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Forest fragments prioritization based on their connectivity contribution for multiple Atlantic Forest mammals

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ABSTRACT

Natural environments worldwide are increasingly restricted to smaller and isolated patches, resulting in major threats to biodiversity. To prioritize conservation efforts, it is important to assess the relative contribution of the habitat remnants to landscape connectivity. We prioritized remnants of Atlantic Forest in Argentina based on their contribution to the connectivity requirements of mammals that are sensitive to landscape transformation by analyzing habitat connectivity and availability for five species with varying habitat requirements and dispersal abilities. We combined graph-based analysis with occupancy models to calculate the resistance matrices and the node attributes, incorporating anthropogenic pressures. Results of connectivity indices were combined for all species so that those that were more sensitive to the loss of connectivity and/or availability had a greater influence on the final prioritization. Five patches had maximum priority for conservation and were vital to maintaining both landscape connectivity and habitat availability. These patches were particularly important for smaller species with low dispersal abilities, for which they constitute suitable habitats. Four percent of the patches were identified as irreplaceable stepping-stones that connected habitat patches for species with intermediate dispersal distances. Patch connectivity was not equally important for all species as they had different dispersal abilities and sensitivity to anthropogenic pressures, which means that the process of territorial planning based on landscape connectivity must include very careful selection of the species involved. With this multi-species model, we generated a spatially explicit tool that proved useful to prioritize forest patches to conserving Atlantic Forest mammals and other fragmented Neotropical forests.

1. Introduction

The loss and fragmentation of natural environments due to the intensification of human activities is one of the greatest threats to biodiversity (Haddad et al., 2015). Natural environments are increasingly restricted to smaller and isolated patches surrounded by a matrix of human land uses (Bennett and Saunders, 2010). Such environments present different challenges for species that must move between habitat patches (Ricketts, 2001), potentially increasing their vulnerability to genetic drift, climate change, and demographic stochasticity due to population isolation (Gaggiotti and Hanski, 2004). In addition, other anthropogenic pressures associated with habitat fragmentation, such as poaching (Peres and Lake, 2003), have negative consequences on some vertebrate populations (Benítez-López et al., 2017; Bogoni et al., 2020). The global process of habitat loss and the lack of protection of most of the remaining patches of natural environment increase the need for territorial and conservation planning to be based on the prioritization of habitat remnants (Margules and Pressey, 2000).

One common approach to prioritizing habitat remnants is by using graph-based analysis to evaluate their contribution to connectivity and habitat availability (Urban and Keitt, 2001). This approach considers habitat patches as nodes connected by links representing functional connections (e.g., the probability of dispersal of an individual; Urban et al., 2009), and ranks them by their importance using various indices (e.g., Saura and Pascual-Hortal, 2007). A major limitation to connectivity assessments is that it is extremely challenging to collect actual

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dispersal data, and thus matrix resistance is usually based solely on expert opinion (Zeller et al., 2018). A more affordable but still rarely used alternative is creating matrix resistance surfaces derived from habitat suitability values (Keeley et al., 2016), which can be estimated empirically using species-specific occurrence information. For that purpose, occupancy models are a valuable tool for estimating the probability of species occurrence throughout the landscape. These models can incorporate the effect not only of the land cover but also of different anthropogenic pressures (MacKenzie et al., 2006; Meyer et al., 2020). Combining empirical data with graph-based analysis enables a biologically realistic prioritization of patches to be developed that can be incorporated into land management plans or protected-area planning (Saura and Rubio, 2010).

Another challenge of territorial planning is how to identify which habitat patches effectively maintain connectivity for entire communities (Cushman and Landguth, 2012). Most large-scale projects aimed at improving connectivity focus on umbrella species, on the assumption that sustaining these will also result in the protection of less habitat-demanding species (Beier et al., 2008; Ripple et al., 2014). However, these umbrellas, usually large-bodied species with high dispersal abilities, well-suited for large-scale analysis, do not necessarily reflect what happens at more local scales, nor ensure the conservation of smaller and/or less mobile species (e.g., rodents or small herbivores) that may perceive the matrix differently and have different habitat requirements (e.g., they may perceive their habitat at different scales; Beier et al., 2009; Nagy-Reis et al., 2017). Since not all species within a community are similarly affected by landscape transformation and anthropogenic pressures (e.g., some species are more sensitive to poaching than others; Iezzi et al., 2019; Peres and Palacios, 2007) it is important whenever possible to consider the requirements of multiple species when prioritizing habitat patches in territorial planning (Brodie et al., 2015; Meurant et al., 2018).

The Atlantic Forest is a global biodiversity hotspot (Myers et al., 2000) but due to a long process of converting native forest to agriculture, it is now one of the most threatened forests in the world, with only 17% of its original cover remaining (Fundación Vida Silvestre Argentina, 2017). The negative effects of this habitat loss and fragmentation have been studied for many species, including mammal assemblages, in areas of the Atlantic Forest where less than 30% of the forest remains and the patches present a high degree of isolation (da Silva et al., 2015; Magioli et al., 2016; Pardini et al., 2010; Pardini et al., 2005). The Argentinean portion of the Atlantic Forest has declined almost 20% in the last 40 years, due to its being converted to perennial crops and commercial tree plantations, but it still maintains large, continuous forest remnants (>300,000 ha), surrounded by a production matrix that contains multiple native forest fragments (Zuleta et al., 2015). Although deforestation has decreased over the last 15 years, a recent study showed that connectivity for jaguars (*Panthera onca*) decreased by 65% in the same period (Martínez Pardo, 2020). This suggests that relatively low forest loss led to key patches for connectivity being lost, or that a threshold was reached at which subsequent loss of forest area significantly affected jaguar functional connectivity. If this occurred for a species with high dispersion and movement abilities like the jaguar, it is of high priority to study how this landscape is affecting habitat connectivity and availability for the entire mammal community, including species with different functional traits and dispersal abilities. As most of the forest remnants are not protected in this area, territorial planning is needed to maintain the mammal community inhabiting this landscape, and this requires prioritization of forest patches to guide conservation efforts (Fundación Vida Silvestre Argentina, 2017).

