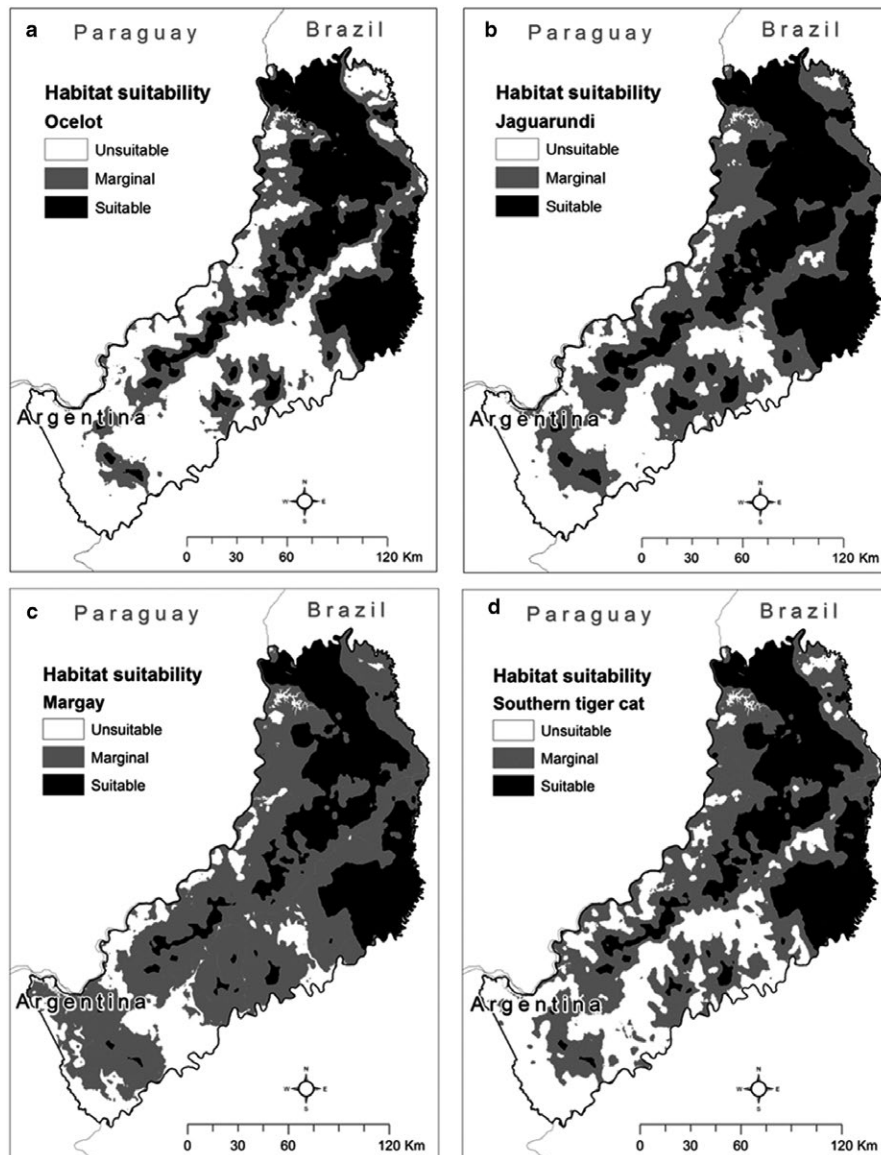
FIGURE 5 Categorical habitat-suitability maps for ocelots (a), jaguarundis (b), margays (c), and the southern tiger cats (d) in the Atlantic Forest of Misiones, Argentina. Each cell of these maps was classified into one of the three categories (unsuitable, marginal, and suitable) according to threshold criteria

grasslands of central Argentina and central Brazil (Caso, de Oliveira & Carvajal, 2015). This result reinforces the hypothesis that other factors associated with forest loss (lower prey availability, higher mortality, etc.) exist in areas of Misiones dominated by land uses without trees that are affecting the populations of this felid.

