

Barriers, corridors or suitable habitat? Effect of monoculture tree plantations on the habitat use and prey availability for jaguars and pumas in the Atlantic Forest



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ABSTRACT

Large carnivores are key elements of natural ecosystems and most of them are declining due to the impacts of human activities. Jaguars and pumas are the largest felids of the American continent, and particularly jaguars are critically endangered in the Atlantic Forest of South America. As with other tropical forests, the Atlantic Forest has been converted to human land uses including forest tree plantations with exotic species. We assessed jaguars and pumas habitat use in a productive landscape of exotic pine plantations and forest areas in the Atlantic Forest of Argentina. We estimated the availability of their main preys in this landscape and evaluated the variables that affect their occupancy pattern. We developed large scale camera traps surveys between 2013 and 2014 in an area that includes pine plantations, protected areas, and unprotected areas covered by native forest and small rural properties. In total, we sampled 274 sampling stations with an effort of 13,347 camera-trap days. We used single-species single-season occupancy models to evaluate the effect of the proportion of pine plantation around the sampling station, the cost of human access, and the distance to the edge of the continuous forest block on the occupancy of the felids and its main prey species. For felids, we also evaluated the effect of the availability of their prey species. With a few exceptions, the occupancy probabilities of most prey were affected by one or two of the landscape variables tested. Habitat use by jaguars and pumas was affected by this anthropogenic landscape change. Even though the relative proportion of plantation to forest around camera stations did not affect the habitat use of either of the two feline species, other factors associated with this anthropic land-use, as human accessibility and distance to the continuous forest, did show an effect on these big cat species. According to our results, relatively small and well-managed areas of exotic tree plantations interspersed with forest areas do not constitute barriers for jaguars and pumas in the Atlantic Forest and can function as potential corridors. Forest plantations as such, do not appear to constitute optimal habitats for these felids. The role of tree plantations as potential corridors or supplementary habitat for pumas, jaguars and their prey relies, to different degrees, on the maintenance of a high proportion of native forest among the plantations, on a good connectivity with the large patches of protected forest, and on the control of poaching.

1. Introduction

Large carnivores are considered keystone species that affect the provision of ecological services, including the maintenance of biodiversity (Estes et al., 2011; Ripple et al., 2014). With a few exceptions (e.g., Chapron et al., 2014), most large carnivore populations are

dwindling, and many of them are endangered as a result of human activities that in many cases cause habitat loss, prey depletion and human-carnivore conflicts (Loveridge et al., 2010; Ripple et al., 2014). The persistence of large carnivore populations in a landscape is highly dependent on the presence of large and connected areas of suitable habitat (Crooks, 2002), with a good prey base (Karanth et al., 2004)

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and free of major edge effects and persecution (Woodroffe and Ginsberg, 1998).

The jaguar (*Panthera onca*) and the puma (*Puma concolor*) are the largest felids of the Americas. They are generalized hyper-carnivores highly dependent on a good prey base of medium to large sized mammals (Currier, 1983; Seymour, 1989). Their trophic position determines that their population densities are naturally low (for jaguars generally < 4 individuals/100 km², Jędrzejewski et al., 2018; for pumas usually < 8 individuals/100 km², Caso et al., 2008; Kelly et al., 2008). As is the case with most other large carnivores, their densities are mostly regulated by habitat productivity and prey density (Di Bitetti et al., 2008a, 2008b; Karanth et al., 2004; Miquelle et al., 2010). Their dependency on good prey availability base also means that they require large home ranges and, consequently, large expanses of suitable habitat relatively free of human pressures to persist in a landscape (Herfindal et al., 2005; Jędrzejewski et al., 2007; Morato et al., 2016).

Their preference for large mammal prey usually bring jaguars and pumas into conflict with cattle raisers, which have habitually persecuted and killed them (Caselli de Azevedo, 2008; Inskip and Zimmermann, 2009; Loveridge et al., 2010; Quiroga et al., 2016; Zimmermann et al., 2005). Even in areas where human-jaguar/puma conflicts are not important, poaching has a negative effect on their populations, either as a result of large cat trophy hunting or as a result of prey depletion (Paviolo et al., 2008, 2009a). Thus, the puma and, particularly, the jaguar, have mostly disappeared from areas of high human population densities, particularly where poaching is common or the alteration of the original landscape has been severe (De Angelo et al., 2011; Jędrzejewski et al., 2018; Woodroffe, 2000). However, the negative impact of human activities on these large felids range from nil or mild, as in well managed logging concessions (Tobler et al., 2018), to drastic, as in landscapes where the original environment has been mostly replaced by annual crops or cattle raising grasslands (De Angelo et al., 2011, 2013; Paviolo et al., 2016).

The global jaguar population is continuously declining and its range is shrinking (Quigley et al., 2017). Although a large population still exists in the Amazon, the jaguar range outside this region has been highly reduced, and most of the remaining populations are small and isolated (de la Torre et al., 2018; Jędrzejewski et al., 2018). In Argentina, the jaguar has been categorized as Critically Endangered (Aprile et al., 2012). It is estimated that about 300 individuals remain in three small and relatively isolated subpopulations in the north of the country (Di Bitetti et al., 2017; Jędrzejewski et al., 2018), with the Misiones province population estimated at around 90 individuals (Paviolo et al., 2016). The non-endangered puma has a much wider distribution and a much larger population, both globally, in Argentina, and in Misiones; and is more resilient than the jaguar to human impacts and landscape transformations (Aprile et al., 2012; Caso et al., 2008; De Angelo et al., 2011; Paviolo et al., 2009b).

Tropical and subtropical forests concentrate high levels of biodiversity (Myers et al., 2000). At the same time, they provide good conditions for forestry production. As a consequence, large expanses of tropical and subtropical forests are being replaced by fast-growing short-rotation plantations that usually contain lower levels of biodiversity (Barlow et al., 2007). In the Atlantic Forest of South America, one of the most endangered biodiversity hotspots on Earth (Ribeiro et al., 2009), *Pinus* and *Eucalyptus* monoculture plantations constitute an important productive activity. In the Atlantic Forest of Misiones province, Argentina, monoculture plantations, totaling about 4058 km² (MA, 2015), have replaced large expanses of native forests in the last few decades (Izquierdo et al., 2008). Most of these plantations are localized in the northern sector of this province, which is one of the last strongholds of the jaguar in the whole Atlantic Forest (Paviolo et al., 2008, 2016). Even though these plantations have negative effects on some taxonomic groups (small felids, Cruz et al., 2018; anurans, Gangenova et al., 2018; small terrestrial mammals, García, 2018; medium-large terrestrial mammals and understory birds, Iezzi et al.,

this issue; spiders, Munévar et al., this issue; birds, Zurita et al., 2006) there have been no assessment of their effects on the wide-ranging large felids, the jaguar and the puma.