Our main objective was to assess the relative importance of forest remnants in a farming landscape of the Argentinian Atlantic Forest, based on their contribution to the connectivity requirements of sensitive mammals. Following Saura and Rubio (2010), we expected that patches that act as connecting elements would be relatively more important for species with higher dispersal abilities, and that patches providing higher habitat availability would be more important for smaller species that could establish their home ranges within them. We used camera-trap databases and occupancy models to estimate the resistance matrices and node attributes for five mammal species. We then used graph theory to analyze habitat connectivity and availability for each species and combined the results from all the species to generate a forest-patch prioritization map. This highlights the patches that are more important for species that are sensitive to connectivity loss and/or habitat availability in this area and at this scale (Fig. 1).

2. Material and methods

2.1. Study area and data collection

We conducted this study in the north of Misiones province, Argentina, in the Upper Paraná Atlantic Forest ecoregion. The natural vegetation is a semi-deciduous subtropical forest. The study area still contains 68% native forest and includes part of the largest fragment of this ecoregion (~370,000 ha, counting portions of Brazil's bordering forests; Fig. 1) and multiple remnants of different sizes and degrees of protection and anthropogenic disturbance, including poaching (Martínez Pardo et al., under review). In addition to native forest, the predominant land uses include commercial tree plantations (mainly pine, *Pinus taeda*, almost 20% of the study area), shrub plantations (mainly yerba mate, *Ilex paraguariensis*, 8%), annual crops (tobacco, corn, and cassava), and pasture for cattle-grazing (both summing 2%; Fig. 1).

The area still retains the original assemblage of native terrestrial mammals, including several sensitive species, such as the jaguar (Paviolo et al., 2016), the lowland tapir (*Tapirus terrestris,* de Bustos et al., 2019)*,* and the ocelot (*Leopardus pardalis,* Cruz et al., 2019a). Previous work in this region aimed at prioritizing forest fragments to improve connectivity in critical areas for jaguars (Martínez Pardo et al., 2017), but there are no studies focused on evaluating forest connectivity and availability for the entire mammal community.

We combined data from two large-scale camera-trap surveys conducted between 2013 and 2014. One of the surveys was aimed at studying mammal and bird assemblages (Iezzi et al., 2018) and the other at estimating jaguar densities (Paviolo et al., 2016). For the former, 184 single-camera sampling stations were active for an average of 49.80 ± 19 continuous days, set up in the native forest or pine plantations, at distances of >50 m from roads or human trails. In the latter, 90 camera-trap stations were deployed for 47.43 ± 14.18 days on infrequently used unpaved roads (2-6 m wide). These consisted of two camera traps facing each other on each side of the road. We excluded records from 32 stations that did not meet the criterion of a distance >500 m from the closest one. Total effort was 11,681 camera-trap days derived from 242 sampling stations with a mean distance between stations of 2223 m. The minimum convex polygon that included all the cameras was 5089 km^2.

2.2. Selection of focal species

Based on previous studies (Cruz et al., 2018; Iezzi et al., 2019), we selected 5 forest specialist mammal species, sensitive to landscape transformation at the scale of our study, and for which we had enough camera-trap records to run robust occupancy models (i.e., they were recorded in more than 30% of the stations): the black-eared opossum (*Didelphis aurita*), Azara's agouti (*Dasyprocta azarae*), red brocket deer (*Mazama americana*)*,* tapir, and ocelot. These species have a wide range of body weights and diet types, including a carnivore with an extensive home range, large and medium-sized herbivores, and smaller species able to establish their home ranges within small patches (i.e., agouti, opossums; Table B1, Fig. 1). The type of land use replacing the forest affects the occurrence of these species, as cattle pastures and annual crops may represent barriers for some of them (Cruz et al., 2019b, 2019c; Iezzi et al., 2019). Also, the agouti, the brocket, and the tapir are frequently hunted species (Giraudo and Abramson, 2000) and are thus