The non-monotonic response of the margay to the lack of tree cover was unexpected since this species is commonly characterized as the most arboreal of the Neotropical felids due to its morphological adaptations to an arboreal environment (de Oliveira, 1998; Emmons & Feer, 1997). Although the response curve of this felid indicates a high probability of occurrence at low and high tree cover values, the confidence interval also increases with the percentage of land uses without trees. This response could be partially explained by a bias in their detectability. At sites with greater tree cover, this felid may be less detected as it spends more time moving through

the canopy. At sites with low tree cover, it may increase its detectability (i.e., by camera trap stations located at ground level) because margays may move more frequently on the ground in environments without a continuous canopy. Notwithstanding this potential bias, our results suggest that the margay can inhabit sites with low tree cover, despite its adaptations for tree climbing (de Oliveira, 1998; Emmons & Feer, 1997).

The distance to the edge of large native forest fragments was also an important covariate, as indicated by the lower AICc value of the models that included this variable. The four felids were negatively affected by increasing distance to the edge of the large native forest fragments. The presence of these felids in small forest fragments may depend on the presence of a close population source, and forest connectivity is essential for the persistence of these felids in productive landscapes. However, the southern tiger cat had a

TABLE 2 Percentage of the total area of Misiones covered by each habitat category for the four felids calculated from the categorical maps

Land uses	Ocelot (%)	Jaguarundi (%)	Margay (%)	Southern tiger cat (%)
Suitable habitat				
Total	32.40	36.12	26.74	28.94
Native forest	28.71	31.79	24.40	26.06
Tree plantation	3.34	3.36	2.23	2.70
Mixed crop	0.16	0.42	0.05	0.08
Herbaceous crop	0.11	0.32	0.03	0.05
Shrub crop	0.08	0.23	0.03	0.05
Wetland	0.00	0.00	0.00	0.00
Bare natural area	0.00	0.00	0.00	0.00
Pasture	0.00	0.00	0.00	0.00
Marginal habitat				
Total	25.26	37.96	58.59	42.75
Native forest	15.42	20.01	30.36	25.50
Tree plantation	5.15	7.34	9.33	8.25
Mixed crop	2.02	4.52	7.70	3.81
Herbaceous crop	1.37	2.85	5.73	2.46
Shrub crop	1.26	3.08	4.77	2.61
Wetland	0.02	0.05	0.18	0.05
Bare natural area	0.01	0.01	0.01	0.01
Pasture	0.01	0.10	0.51	0.05
Unsuitable habitat				
Total	42.34	25.92	14.68	28.31
Native forest	16.32	8.64	5.67	8.88
Tree plantation	5.24	3.04	2.18	2.78
Mixed crop	8.13	5.37	2.57	6.42
Herbaceous crop	4.79	3.11	2.45	3.76
Shrub crop	6.87	4.90	1.47	5.55
Wetland	0.30	0.26	0.13	0.27
Bare natural area	0.00	0.00	0.00	0.00
Pasture	0.69	0.61	0.20	0.66

TABLE 3 Niche breadth and niche overlap and their confidence intervals (95%) estimated with *Levins index* and *Hellinger index*, respectively, using the ENMTools program

	Niche amplitude	Niche overlap			
		Ocelot	Jaguarundi	Margay	Southern tiger cat
Ocelot	0.476 (0.469–0.483)	1	0.952 (0.946–0.957)	0.914 (0.899–0.930)	0.920 (0.913–0.928)
Jaguarundi	0.691 (0.621–0.761)	X	1	0.969 (0.963–0.975)	0.977 (0.972–0.982)
Margay	0.762 (0.716–0.807)	X	X	1	0.990 (0.987–0.992)
Southern tiger cat	0.770 (0.751–0.789)	X	X	X	1

greater tolerance to increasing distances from the continuous forest than the other felids, supporting our prediction that the southern tiger cat has a greater tolerance to fragmentation than the ocelot. Also, the observed differences from the margay's and jaguarundi's responses might be due to the fact that, being the smaller of the cats, the southern tiger cat could satisfy its habitat requirements in smaller fragments than the other felids as a result of its smaller home-range size (Kasper et al., 2016).