Using camera-trap records in combination with occupancy models (MacKenzie et al., 2006; Wearn and Glover-Kapfer, 2017), we investigated jaguar and puma habitat use in a productive landscape that includes pine plantations and forest areas in northern Misiones province. We estimated the availability of their main preys in this landscape and evaluated the variables that affect their occupancy pattern. For jaguars, pumas and prey species, we predicted a lower probability of use and occupancy of camera-trap sites with higher relative percentage of plantations vs. native forest in their surroundings. We also predicted a positive effect of the cost of human access to a site (a proxy variable negatively related to poaching intensity) on the probability of it being used by these large felids and in the probability of occupancy of the commonly-poached species in the region. We also expected the probability of use of a site by these felids and the probability of occupancy of the prey species to decrease with the distance to the large and better-protected forest block, under the assumption that it constitutes the main population source for these species. Finally, we predicted a positive relation between prey abundance and the large cats' probability of use of a site.

2. Materials and methods

2.1. Study area

We conducted this study in northern Misiones province, Argentina (Fig. 1; 54°15'30.60"W, 25°55'52.32"S). The study area contains one of the largest continuous remnants of Atlantic Forest (AF) in the World. The natural vegetation of this region is a semi-deciduous subtropical forest and the study area still holds the complete regional native mammal assemblage (Galindo-Leal and de Gusmão Câmara, 2003; Giraudo and Abramson, 2000). This study area comprises a central portion with several contiguous public and private protected areas (Iguazú National Park, Urugua-í Provincial Park, San Jorge Forest Reserve, Urugua-í Wildlife Reserve, etc.) that together constitute a large block of continuous native forest of more than 2700 km² (Fig. 1). To the West, the landscape is dominated by pine (*Pinus taeda*) plantations and native forest remnants of different sizes and degree of connectivity with the continuous native forest. Pine monoculture plantations have a high density of trees (1670 individuals per ha), and the stands are neither pruned nor thinned. This western portion of the study area has an extensive network of dirt roads that provide access to the pine plantation stands. Some of these roads are closed to public traffic, but others have no restricted access. To the East, the study area contains a matrix of small-scale (10–200 ha) rural properties with agricultural production (yerba mate, tobacco, maize), and small pastures with cattle and swine. There are also small (usually < 100 ha) forest fragments in these properties and medium-sized (100–5000 ha) public and private protected areas (Fig. 1).

2.2. Data collection

For this study, we joined data from two overlapping (both in space and time) large-scale camera-trap surveys developed in the area between 2013 and 2014. In total, we developed 274 sampling stations with an effort of 13,347 camera-trap days. Mean distance between nearest camera-trap stations was 1.8 km. The minimum convex polygon that included all the cameras was of 5089 km² including 66% of native forest, 17% of pine plantations and 17% of other land uses such as pastures, cities, water, etc. (Fig. 1). One of the surveys was developed between February and July 2014 with the main objective of estimating jaguar densities (Paviolo et al. 2016). During this survey, 90 camera trap stations were deployed on infrequently used unpaved roads (2–6 m wide). Each station consisted of two camera traps facing each other on

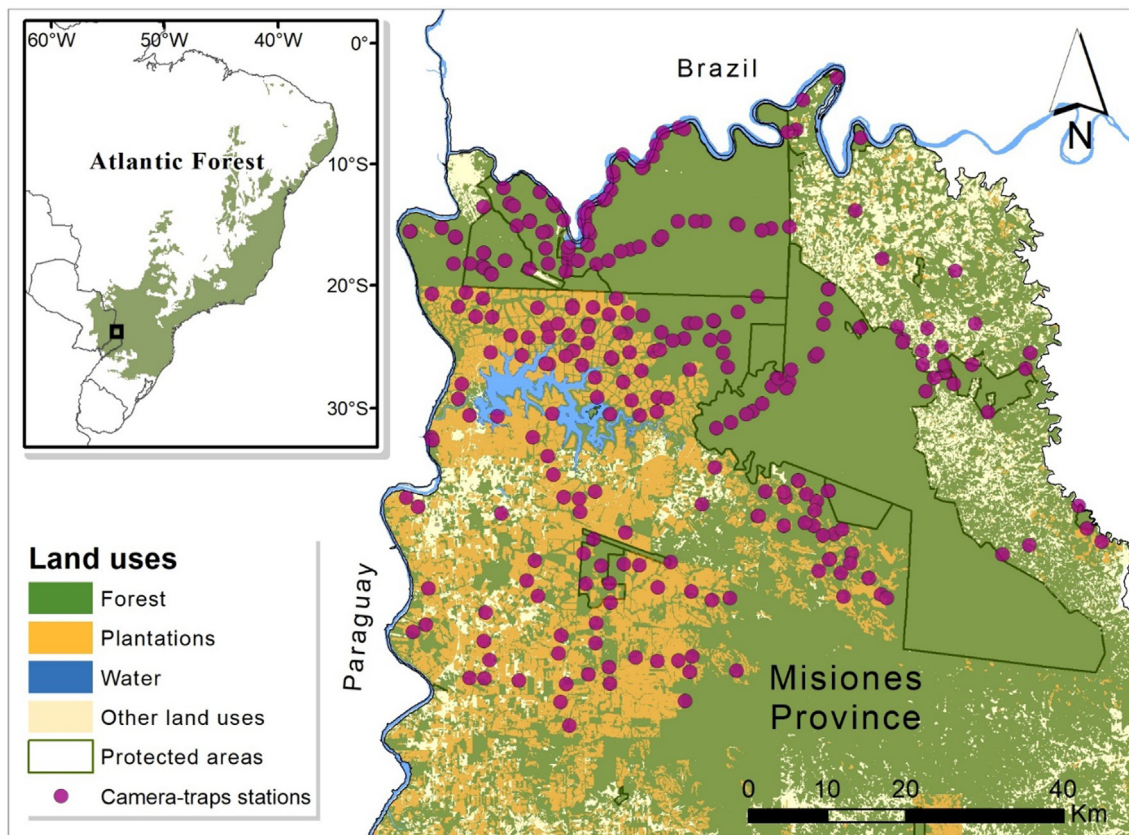


Fig. 1. The study area located in the Northern part of Misiones Province. Forest, pine plantations and other land uses are shown in different colors. The location of the survey stations are represented by points.

both sides of the road. Stations were active for an average of 47.43 (± 14.18) continuous days totalizing a sampling effort of 4269 camera trap days.

The other survey was conducted between May 2013 and December 2014. This survey was aimed at studying mammal and bird assemblages (Iezzi et al., this issue). Sampling stations consisted of a single camera-trap, settled inside the native forest or pine plantation stand, at distances of > 50 m from a road or human trail. During this survey, 184 camera trap stations were active for an average of 49.80 (± 19) continuous days with a total sampling effort of 9171 camera trap days. No baits were used in any survey.

2.3. Habitat use data analysis

2.3.1. Environmental and anthropogenic variables

With the aim of testing the hypotheses stated in the Introduction, we estimated at each station the values of four different variables: (1) The percentage of the pine plantation cover minus the percentage of native forest cover in a concentric radius around each sampling station (“%P-F”), (2) the cost of human access, (3) the distance to the continuous forest block border (“distance”), and (4) the availability of prey species for pumas and jaguars.