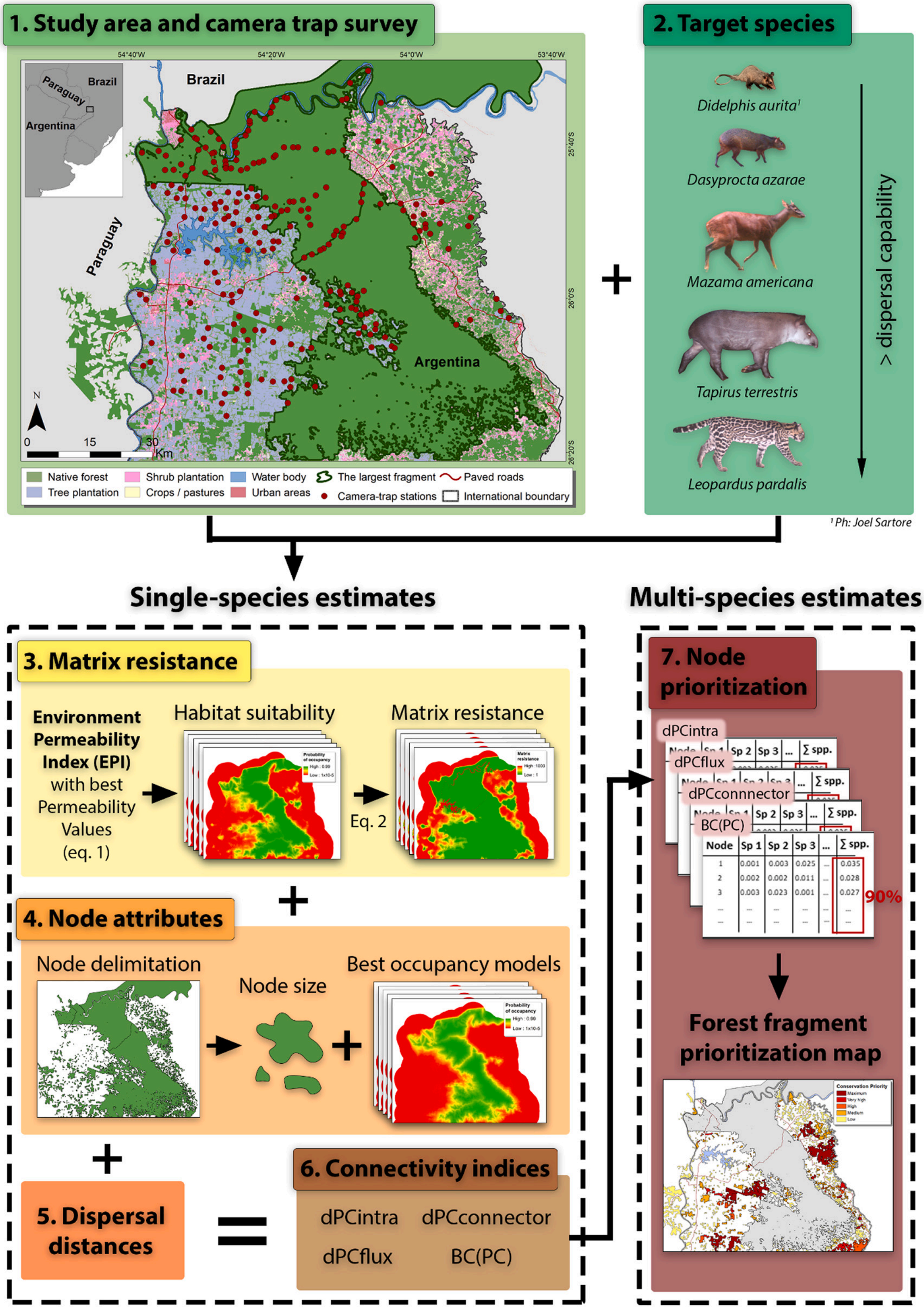

Fig. 1. Methodological steps to identify priority forest remnants for mammal conservation in the Atlantic Forest of Argentina. We developed a camera-trap survey ($N = 242$ stations) in a fragmented landscape (1) and selected 5 target species (2). We assessed permeability and developed resistance matrices (3) and node attributes (4) which were used in conjunction with the dispersal distances of the species (5) as inputs for the connectivity models for each species. We estimated 4 connectivity indices (6) and combined single-species estimates in a multi-species forest fragment prioritization map (7).

less abundant in more accessible and unprotected areas (Di Bitetti et al., 2008; Paviolo et al., 2018; Paviolo et al., 2009).

2.3. *Estimation of resistance matrices using occupancy models*

To develop species-specific prioritization of patches, we first estimated resistance matrices (Fig. 1). These are necessary to estimate effective distances between each pair of nodes that would represent the graph links (Pascual-Hortal and Saura, 2006; see Section 2.5). We developed the resistance matrices for each species based on habitat suitability models, which were defined by the probability of occupancy of the species in the landscape. Occupancy models estimate the probability that a site is being used (occupied) by a species (ψ), and the probability of detecting the species (p) at each camera-trap station when the station is occupied (MacKenzie et al., 2006). Since we did not place camera-trap stations in all land-use types, to better predict habitat suitability in the entire landscape we estimated the effect of an environment permeability index (EPI) on the occupancy of each species. The EPI evaluates the effect of the land uses immediately surrounding the sampling station (Iezzi et al., 2019). This index was estimated following da Silva et al. (2015), based on the proportion of each land use in a buffer around each station, weighted by a Permeability Value (PV) that represents the cost for movement of the species, using the following formula:

$$\mathrm{EPIb} = \frac{\sum(\mathrm{PVs}^{*}\mathrm{As})}{\mathrm{Ab}} \tag{1}$$

where *EPIb* = Environment Permeability Index for station *b*; *PVs* = Permeability Value of land-use type *s*; *As* = Area occupied by land-use type *s*; *Ab* = Total buffer area around station *b*; *b* = Sampling station; *s* = Land use (native forest, tree plantation, shrub plantation, crops or pastures, urban areas; see Fig. 1). As we did not have movement data to directly estimate PVs, we assumed that the effect of the land cover in the surroundings of the study sites is reflected in the probability of occupancy of each species. Thus, we estimated different variants of EPI that combine different PVs, and selected the combination that best predicted the probability of occupancy of each species. To do this, we used single-species, single-season occupancy models and conducted a two-step modeling approach. The first step was to select the best radius for the EPI for each species to find the appropriate scale at which the probability of occupancy is best predicted by the landscape structure in the surroundings (Jackson and Fahrig, 2015; Table B2). The second step was to select the best combination of PVs to estimate the variant of EPI that best predicted the probability of occupancy of each species, using the radii selected in the first step (Table B3).

For the first step, we estimated different variants of EPI using radii of 100, 200, 500, 1000, and 2000 m and using PVs for a generic medium-large native mammal, following Iezzi et al. (2019). For the second step, we estimated different variants of EPI that combine different PVs, with the condition that the native forest always had a value of 1 (highest permeability), and other land uses had values that increase as their structural similarity with the native forest decreases (i.e., $\mathrm{PV}_{\text{native forest}} = 1$ and $\leq \mathrm{PV}_{\text{tree plantation}} \leq \mathrm{PV}_{\text{shrub plantation}} \leq \mathrm{PV}_{\text{crops/pastures}} \leq \mathrm{PV}_{\text{urban areas}}$). Water bodies were excluded from the EPI estimates (and therefore from the habitat suitability maps) because they could represent barriers for species to cross but at the same time could be attractive to them as a resource. To select the variant of EPI with the best radius for each species and with the best combination of PVs, we compared each model using the Akaike Information Criterion for small samples (AICc) and selected the variant included in the model with the lowest value. To better predict habitat suitability considering other anthropogenic pressures present in the area, we also included the cost of human access as an indirect measure of human impact and poaching, affecting the ψ and/or p of game species (Table 1). We also included some other covariates of p based on previous studies (Cruz et al., 2019b, Cruz et al., 2018; Paviolo et al., 2018; Table 1, see Appendix A for details).

Finally, we generated habitat suitability maps for each species, extrapolating the probability of occupancy of each one to the entire landscape. We used a negative exponential transformation to translate habitat suitability into resistance matrices, following Meyer et al. (2020) and Trainor et al. (2013):

Table 1

Description and justification of the variables included in occupancy models to estimate habitat suitability and nodes attributes, and that can be affecting the detectability (p) and probability of occupancy (ψ) of the five mammal species (see Appendix A for more details).