The distribution of suitable habitats was similar for the four felids, covering one-third of the total area of Misiones. This represents a large reduction in the suitable habitat if we consider that, originally, these species may have had continuous habitat over the whole Misiones Atlantic Forest (IUCN, 2016). Most of the area identified as suitable habitat corresponds to native forest sites, suggesting a great dependence for the four felids on this environment. Half of the suitable area has some protection status. The native forest must be preserved in order to ensure the availability of suitable habitat for the small- and medium-sized felids and other wildlife of Misiones (e.g., jaguars and pumas, Paviolo et al. (2008, 2009), De Angelo, Paviolo, Wiegand, Kanagaraj and Di Bitetti (2013); tapirs, Cruz, Paviolo, Bó, Thompson and Di Bitetti (2014); red brocket deer, Di Bitetti, Paviolo, Ferrari, De Angelo and Di Blanco (2008)). In addition, conversion of the unprotected native forest to other types of land use, mainly crops, would imply a significant loss of optimal habitat for these species.

The ocelot had the narrowest niche of the four felids. The habitat-suitability maps suggest that its optimal habitat is limited to areas with a large percentage of native forest. Ocelots are more strongly associated with the native forest than the other felids, confirming our hypothesis that ocelots are more sensitive to human impacts. The three small cats, and specially the margay, had a broader niche due to their higher tolerance of human impacts and fragmented environments (de Oliveira et al., 2010; Di Bitetti et al., 2010; Kasper et al., 2016; Rinaldi et al., 2015). However, sites with high suitability for ocelots correspond to highly suitable sites for the small felids as well, so niche overlap among the four felids was high. These results are similar to those observed for the big felids (pumas and jaguars) in the Upper Parana Atlantic Forest. The jaguar, the largest felid, showed a narrower niche breadth than the puma (De Angelo, Paviolo & Di Bitetti, 2011), the latter demonstrating a larger capability to use areas with higher human impacts since jaguars disappeared from those areas. However, niche overlap between the two large cats is high, with a similar distribution of the suitable habitat for both species, mainly well-protected native forests.

At the scale of this work, where a great variety of environments were included (from continuous native forest sites to areas without tree cover), the suitable habitat of the four felids was almost entirely restricted to the native forest. The highest probability of occurrence for all four species occurs in the largest native forest remnants, mostly within protected areas. At a more local scale, in the northern part of Misiones, in an area mainly dominated by high tree cover (i.e., native forest and pine plantations), native forest loss negatively affected these species (Cruz et al., 2018). However, the main factor negatively affecting the occurrence of the southern tiger cat at this scale was the presence of the ocelot and not the lack of native forest (ibid.). This suggests that the main factors affecting the habitat use of these felids can vary according to the scale of analysis, and at a more local scale, interspecific competition gains importance (Jiménez, 1996; Mitchell & Banks, 2005).

Habitat-suitability models are very useful tools for generating management and conservation recommendations since they are spatially explicit and allow the identification of specific areas where actions should be implemented (De Angelo et al., 2013; Ferraz et al., 2012; Thorn, Nijman, Smith & Nekaris, 2009). For example, in the southern part of Misiones, several small areas have been identified as suitable habitat for these felids. However, they are highly fragmented and relatively isolated and it is not clear whether they can sustain populations or not of these species. Further research should be concentrated in these fragments where little or no studies have been conducted, particularly on the population status of these species and on the functional connectivity of their habitat. Also, these models are useful to understand how the species are affected by landscape transformation by humans, something that is particularly important for little known species or for those difficult to study or with scant records, like the margay and the jaguarundi. The results of this work suggest that, even though the smaller cat species show a slightly higher tolerance for human disturbance than the ocelot, the survival of all the wild felids of the Atlantic Forest (including jaguar and pumas; see De Angelo et al. (2013), Paviolo et al. (2016)) is highly dependent on the protection of the remaining native forests.

DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sq7072h (Cruz et al., 2019).

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SUPPORTING INFORMATION

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