(1) The %P-F is a variable that represents the relative abundance of pine plantations vs native forest within a circle centered on the surveying station. We use the relationships between these two land uses and not as separate variables, because these they were highly and negatively correlated in our study area (negatively). The %P-F can take values ranging from -100 when the surrounding area is completely covered by native forest to 100 , when the area was completely covered by pine plantations and no native forests remain. Other land uses were not considered in this variable, but for

the analysis we only included surveying stations that have more than 75% of tree cover land uses (% pine plantation + % native forest $\geq 75\%$). The radiuses values used to estimate this variable were less than or about equal to the estimated mean radius of the home range of the studied species in the AF (De Angelo et al., 2013; Kanagaraj et al., 2011; Schadt et al., 2002). Thus, we used radius of 0.1 km for armadillo (*Dasypus novemcinctus*), opossums (*Didelphis* sp., either *Didelphis aurita* or *Didelphis albiventris*), agouti (*Dasyprocta azarae*) and paca (*Cuniculus paca*) ($n = 273$ stations with $> 75\%$ tree cover); a radius of 0.5 km for brocket deer (three *Mazama* species are present in the study area: *Mazama americana*, *Mazama nana* and *Mazama gouazoubira*) ($n = 264$ stations); and a radius of 1 km for coatis (*Nasua nasua*), peccaries (*Tayassu pecari* and *Pecari tajacu*) and tapirs (*Tapirus terrestris*) ($n = 261$ stations). For jaguars and pumas, we used two different radiuses of 2 km and 4 km, and the number of stations used for these species was 247.

(2) The cost of human access is the estimated time that would need a person to reach the station from the closest town or city. To build this variable we used estimates of mean human speed when traversing different kinds of roads (i.e. by car or motorcycle) or land uses (i.e. by walk). A detailed explanation of the methodology used to estimate this variable could be found in De Angelo et al. (2011) and Iezzi et al. (this issue). Higher values of this variable may represent a reduction of anthropogenic impacts such as poaching intensity, logging, abundance of dogs and other domestic animals, among others (De Angelo et al., 2011, 2013).

(3) As we expect the forest block to be the main population source of most native mammals of this region (Iezzi et al., this issue; Sunarto et al., 2012; Yue et al., 2015), we estimated the distance to the edge of the continuous forest block following the methodology used by Iezzi et al. (this issue). For that purpose, we used the Cost-Distance function to estimate the accumulated costs of an animal moving

through the least-cost paths from the native forest block to the station, taking into account the distance (in km) from its border and the heterogeneity and friction effect of the landscape matrix (Adriaensen et al., 2003; Epps et al., 2007; Iezzi et al., this issue). Stations that were inside the native forest block had negative values. To estimate the effect of this variable on the occupancy of prey, we used a grid assigning movement costs to each landscape element for a generic medium or large native animal created by Iezzi et al. (this issue). In this grid, pine plantations are five times costlier than the native forest for a mammal to move through (“dist5”, Iezzi et al., this issue). As such, cost is a variable aimed at representing the tendency of animals to move through different landscape features, since cost is not measured exclusively as time or energy expenditure, but includes the risk of predation, poaching or road kill (e.g., the more open plantations do not provide as good concealment as a forest and animals may perceive it as a more risky habitat), which add to the proneness of animals to use that particular type of environment (Iezzi et al., this issue). To evaluate if pine plantations are barriers or work as corridors or suitable habitat for the big carnivores, we modified the cost of pine plantations of the original grid and created three variants of the variable “distance” using: (1) a grid where pine plantations have the same cost as the native forest (“dist1”); (2) a grid where pine plantations have twenty times the cost of forest (“dist20”) and (3) a grid where pine plantations have fifty times (“dist50”) (see Iezzi et al., this issue).

(4) To evaluate prey availability for jaguars and pumas at each camera trap site we generated an index based on a model that took into account prey species occupancy probability and the contribution of each prey species to biomass consumption by the two felid species. The mean biomass contribution of each prey species for pumas and jaguars was obtained from three previous studies developed in the region (Cascelli de Azevedo, 2008; Crawshaw, 1995). We only included prey species that have contributed at least 5% to the total biomass consumed by the large felids in at least one of these studies. As in the diet studies some species were not identified at the species level, we gathered together the two species of peccaries as only one item, and we did the same with the three species of *Mazama* and the two species of *Didelphis*. We excluded the black and white tegu (*Salvator merianae*) from this analysis due to its extremely seasonal activity pattern, and the capybara (*Hydrochaeris hydrochaeris*) due to the lack of records of this species during our surveys, but none of these two species contributed > 15% of biomass in any one of the previous studies. To estimate prey availability for jaguars and pumas at each station, we developed an index of prey availability for each predator by combining the relative contribution of each prey species to the biomass consumed by each felid with the estimated occupancy probability of each prey species following the models:

$$\begin{aligned} \text{Jaguar prey availability} &= \psi \text{ peccaries} * 0.544 \\ &+ \psi \text{ brocket deer} * 0.151 \\ &+ \psi \text{ coati} * 0.125 + \psi \text{ agouti} * 0.065 \\ &+ \psi \text{ armadillo} * 0.064 \\ &+ \psi \text{ opossum} * 0.026 + \psi \text{ tapir} * 0.025 \end{aligned}$$

and

$$\begin{aligned} \text{Puma prey availability} &= \psi \text{ brocket deer} * 0.307 \\ &+ \psi \text{ peccaries} * 0.278 + \psi \text{ agouti} * 0.180 \\ &+ \psi \text{ coati} * 0.134 + \psi \text{ paca} * 0.102 \end{aligned}$$

Another variable that we included in the models to control for its potential effect was the location of the camera trap stations, since this could highly affect the detectability of some Neotropical mammals (Cusack et al., 2015; Di Bitetti et al., 2014). Since our sampling stations

were placed at locations with potentially different detection probabilities, and in order to control for this potential bias in detectability, we included in the models location, as a categorical variable with three levels: roads, inside forest and inside pine plantations.

2.3.2. Single-species occupancy models

We analyzed the patterns of habitat use by jaguars, pumas, and their prey with single-species single-season occupancy models with a likelihood-based approach using PRESENCE 2.12.9 program (Hines, 2006; MacKenzie et al., 2006). These models provide an unbiased estimate of the probability that a species occupies an area (ψ) when detection probability (p) is < 1 while allowing modeling the effects of variables on ψ or p (MacKenzie et al., 2002; MacKenzie et al., 2006). The probability of detection (p) is estimated by repeated sequential samplings of a specific area (MacKenzie et al., 2006). To increase the probability of detection we combined every eight consecutive trap days into a trapping occasion. In this work we consider the estimate of ψ at a camera trap site as an indicator of the probability of occurrence of the species with smaller home ranges (agouti, opossum, brocket deer, etc.) at that camera trap site. For species with larger spatial requirements (peccaries, tapirs, felines) ψ is considered an estimate of the probability of use of the specific site where a camera trap was placed (MacKenzie et al., 2006).