	Variable	Description	Justification
Habitat suitability			
p	Location of camera trap (LOC)	Categorical variable that defines the location of the camera trap: roads, inside forest, or inside pine plantations.	The dataset belonged to two different survey designs and the location of camera traps could highly affect p of some mammals (di Bitetti et al., 2014; Paviolo et al., 2018).
	Cost of Access (CostAccess)	Continuous variable representing human accessibility as a proxy of the human impact and hunting pressure (Ferreguetti et al., 2018; Martínez Pardo et al., under review).	In areas with high poaching, large ungulates and carnivores may change their behavior and become more elusive (Mendes et al., 2020) affecting p of brocket, ocelot, and tapir (Paviolo et al., 2018).
	Reproductive seasonality (Season)	Categorical variable describing the reproductive seasonality of the opossum (only included in opossum models).	The abundance and activity of opossums vary seasonally according to reproductive activity and resource availability (Cáceres, 2003) affecting p of this species (Cruz et al., 2019b).
ψ	Environmental Permeability Index (EPI)	Continuous variable representing the proportion of each land use in a buffer around each station, weighted by a Permeability Value (see Eq. 1).	Since we did not place camera-trap stations in all land uses, to better predict habitat suitability in the entire landscape we estimated the general effect of the landscape permeability using this index (da Silva et al., 2015; Iezzi et al., 2019).
	Cost of Access	Same as estimated for p.	Poaching has negative consequences on populations of many large mammal species, affecting ψ of the commonly poached species in the region: agouti, brocket, ocelot, and tapir (Cruz et al., 2018; Di Bitetti et al., 2008; Paviolo et al., 2018, Paviolo et al., 2009).
Nodes attributes			
p	Same variables than included in habitat suitability models.		
ψ	Environmental Permeability Index*	Same as estimated for habitat suitability.	To evaluate the effect of the proportion of the different land uses surrounding the camera-trap station (da Silva et al., 2015; Iezzi et al., 2019).
	Percentage of forest around each station (% forest)*	Continuous variable representing the percentage of forest in a buffer around each station.	The amount of forest in the landscape is a variable that affects the occupancy of several mammal species in the Atlantic Forest (Beca

(*continued on next page*)

Table 1 (*continued*)

Variable	Description	Justification
		et al., 2017; Cruz et al., 2019c; Paviolo et al., 2018). EPI also considers the proportion of forest in the buffer, but the occurrence of some species may be more affected by the amount of forest than the land use type in the environment (Iezzi et al., 2019).
Diversity of land uses around each station (heterogeneity)*	Continuous variable representing the diversity of land uses estimated with the Shannon–Wiener index (only included in opossum models).	The presence of different land uses in the landscape may offer a variety of resources affecting ψ of the opossums (Cruz et al., 2019b).
Distance to the largest fragment (Distance)*	Continuous variable representing the distance from each station to the largest forest fragment.	Very large forest patches are critical as population sources of mammal species and may affect their occurrence (Cruz et al., 2018; Iezzi et al., 2018; Paviolo et al., 2018).
Cost of Access	Same description and justification than for habitat suitability	

[*] Most of these variables are highly correlated (Spearman coef. > 0.7) thus we generated models with all possible combinations of non-correlated variables.

$$R = 100 - 99\frac{(1 - e^{-8HS})}{1 - e^{-8}} \quad (2)$$

where *R* is the resistance value and *HS* is habitat suitability (i.e., ψ). With this transformation, resistance values ranged from 1 to 100 and increased dramatically at very low habitat suitability values. As roads are linear structures that are only one pixel wide but can be a barrier and a death risk for all species, once we obtained resistance matrices, we assigned these a higher resistance value of 1000. To water bodies (not included in EPI estimations), we assigned a resistance value of 100 for water-tolerant species (brocket and tapir), 500 for the ocelot, and 1000 for the smaller species that are very unlikely to cross water bodies larger than the size of one pixel (30 m).

2.4. *Delimitation of nodes and their attributes*

We considered as nodes those forest patches containing a core forest area not affected by edge effects. Following Iezzi et al. (2019), the edge width was defined as 200 m, and thus a core area was an area within a fragment more than 200 m away from any abutting non-forest areas (Saura et al., 2011). We also split fragments traversed by paved roads. Using these criteria, we identified 843 nodes, ranging from 13 to 205,315 ha (median = 35.5 ha), including 46 nodes located in neighboring countries close to the international border. For each species, nodes were characterized by adding up the predicted probability of occupancy of their pixels, thus weighting the node area by its use (Fig. 1). Since occupancy models developed to estimate resistance matrices (Section 2.3) may not necessarily be the models that best predict species occupancy (i.e., other landscape variables that specifically characterize forest patches may better explain species occupancy but may be highly correlated with EPI), we decided to evaluate the importance of other variables affecting ψ that also describe forest configuration and heterogeneity of land uses in the landscape, based on previous works (Cruz et al., 2018; Cruz et al., 2019b; Paviolo et al., 2018; Tables 1 and B4). We ranked models by their increasing AICc value (Burnham and Anderson, 2002) and selected the model with the lowest AICc to predict the probability of occupancy of each species (see Appendix A for more details).

To delimit the nodes and to estimate the variables, we used a land-use raster layer (pixels of 30 × 30 m) created for 2013–2014 by Zuleta et al. (2015). We used ArcGIS 10.3.1 (ESRI Inc.) to create the variables, generate habitat suitability maps and resistance matrices, and characterize the nodes. Occupancy models and model selection were performed using "*camtrapR*", "*unmarked*", and "*MuMIn*" packages in R ver. 4.0.3 (Appendix A).

2.5. *Graph links among nodes*

In a graph-based approach, the landscape is represented as a set of nodes that are functionally connected by links (Urban and Keitt, 2001). In a probabilistic connection model, graph links represent the probability of direct dispersal of a species between two nodes, which is obtained as a function of the distances between nodes and the dispersal distance of the species under analysis (Pascual-Hortal and Saura, 2006). We estimated the distances between nodes as effective distances which consider the facility of movement and death risk of individuals through each land use, represented by the resistance matrices previously created (Section 2.3; Adriaensen et al., 2003). The effective distances between each pair of nodes were obtained through least-cost path algorithms using Linkage Mapper 0.9 (McRae and Kavanagh, 2011) in ArcGIS 10.3.1. The effective distances were transformed into probabilities of movement for each species using a negative exponential function, with a decay parameter estimated using the median dispersal distance for each species, estimated as a function of body size following Sutherland et al. (2000; Table B1). We transformed these Euclidean dispersal distances into effective distances (cost units) by multiplying them by the average resistance value within a buffer (same radius selected for EPI for each species) around camera-trap stations that had occupancy values greater than the average (Table B1).