We first run occupancy models for the prey species. We included, as variables affecting ψ : (1) %P-F around the sampling station, using “%P-F 0.1 km”, “%P-F 0.5 km”, “%P-F 1 km” depending on the analyzed species, (2) the cost of access for humans (“access”), and (3) the distance to the continuous forest block border, with the pine plantations being five times as costly as the native forest (“dist5”). The variables affecting p were: (1) Location of the camera trap (Loc road, Loc forest, Loc pine; categorical variable with Loc pine in the intercept), and (2) the cost of human access (“access”). We tested for collinearity among the continuous variables through Spearman correlations using the Infostat program (Di Rienzo, 2009). Given that “dist5” was correlated with “%P-F 0.5 km” and “%P-F 1 km” variables, with a $\rho > 0.70$, these variables were run in separate models.

We modeled all combinations of non-correlated variables since we were interested in analyzing the importance of each variable and its effect on ψ and p (Anderson, 2007; Burnham and Anderson, 2002). Models were ranked using Akaike’s information criterion (AIC). We selected the top models with $\Delta\text{AIC} \leq 2$. Models containing “pretending variables” were discarded for the analysis (Anderson, 2007; Arnold, 2010; Burnham and Anderson, 2002). The pretending variables were corroborated analyzing their confidence intervals (CI), i.e. variables whose 95% CI included zero (Anderson, 2007). We then averaged the remaining models to estimate the values of the betas for each variable. The variables with 95% CI that did not overlap 0 were considered to have strong evidence of an effect on the parameters (Anderson, 2007; Dugger et al., 2015).

For the occupancy models of jaguars and pumas, we used as potential variables affecting ψ : (1) %P-F around the station, using a 2-km radius (“%P-F2km”) or a 4-km radius (“%P-F4km”), (2) the cost of human access (“access”), (3) the distance to the continuous forest block border, considering different relative costs of moving through a pine plantation compared to the native forest (“dist1”, “dist5”, “dist20” or “dist50”), and (4) the prey occupancy probability (“prey”). The variables affecting p were: (1) Location of the camera trap (Loc road, Loc forest, Loc pine; categorical variable with Loc pine in the intercept), and (2) the cost of human access (“access”).

For the occupancy models, we used a two-step approach. First, we assessed the “distance to the continuous forest block border” and the spatial scale of “%P-F” that best represents the species’ response. Then we analyzed the most influential variables for occupancy and detectability parameters for each felid (MacKenzie et al., 2006; Nagy-Reis et al., 2017). Because the four distances to the continuous forest block were highly correlated among each other (i.e. $\rho > 0.95$), for each

felid we ran and compared the models that included each of the four variants of this variable (dist1, dist5, dist20 and dist50) along all other non-correlated variables considered to have an effect on ψ and p (four full models). We ranked these four models using AIC and we selected the one with the lowest AIC value. We followed the same protocol to determine the best spatial scale of “%P-F” (comparing a 2 vs a 4-km radius) for each felid. Finally, to determine the most influential variables for occupancy and detection probability parameters for each felid, we run occupancy models for all combinations of the selected and non-correlated variables. Given that “%P-F” was correlated with “distance” and “prey” (i.e. $\rho > 0.70$) we run these variables in separate models. The best models were selected following the same methodology we used with the prey species occupancy models.

3. Results

3.1. Occupancy models for preys

We obtained 1073 independent (i.e. > 1 h apart) records for agouti, 490 for armadillo, 75 for paca, 651 for opossums, 1180 for brocket deer, 204 for coati, 238 for peccaries, and 526 for tapir. For the agouti, mean detection probability (p) was $0.45 (\pm 0.25)$. The detection probability was affected by the location of the sampling station, being lower at stations located in pine plantations. Mean occupancy probability (ψ) of agouties was $0.49 (\pm 0.28)$ and was negatively affected by the relative increase of pine plantations (%P-F) and positively by the cost of human access (Table 1, Supplementary 1, Fig. 2A).

For the paca, mean p was relatively low (0.13 ± 0.12) and it was lower in stations located in pine plantations and higher in sites with higher cost of human access. Mean ψ was $0.29 (\pm 0.06)$ and none of the variables had an important effect on it (Table 1, Supplementary 1, Fig. 2B).

For opossums, mean p was $0.31 (\pm 0.17)$ and no variable had an effect on our estimate of this parameter. Mean ψ was $0.49 (\pm 0.26)$ and was negatively affected by the relative increase of pine plantations (%P-F) (Table 1, Supplementary 1, Fig. 2C).

For the armadillo, mean p was $0.28 (\pm 0.09)$ and it was higher at stations located in native forest. Mean ψ was $0.63 (\pm 0.23)$, and it increased with the distance to the continuous forest block border and decreased with the cost of human access (Table 1, Supplementary 1, Fig. 2D).

For brocket deer, mean p was $0.48 (\pm 0.12)$ and its value increased with the cost of human access. Mean occupancy probability was quite high for brocket deer (0.83 ± 0.02) and none of the variables had an effect on it (Table 1, Supplementary 1, Fig. 3A).

For peccaries, mean detection probability was estimated at $0.20 (\pm 0.08)$, and was higher on stations located on roads. Mean ψ was $0.52 (\pm 0.21)$ and was negatively affected by the relative proportion of pine plantations to forests (%P-F) (Table 1, Supplementary 1, Fig. 3B).

For the coati, mean p was $0.14 (\pm 0.11)$ and was higher at sites located inside the forest and with low cost of human access. The mean ψ estimated for the coati was $0.70 (\pm 0.02)$ and none of the variables had an important effect on it (Table 1, Supplementary 1, Fig. 3C).

For the tapir, estimated p was $0.33 (\pm 0.13)$ and was lower at sites inside pine plantations and higher inside native forest sites. Estimated ψ was $0.38 (\pm 0.28)$ and it was negatively affected by the distance to the border of the continuous forest block and positively by the cost of human access (Table 1, Supplementary 1, Fig. 3D).

According to the model that estimated the spatial variation in prey availability for felids, our index of prey availability for pumas varied between 0.38 and 0.77, and between 0.32 and 0.75 for jaguars (Fig. 4A and B). The largest values of prey availability for the two species were from stations located in protected areas and the less accessible sites (Fig. 4A and B).

Table 1
Beta estimates and their confidence intervals (CI 95%) for each variable included in the best model(s) for pumas, jaguars and its preys. Models were selected using the $\Delta AIC \leq 2$ for criteria and models with pretending variables were discarded. The estimated values of the beta coefficient whose confident intervals did not include 0 were considered to have strong evidence of an effect on the parameters p and ψ , and are shown in bold.