2.6. *Graph-based connectivity models*

To evaluate the relative importance of each node in habitat connectivity for each species, we estimated the three fractions of the probability connectivity index (PC). The PC index is based on the concept of habitat availability, as it considers not only the degree to which the nodes are connected but also their attributes, in this case, a combined measure of patch size and species occupancy (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007):

$$PC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j p_{ij}^{*}}{A_L^2} \quad (3)$$

where *n* is the total number of nodes in the study area, a_i and a_j are the attributes of the nodes *i* and *j*, in our case estimated as a combination of patch size and the species occupancy (see Section 2.4 above). p_{ij} refers to the connections between nodes and represents the dispersal probabilities of the species, estimated for our analysis by the least-cost paths through resistance matrices for nodes *i* and *j* (see Sections 2.3 above) combined with the dispersal distance of the species (see Sections 2.5 above). Finally, A_L is the total study area, and p_{ij}^* is defined as the maximum product probability of all possible paths between patches *i* and *j*. To prioritize the nodes, we estimated the percentage of variation in the PC index (dPC) that measures the decrease in habitat connectivity and availability resulting from the loss of a given node in the landscape (Saura and Pascual-Hortal, 2007). We discriminated dPC in the three fractions: dPCintra, dPCflux, and dPCconnector. dPCintra evaluates the contribution of a node in terms of its attribute, regardless of its position in the landscape network; dPCflux evaluates how well connected a node is with the rest of the nodes in the landscape, using an area-weighted dispersal function that depends on the attribute of a node and its position within the landscape network; and dPCconnector evaluates how irreplaceable a node is as a connecting element or stepping stone between the rest of the nodes in the landscape (Saura and Rubio, 2010). Additionally, we estimated the BC(PC) centrality index, which is developed using the same probabilistic model as used for PC (Bodin and Saura, 2010). Both the dPCconnector and the BC(PC) indices quantify the importance of nodes as connecting elements, with the difference that the latter quantifies this aspect in the current landscape, without making patch removal experiments, while dPCconnector quantifies the connectivity reduction by the connections that cannot be replaced if a node is removed from the landscape (Bodin and Saura, 2010). The largest forest fragment of our study area (a fragment composed of 4 nodes separated by paved roads, Fig. 1) was included in this part of the analysis because of its relevance as a source and destination of connections with other nodes, but it was excluded for the node prioritization (Section 2.7) as its high priority is already well established (Iezzi et al., 2018, 2019). We performed connectivity analyses with software Conefor 2.6 (Appendix A).

2.7. *Multi-species node prioritization*

To generate a node prioritization map, we first worked with each connectivity index separately, summing for each node the value obtained for the five species, following Hartfelder et al., 2020; Fig. 1. Then, for each index, we ranked nodes according to the sum of their index values and selected the minimum number of nodes or patches (MNPC) needed to maintain 90% of the connectivity, considering them as “key patches” (Martínez Pardo et al., 2017). Following this procedure, the species that were more sensitive to the loss of connectivity and/or availability (i.e., species with higher index values) had a greater influence on the final node prioritization than the less sensitive ones. We evaluated the influence of each species on the MNPC selection by estimating the proportional contribution of each species index value to the sum of the index values considering all the species. Finally, we classified the key patches into 5 conservation categories: 1) “maximum priority” were those patches included in the MNPC for all indices; 2) “very high priority” were the patches selected in 3 groups of MNPC (i.e., 3 indices); 3) “high priority” were those selected in 2 groups of MNCP; 4) “medium priority” were included within the MNPC by only one index; 5) “low priority” patches were those not included in the MNPC for any of the indices, and consequently, less important for landscape connectivity.

3. Results

3.1. *Single-species estimates*

The species studied were recorded in 31–46% of the stations, with a mean of 89 ± 17 stations per species (range 74–111 stations). The permeability values included in the EPI that best predicted occupancy probability differed between species (Tables 2 and SB3). The ocelot and the tapir were the species most affected by the presence of production land uses in the surroundings (2-km radius), as habitat suitability was best predicted by models with higher PVs (Table 2). In contrast, anthropogenic land uses had low PV in the best-ranked occupancy models for the agouti (Tables 2 and B3). The best-ranked occupancy models for the opossum and brocket had intermediate PVs.

Variables that best-predicted mammal occupancy varied between species, and thus node attributes were considerably different for each species (Tables 2 and B4). The probability of occupancy of the brocket and the tapir were more affected by the distance to the largest forest fragment than by the EPI (Tables 2, B4, and B5), and thus predicted occupancy was higher in the largest forest fragment and its surroundings (Fig. B1). The occupancy of all species (except the opossum, for which we did not predict an effect of the cost of access and therefore did not model its effect; Table B5) was negatively affected by human accessibility.

Table 2

Beta estimates for each variable included in the occupancy models used to estimate habitat suitability and node attributes for each species (see Table B5 for EE and IC).

Species	Model	
	p	ψ
Habitat suitability		
Black-eared opossum	1.72–2.11*LOC_road[a] - 3.16*LOC_pine[a] - 0.79*Season	1.49–0.07*EPI(tree50/shrub80/crop80/urban80)2000 m[b]
Azara's agouti	0.34–0.19*LOC_inside[a]	0.88 - 1.09*EPI(tree5/shrub5/crop5/urban5)100 m + 1.43*CostAccess
Red brocket deer	−0.75 - 0.06*LOC_road +0.21*LOC_pine +0.61*CostAccess	−1.356 - 0.202*EPI(tree5/srhub10/crop10/urban10)100 m + 2.447*CostAccess
Tapir	−1.31 + 0.78*LOC_road - 0.15*LOC_pine[1] + 0.33*CostAccess	−1.29 - 0.04*EPI(tree50/shrub200/crop200/urban200) 2000 m + 2.33*CostAccess
Ocelot	−2.89 + 2.05*LOC_road - 1.24*LOC_pine[1] + 0.53*CostAccess	0.98–0.04*EPI(tree50/shrub200/crop200/urban200)2000 m + 0.77*CostAccess
Node attributes		
Black-eared opossum	same model as habitat suitability	
Azara's agouti	same model as habitat suitability	
Red brocket deer	−0.08 - 0.18*LOC_road +0.19*LOC_pine +0.69*CostAccess	−0.80 + 1.50*CostAccess - 0.08*Distance
Tapir	−1.34 + 0.79*LOC_road - 0.03*LOC_pine +0.33*CostAccess	−1.53 + 2.31*CostAccess - 0.01*Distance
Ocelot	same model as habitat suitability	

[a] Location of the camera-trap: roads (LOC_road), inside forest (intercept), and inside pine plantations (LOC_pine). For the agouti there were only two categories (LOC_road vs. LOC_inside) since there were no records inside the pine plantations.

[b] EPI = Environment Permeability Index at the best radius selected for each species. In parentheses, the selected combination of Permeability Values (PV) is detailed for each land use (tree plantations / shrub plantations / annual crops and pastures / urban areas).

Node prioritization was very similar between species (Fig. B2-B5). However, node prioritization estimates for the tapir based on dPCintra correlated poorly with those of the two smaller species (Spearman correlations ≤ 0.5, Fig. B6).

3.2. *Multi-species prioritization*

One hundred ninety-eight nodes (23% of the total) were selected as key patches, representing 90% of the connectivity outside the largest forest fragment according to at least one of the indices (Table 2). Only 8 key patches belonged (at least partially) to protected areas, which represents 14% (9547 ha) of the total area of the key patches. The contribution of each species to node selection was variable, with the tapir's indices estimates weighting less than those of the other species (Fig. 2, S2-S5). Smaller species (agouti and opossum) had a significant influence on the selection of MNPC for the dPCintra. The ocelot had a great influence on the selection of MNPC for the dPCflux and BC(PC) indices, and the agouti on the selection of MNPC for the dPCconnector and BC (PC) (Fig. 2).

Only 5 nodes, the biggest patches outside the largest forest fragment, had a maximum priority for conservation (2.5% of key patches; Fig. 3, Table 3). Only 24% of their area is under protection, and 2 of them are completely unprotected (Fig. 3, Table 3). Fifty-eight nodes were classified as “very high” and “high” priority. Almost all of these were considered important as connecting elements (were selected for BC(PC) and/or dPCconnector) and half are irreplaceable for maintaining

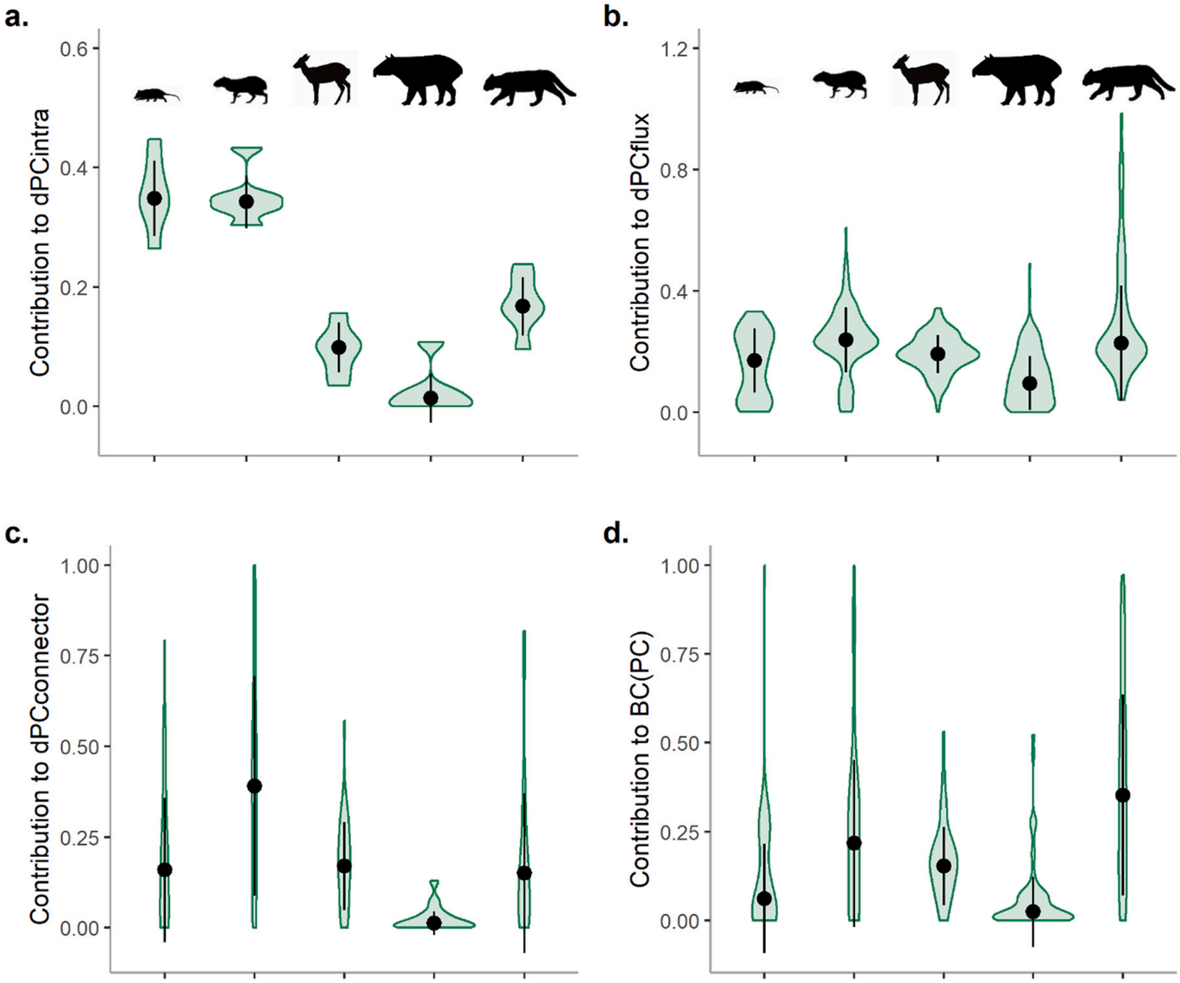

Fig. 2. Kernel probability densities of the proportional contribution of the five species to selected nodes based on a. dPCintra ($N = 6$ nodes), b. dPCflux ($N = 168$ modes), c. dPCconnect ($N = 37$ nodes), and d. BC(PC) ($N = 76$ nodes). Dots show the median values and black lines the SD. Nodes correspond to the minimum number of patches (MNPC) needed to maintain 90% connectivity and were selected using the sum of index values of all species. From left to right: black-eared opossum (*Didelphis aurita*), Azara's agouti (*Dasyprocta azarae*), red brocket deer (*Mazama americana*), tapir (*Tapirus terrestris*), and ocelot (*Leopardus pardalis*). Graphs made with "ggplot2" R package (Wickham, 2014).

connectivity among the remaining nodes (Table 3, Fig. B7). Only 2 of these nodes are partially protected (Fig. 3, Table 3).