Species	ψ					p				
	Intercept	Distance	%P-F	Access	Prey	Intercept (Loc pine)	Loc road	Loc forest	Access	
Agouti	-0.22 (-0.59 to 0.14)	-	-1.41 (-1.92 to -0.90)	0.47 (0.18-0.76)	-	-25.40 (-26.26 to -24.54)	26.00 (25.13-26.87)	25.54 (24.67-26.40)	-	
Paca	-0.92 (-1.47 to -0.38)	-0.19 (-0.46 to 0.09)	-0.10 (-0.30 to 0.09)	-0.34 (-0.72 to 0.04)	-	-4.31 (-6.18 to -2.45)	1.99 (0.06-3.92)	2.90 (1.01-4.79)	0.66 (0.29-1.04)	
Opossums	-0.17 (-0.52 to 0.18)	-	-1.31 (-1.73 to -0.90)	-	-	-1.27 (-2.57 to 0.03)	-0.64 (-1.99 to 0.70)	1.28 (-0.02 to 2.59)	-	
Armadillo	0.77 (0.21-1.33)	1.22 (0.29-2.16)	-	-0.74 (-0.79 to -0.14)	-	-1.09 (-1.39 to -0.78)	-0.52 (-1.05 to 0.00)	0.57 (0.24-0.91)	-	
Brocket deer	1.58 (1.26-1.90)	-0.02 (-0.07 to 0.02)	-0.07 (-0.20 to 0.05)	0.10 (-0.05 to 0.25)	-	-0.09 (-0.24 to 0.06)	-0.01 (-0.09 to 0.07)	0.06 (-0.04 to 0.16)	0.52 (0.41-0.63)	
Peccaries	0.80 (-0.31 to 0.46)	-	-0.90 (-1.27 to -0.53)	-	-	-1.30 (-1.79 to -0.81)	0.32 (0.16-0.48)	-0.84 (-1.44 to -0.24)	0.30 (-0.23 to 0.84)	
Coati	0.88 (0.26-1.50)	0.10 (-0.09 to 0.28)	0.13 (-0.16 to 0.42)	-0.08 (-0.23 to 0.07)	-	-2.58 (-3.12 to -2.04)	-0.93 (-1.69 to -0.17)	1.56 (1.01-2.10)	-0.13 (-0.21 to -0.04)	
Tapir	-0.87 (-1.23 to -0.50)	-1.50 (-2.12 to -0.89)	-	0.80 (0.39-1.21)	-	-1.10 (-1.55 to -0.65)	0.24 (0.08-0.39)	1.01 (0.50-1.53)	-0.01 (-0.53 to 0.52)	
Puma	0.11 (-0.64 to 0.86)	-1.88 (-3.25 to -0.51)	-	-	-0.99 (-1.98 to 0.01)	-4.35 (-5.60 to -3.10)	2.95 (1.70-4.20)	1.13 (-0.21 to 2.46)	0.39 (0.17-0.61)	
Jaguar	1.01 (-0.12 to 2.13)	-1.09 (-2.53 to 0.36)	0.16 (-0.16 to 0.48)	1.26 (0.04-2.48)	0.10	-4.13 (-5.22 to -3.04)	3.19 (2.09-4.29)	-0.71 (-2.12 to 0.69)	0.16 (-0.01 to 0.33)	

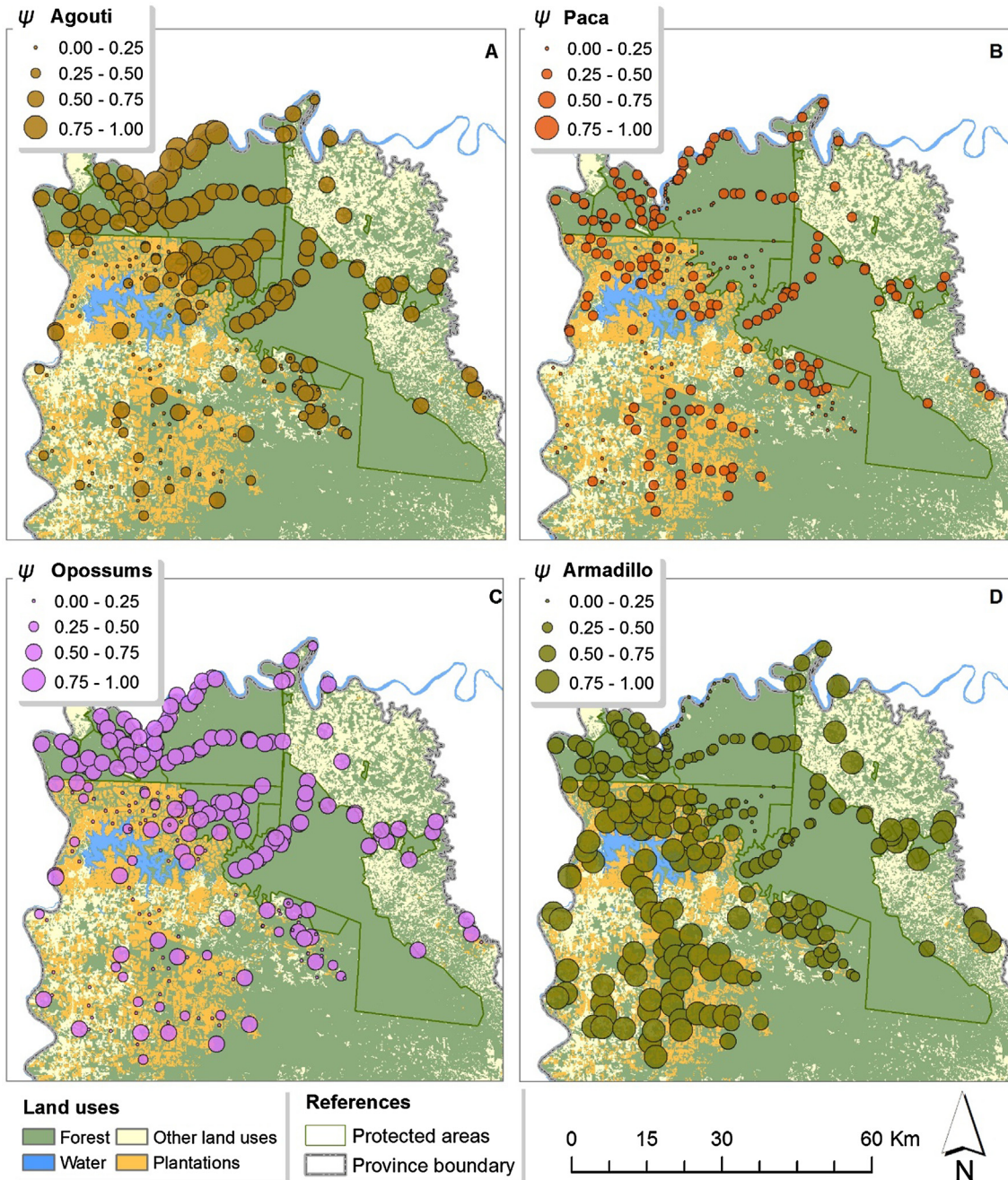


Fig. 2. Occupancy values estimated for different prey species using the better model or the averaging model of the models of $\Delta AIC \leq 2$: (A) Agouti, (B) Paca, (C) Opossums, and (D) Armadillos. The points symbolize the location of survey stations, and the size symbolize the occupancy value estimated using the top model or the model averaging.

3.2. Occupancy models for pumas and jaguars

During the surveys, we obtained 98 records of pumas and 213 jaguar records. For the variables distance and relative proportion of pine plantations to forests the variants that gave a better fit to the models (the first step in the modelling approach) were “%P-F 4 km” for both felids and “dist5” for pumas, “dist50” for jaguars. However, the AIC of the models using different values of “dist” (1, 5, 20 and 50) were very similar.

For pumas, there were two models with $\Delta AIC \leq 2$ but the second best ranked model was discarded because it had a pretending variable (Table 2). The top ranked model suggests that mean p was 0.10 (± 0.11) and is lower inside pine plantations and higher on roads, and that is positively affected by the cost of human access. This model

suggests that mean estimated ψ for pumas was 0.55 (± 0.23), and is being negatively affected by the distance to the continuous forest block border (Table 1, Fig. 5A).

For jaguars, there were five models with $\Delta AIC \leq 2$ (Table 2). The top ranked models suggests that mean p was 0.11 (± 0.14), and is being affected by the location of the camera trap station, being lower inside pine plantations and higher on roads. The mean estimated value of ψ was 0.68 (± 0.22), and this parameter is being positively affected by the cost of human access (Table 1, Fig. 5B).

4. Discussion

Using large-scale camera-trap data in combination with occupancy models we assessed the probability of habitat use by jaguar and puma,

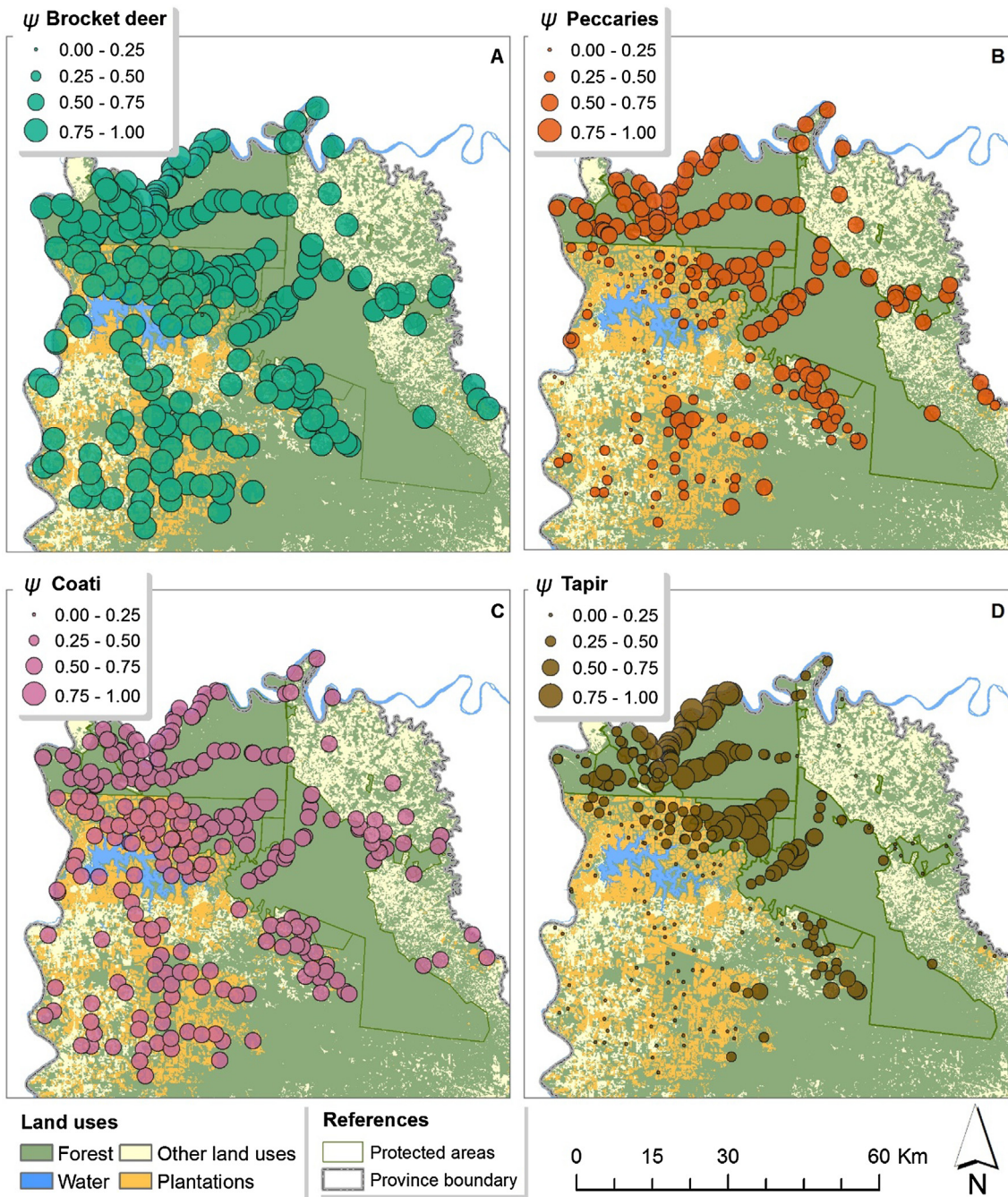


Fig. 3. Occupancy values estimated for different prey species: (A) Brocket deer, (B) Peccaries, (C) Coatis, and (D) Tapirs. The points symbolize the location of survey stations, and the size symbolize the occupancy value estimated using the top model or the model averaging.

and estimated the occupancy probability of their main prey in a landscape modified by forest plantations in the Atlantic Forest. Even though the relative proportion of plantation to forest remaining in the landscape did not strongly affect the habitat use of either of the two feline species, other factors associated with this anthropic land-use changes (distance to the source forest and human accessibility) did show an effect on these big cat species.

The occupancy probabilities of most prey were affected by one or two of the landscape variables, and in most cases (armadillos being the exception) the variables had the predicted effect on ψ . Agoutis, opossums, and peccaries were negatively affected by an increasing proportion of pine plantations in the landscape. The pine plantations are generally areas with a highly simplified plant structure (Iezzi et al., this issue), which may increase predation risk, and probably have less food

available for these omnivorous and frugivorous prey, since fruits, small vertebrates and arthropods are less abundant in this environment (Gangenova et al., 2018; García, 2018; Iezzi et al., this issue; Munévar et al., this issue; Zurita et al. 2006). It is probable that lower food availability and increased perception of predation risk may result in lower occupancy or habitat use by these species in areas mostly covered by pine plantations.