4. Discussion

Adequate territorial planning and conservation efforts require a prioritization within degraded and fragmented forests. The Argentinian Atlantic Forest still preserves large forest fragments that act as population sources for many mammal species. It also contains multiple smaller remnants immersed in a production matrix (Iezzi et al., 2018, 2019), most of which are currently unprotected. Here we prioritized these remnants using a multi-species approach and identified those where conservation action should be implemented to promote connectivity for the mammal assemblage and achieve a sustainable production landscape.

We evaluated forest connectivity using a graph-based approach that allowed us to characterize the landscape in a spatially explicit manner. As in other fragmented landscapes, the percentage of variation in the probability of connectivity index (dPC) was a useful tool to evaluate the relative importance of habitat patches for maintaining habitat availability and connectivity (e.g., Engelhard et al., 2017; Pereira et al., 2011). Also, a combination of graph-based analyses and occupancy models allowed us to incorporate the effect of other anthropogenic pressures when developing the forest fragment prioritization, an innovative approach in this kind of studies.

A low percentage of the patches outside the largest forest fragment concentrate most of the connectivity (90%). The loss of these few key patches would have a strong impact on the functioning of the network of remaining patches. The few patches selected based on dPCintra are highly important to maintain habitat availability, and particularly so for smaller species with low dispersal abilities (as Saura and Rubio, 2010, described). The patches selected based on dPCconnector are irreplaceable as stepping stones for species with intermediate dispersal distances, as these need connecting elements to move between habitat patches (Saura and Rubio, 2010). In addition, for species with larger dispersal distances (the ocelot in this case), patches selected based on dPCflux are very important, as this index best describes immigration rates (Poli et al., 2020; Saura and Rubio, 2010).

We studied mammal species that varied in body size and dispersal ability to be able to represent the Atlantic Forest mammal assemblage. Multi-species connectivity models, though poorly studied and applied (e.g., Albert et al., 2017; Liu et al., 2018; Meyer et al., 2020), are important, as species differ in their habitat and connectivity requirements (Beier et al., 2008). In our study area, where there are also other anthropogenic pressures such as poaching, connectivity of small fragments was not equally important for all species, which emphasizes the need to be careful when selecting species to carry out territorial planning based on landscape connectivity. The tapir, for example,

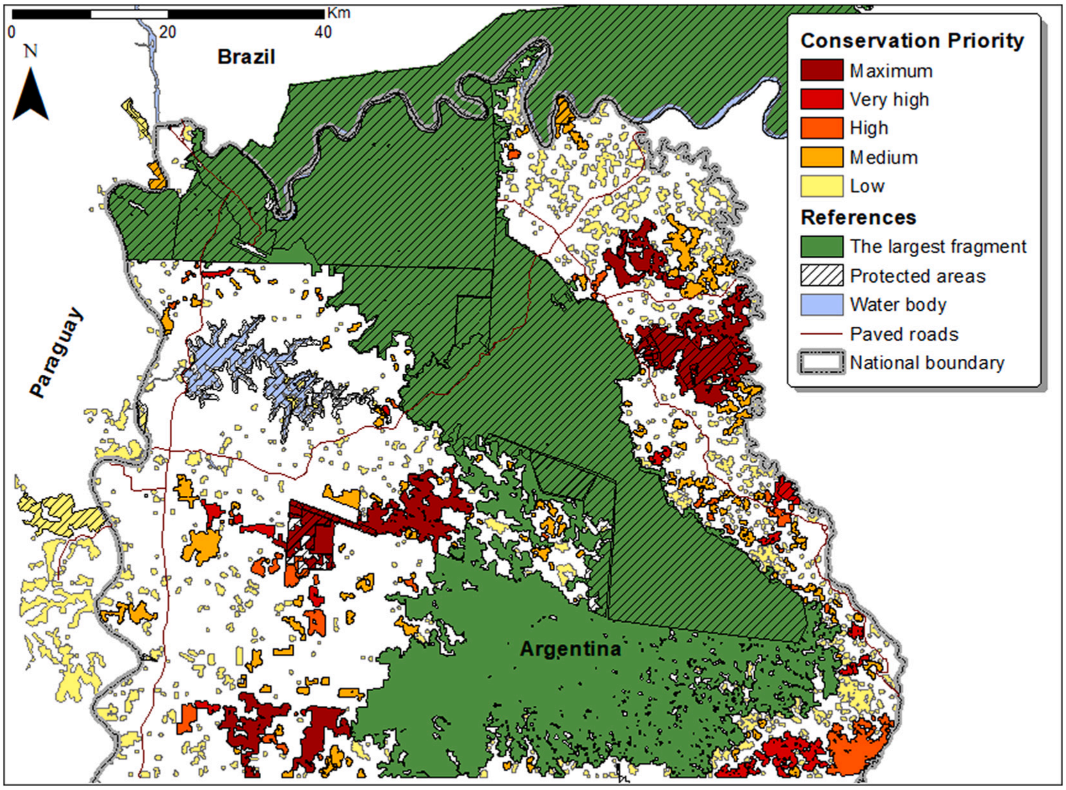

Fig. 3. Importance of each forest patch in the Atlantic Forest of Argentina according to its prioritization category, based on its contribution to the maintenance of overall landscape connectivity as measured by dPCintra, dPCflux, dPCconnector and BC(PC) indices. To see details of the indices that were important for each patch and their interpretation, see Fig. B7 and Table 2.

Table 3
Description of the prioritization categories of nodes to preserve habitat connectivity for sensitive mammal species, including the number of nodes and area covered by each category, and the percentage of nodes and area that belong to protected areas within each category.