Another variable that had an effect on some of the prey species was the cost of human access which, as predicted, had a positive effect on the occupation probability of tapirs and agoutis (but a negative effect on armadillos). Increasing values of cost of access are a good indicator of decreasing human disturbances, particularly poaching (De Angelo et al., 2011; Espinosa et al., 2018; Paviolo et al., 2009a), which is a widespread activity in the Atlantic Forest (Giraud and Abramson,

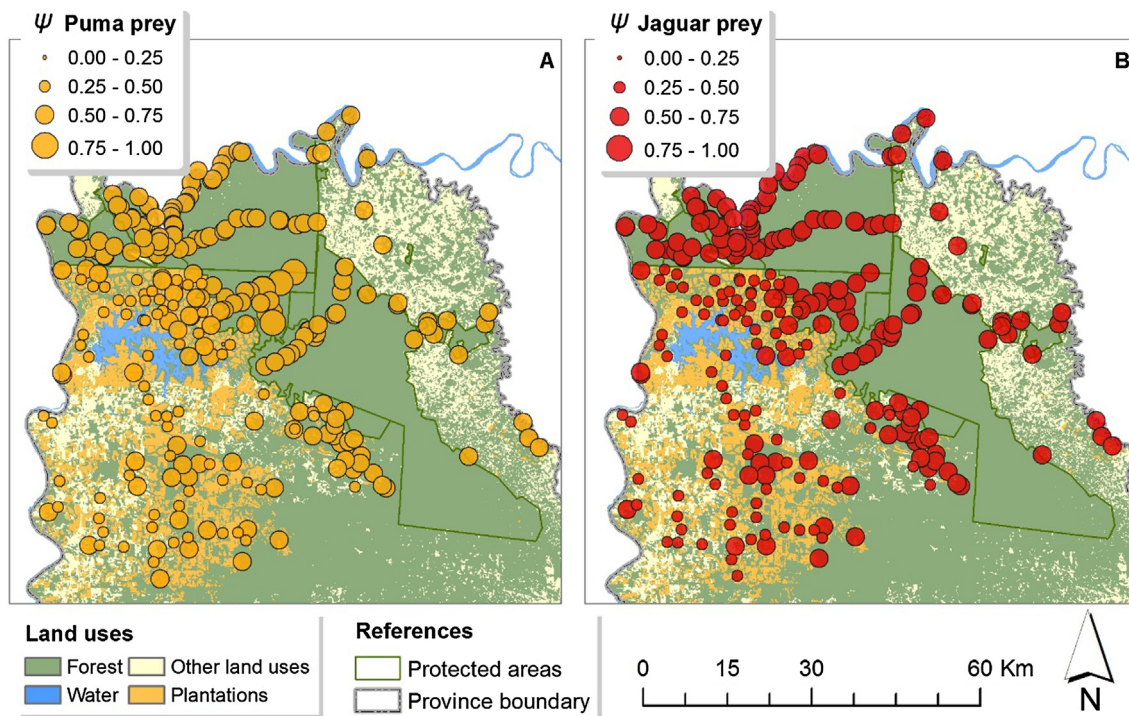


Fig. 4. Index of prey availability for large felids in the study area: (A) availability of puma preys; (B) availability of jaguar preys. The points symbolize the location of survey stations, and the size symbolize the occupancy value estimated using the top model or the model averaging.

Table 2

Single-species single-season models for pumas and jaguars to analyze variables affecting ψ and p . Models were ordered according to the lowest value of AIC and were selected using the $\Delta AIC \leq 2$ for criteria. Only models with $\Delta AIC \leq 2$ and the null model are presented here. Variables whose 95% CI do not include 0 are depicted in bold.

Model	AIC	ΔAIC	AIC weight	N° Par.	-2LL
<i>Models for puma</i>					
ψ (dist5, prey), p(Loc, access)	531.67	0	0.6569	7	517.67
ψ (dist5, access, prey), p(Loc, access)	533.66	1.99	0.2429	8	517.66
ψ (.), p(.)	609.5	77.83	0	2	605.5
<i>Models for jaguar</i>					
ψ (dist50 km, access, prey), p(Loc, access)	594.29	0	0.3078	8	578.29
ψ (dist50 km, access, prey), p(Loc)	595.13	0.84	0.2022	7	581.13
ψ (%PF4 km, access), p(Loc, access)	595.44	1.15	0.1732	7	581.44
psi(access, prey), p(Loc, access)	595.64	1.35	0.1567	7	581.64
ψ (access), p(Loc, access)	595.89	1.6	0.1383	6	583.89
ψ (.), p(.)	730.97	136.68	0	2	726.97

2000; Paviolo et al., 2009a; Sousa and Srbek-Araujo, 2017). The lowland tapir is perhaps the most sensitive Neotropical ungulate to poaching, due to its low reproductive rate (Bodmer et al., 1997). Consequently its populations decline in areas more accessible to humans and with less protection against hunting (Cullen et al., 2000; Paviolo et al., 2009a; Cruz et al., 2014; Espinosa et al., 2018). Tapir occupation probability also decreased with the distance to the continuous forest (armadillos again showing the opposite pattern). This could indicate that tapirs, being very sensitive to poaching, show a very neat source-sink dynamics in this landscape (Novaro et al., 2005).

The agouti is also a species frequently hunted in the region (Giraud and Abramson, 2000), and it has been documented that the species declines in areas with lower protection in the Atlantic Forest (Paviolo,

2010). This species is likely to be affected not only by higher levels of poaching, but also by the increasing presence of domestic carnivores in areas close to villages. Iezzi et al. (this issue) consider that both tapir and agouti can be considered as continuous and well conserved forest indicator species in the Atlantic Forest.

The occupation probability of the paca, the coati and brocket deer was not affected by any of the variables assessed in this study. In the case of the paca, the low number of records may not have allowed the identification of clear patterns of the effect of the variables on this species. In the case of brocket deer, the lack of effect of the variables on the occupation probability is probably due to the fact that in this analysis we considered the three species that inhabit the Atlantic Forest (*M. americana*, *M. nana* and *M. gouazoubira*) as a single group of species. However, these species have different responses to hunting pressure and environmental transformation (Di Bitetti et al., 2008b; Paviolo et al., 2009a, Iezzi et al., this issue). For example, *M. americana* is very sensitive to hunting pressure and environmental change, and may show in this landscape a source-sink dynamics similar to the tapir, while *M. nana* is more abundant in areas with lower levels of protection against poaching (Di Bitetti et al., 2008b; Paviolo et al., 2009a), and *M. gouazoubira*, in the Atlantic Forest, is more frequently recorded in pine plantation stands (Iezzi et al., this issue).

For none of the two big cats the relative increases in the area of pine plantations had a significant effect on habitat use. It is likely that this result is due to the adaptability of both species to live in environments with very diverse plant structures including closed forests, open forests, savannas and scrublands (Currier, 1983; Seymour, 1989). The landscape where we developed this study contains a continuous native forest block surrounded by a matrix of agricultural lands or pine plantation stands < 3 km² where forest remnants of different sizes are embedded. This meant that the area analyzed still preserves enough proportion of native forest at the scales that these species perceive and move along the landscape (a scale of 4 km radius was selected by our models).

In relation to this, we observed that the probability of habitat use for pumas was strongly affected by the distance to the continuous forest but

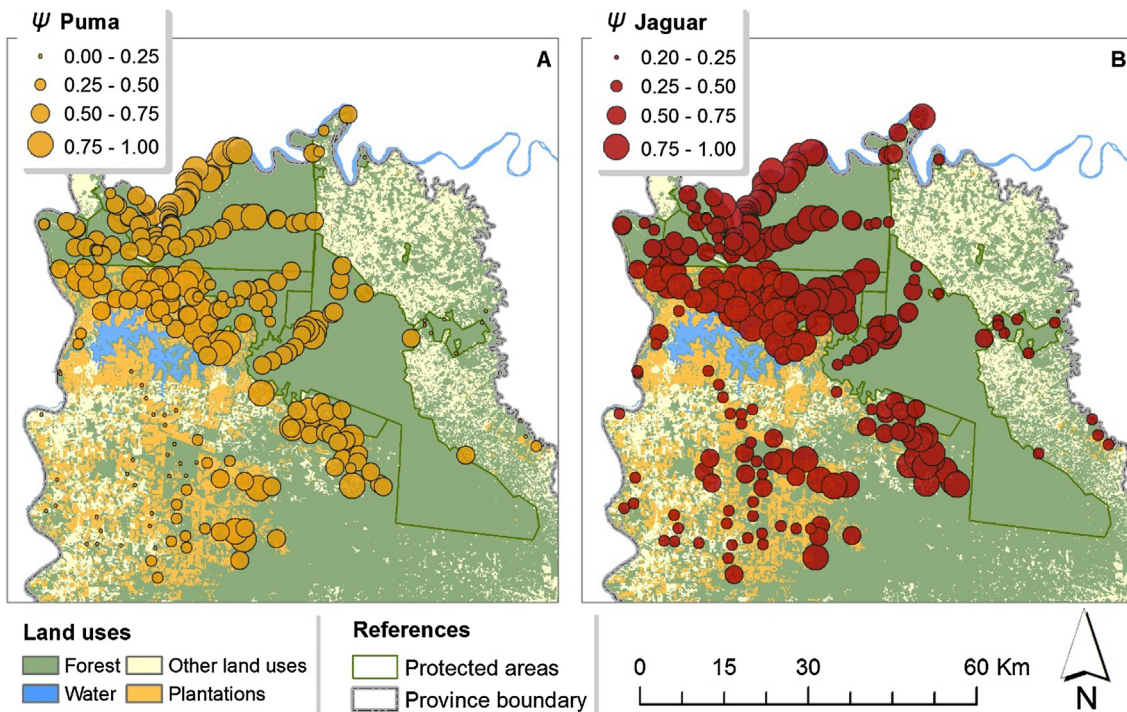


Fig. 5. Occupancy values estimated for jaguars and pumas in the study area. The points symbolize the location of survey stations, and the size symbolize the occupancy value estimated using the top model or the model averaging.

this affected jaguars to a lesser extent. This may evidence that pumas are dependent on the presence of continuous forest, or that distant areas may be population sinks (De Angelo et al., 2011; Newby et al., 2013; Robinson et al., 2008). The lesser effect of this variable on jaguars is striking, because jaguars are generally considered more sensitive to environmental changes than pumas, and particularly in the Atlantic Forest they are more dependent on the presence of blocks of continuous forest than pumas (De Angelo et al., 2011). However, considering the greater displacements of jaguars with respect to pumas in the Atlantic Forest (Morato et al., 2016; Paviolo et al., unpublished data), it is likely that the area of study where we carry out this work does not have much stations at distances large enough for the effect to be quantifiable for jaguars.

Jaguars and pumas used areas with higher levels of human accessibility less frequently, but the effect was strong only on jaguars. The effect of human accessibility on the presence and density of jaguars has been well documented (De Angelo et al., 2011, 2013; Espinosa et al., 2018; Paviolo et al., 2016). Increasing accessibility values are generally associated with increased poaching pressure which has a major impact on jaguar abundance in the Atlantic Forest (Paviolo et al., 2008, 2016). The reduction of protection against poaching thus appears as a top priority action to achieve the conservation of jaguars in this landscape. Achieving better protection would increase the use of plantation-forest mosaics by this species.

The lack of a positive effect of prey abundance on the probability of habitat use by the two feline species is contrary to our *a priori* prediction. However, there are numerous studies that find that the use of space or time between predators and their prey does not always have high levels of overlap (Arias del Razzo et al., 2012; Laundré, 2010; Polisar et al., 2003; Weckel et al., 2006). The landscape of fear hypothesis predicts that the distribution of predators and prey will not overlap significantly and that prey will accommodate their use of space to avoid being preyed upon, and predators will do their part to have access to prey (Laundré, 2010). In our case, it is likely that the lack of relationship between the habitat use of predators and their main prey is an effect of what is predicted by this model.

5. Exotic tree plantations and the conservation of large felids in the Atlantic forest

According to our results, exotic tree plantations like the ones we studied do not constitute barriers for the large felids in the Atlantic Forest, and their occurrence in a plantation dominated landscape may indicate that well managed plantations intermixed with patches of forest can function as medium quality habitat, or at least as potential corridors. However, the results found in this work are based on data obtained from forest plantations that are close to some of the largest and best protected fragments of Atlantic Forest (Paviolo et al., 2016). Also, the pine plantations of this area are exploited by large companies that control the access to some areas, and invest resources in the control of poaching and other illegal activities. So, the conclusions of this work should not be extrapolated to other exotic timber producing landscapes without considering these issues.

According to our results this mosaic of tree-plantations and native forest does not constitutes optimal habitat for pumas and jaguars. The occupation probability estimated for some of the important jaguar and puma prey species was negatively affected by an increase in the proportion of pine plantations in the landscape, by the distance to the continuous forest, and by human accessibility. Among this group of species, peccaries are an important resource for pumas and a key resource for jaguars. Other species were not affected by these conditions or even their occupation increased, and they could constitute important alternative resources for individual jaguars and pumas whose home ranges include forest plantations or during dispersal movements through these modified landscapes. The plantation landscape with large proportion of native forests as the one we studied, may function as areas that help to meet the energetic requirements of large felids, to maintain young individuals waiting for a territory or to disperse between patches of continuous forest.

It is expected that exotic tree plantations with lower proportion of forest patches, distant to large continuous forest blocks, and highly accessible by humans present lower abundance of prey species, and worse conditions to support jaguar and puma individuals, or even to

allow the movements of these species. To improve the value of this plantation landscape for the conservation of these felids, it would be important to maintain a high proportion of native forest among the exotic tree plantations, and the connectivity of the native forest fragments with large blocks of forest. Also, the reduction of the accessibility of poachers will help to increase the prey base and reduce the risk of the elimination of individuals.

The landscape dominated by monoculture forest plantations seems to have less impacts on jaguars and pumas than alternative productive landscapes. One of the reasons is probably that jaguars and pumas are not perceived as conflictive animals in this landscape, as they usually are in agricultural landscapes where cattle or other domestic animals are preyed upon by jaguars and pumas and, consequently, these large felids are persecuted and eradicated (Caselli de Azevedo, 2008). This is because pine plantations are managed by large timber companies in large properties, with few domestic animals and people in the field, and with time lags of several years between interventions. Thus, low occurrence of conflicting situations may probably increase the survivorship of these felids in this landscape when compared to other land uses.

Our results indicated that the role of tree plantations as potential corridors or supplementary habitat for pumas, jaguars and their prey relies, to different degrees, on the maintenance of a high proportion of native forest among the plantations (e.g. peccaries), the connectivity with the large patches of protected forest (e.g. for pumas and tapirs), and at least for jaguars, tapirs, and agouties, on the control of poaching.

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Declaration of interest

None.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.foreco.2018.08.029>.

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