Conservation Priority	# Nodes	Indices included	Description	Area (ha)	% Protected areas
Maximum	5	dPCintra; dPCflux; dPCconnector; BC(PC)	These are large and/or with high species occupancy. They are highly connected. They are important as connecting elements in the current landscape and are also irreplaceable for this role.	Total: 30402 Mean: 6080	Nodes: 60% Area: 24%
Very high	17	dPCflux; dPCconnector; BC(PC)	These are highly connected. They are important as connecting elements in the current landscape and are also irreplaceable for this role.	Total: 7259 Mean: 427	Nodes: 6% Area: 6%
High	14	dPCconnector; BC(PC)	These are important as connecting elements in the current landscape and are also irreplaceable for this role.	Total: 8824 Mean: 205	Nodes: 2% Area: 3%
	1	dPCflux; dPCconnector	This is highly connected. It is irreplaceable as a connecting element.		
	25	dPCflux; BC(PC)	These are highly connected. They are important as connecting elements in the current landscape.		
	1	dPCintra; dPCflux	This is large and/or with high species occupancy. It is highly connected.		
Medium	15	BC(PC)	These are important as connecting elements in the current landscape.	Total: 21179 Mean: 158	Nodes: 2% Area: 6%
	119	dPCflux	These are highly connected.		
Low	645	–	These are not within the group of patches that comprise 90% of connectivity for any indices.	Total: 41608 Mean: 64	Nodes: 1% Area: 10%

despite its great dispersal ability, was the species with the lowest contribution to node selection, probably because it is very sensitive to hunting pressure (Bogoni et al., 2020) and thus its habitat use (occupancy) was strongly affected by proximity to the largest well-protected forest fragments (population sources) more than by landscape connectivity (Table 2, Fig. 3 and B1). Therefore, species with these features, even though usually endangered, are not good targets for developing connectivity models aimed at promoting connectivity for the entire assemblage, at least at the scale of our analysis. A combination of highly dispersed species (e.g., medium-large felids) with smaller species that find small patches as suitable habitats (e.g., rodents, opossums) is a better option if just a few species are to be selected to represent the whole assemblage.

Human accessibility, a proxy of poaching (Ferreguetti et al., 2018; Martínez Pardo et al., under review), highly affected patch prioritization, as it affected the probability of habitat use by most of the selected mammal species. These results are consistent with what other studies have suggested: in landscapes that still have a high proportion of native vegetation cover, as is the case of northern Misiones, it is expected that the quality of the environment becomes highly important, sometimes even more than the configuration of fragments, for conserving biodiversity at landscape level (Iezzi et al., 2019; Pardini et al., 2010). In our study area, most patches outside the largest are very accessible, have no or weak protection, and are thus highly affected by poaching (Martínez Pardo et al., under review). In this context, species such as the tapir and the brocket, which are sensitive to hunting (see Table 2), would be more dependent for their conservation on anti-poaching measures rather than on improving forest connectivity. Since poaching affects populations of large Neotropical mammals (Bogoni et al., 2020) and protected areas are usually only a minor portion of remaining tropical forests, it is important to consider its indirect effect on forest patch prioritization when developing land management plans.

Forest prioritization was highly influenced by patch configuration and anthropogenic pressures, but also by matrix resistance. Our results suggest that the type of land use that replaced the forest affected mammal species occupancy differentially. Although the mammal assemblages recorded in pine plantations are depauperate compared to those of the largest forest fragment (Iezzi et al., 2018), these plantations constitute a more permeable matrix than other crops and cattle pastures for several Atlantic Forest mammals (see also Cruz et al., 2019c; Iezzi et al., 2019; Paviolo et al., 2018). Since the presence of canopy trees seems to promote the presence of forest mammals, agroecological crops grown under forest cover are a good alternative to promote a more permeable matrix (Cassano et al., 2012). A more permeable matrix scenario would likely result in a different prioritization map, changing the role of the different patches according to their location and/or increasing the relative importance of patches that are now isolated in the most disturbed areas. Despite this general suggestion, studies are still needed to assess the effects of different agricultural modes of production on matrix permeability in order to promote biodiversity-friendly production systems. Also, more integrative studies that combine multiple taxa are important, as a different prioritization of patches might have resulted if species with different habitat requirements had been included in the analysis (e.g., volant or arboreal species highly dependent on trees).

4.1. *Conclusions and recommendations*

We generated a spatially explicit tool that proved useful to identify the forest patches immersed in a production landscape that are a priority for the conservation of a mammal assemblage. Most of these high-priority patches are not legally protected and belong to forestry companies and small farmers, and thus creating new protected areas is not always a viable option. In Argentina, forest preservation is regulated by law (National Law N°26.331) but illegal clearcutting, selective logging, and poaching are still major threats in the region. It is therefore important to encourage the use of economic incentives to prevent these activities and to make landowners aware of the importance of maintaining and protecting the forest remnants within their properties. Also, forestry companies can use these prioritization strategies to promote sustainable production landscapes (see Mesquita et al., 2012) and would benefit from certification schemes that encourage them, such as FSC (FSC, 2015). It is also important to reduce poaching in the priority patches as this has negative effects on several mammal populations. All these actions together will facilitate the movement and survival of sensitive mammal species, promoting the conservation of the entire community in a production landscape, which is essential to confront the negative effects of forest fragmentation on biodiversity.

Data statement

The complete data that support the findings of this study are available from the corresponding author upon request. Part of the data is available in:

Iezzi, M.E., De Angelo, C.D., Cruz, P., Varela, D., Cirignoli, S., Di Bitetti, M.S., 2021. Data from: Are tree plantations promoting homogenization of mammal assemblages between regions with contrasting environments? Dryad dataset, https://doi.org/10.5061/dryad.2280gb5qv

Lima, F., Beca, G., Muylaert, R. L. R. L., Jenkins, C. N. C. N., Perilli, M. L. L. M. L. L., Paschoal, … Galetti, M., 2017. ATLANTIC-CAMTRAPS: a dataset of medium and large terrestrial mammal communities in the Atlantic Forest of South America. Ecology, 98(11), 2979. https://doi.org/10.1002/ecy.1998

Nagy-Reis, M.B., de Faria Oshima, J.E., Kanda, C.Z., Palmeira, F.B.L., de Melo, F.R., Morato, R.G., … Ribeiro, M.C., 2020. NEOTROPICAL CARNIVORES: a data set on carnivore distribution in the Neotropics. Ecology ecy.3128. https://doi.org/10.1002/ecy.3128

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Adriaensen, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., Matthysen, E., 2003. The application of ‘least-cost’ modelling as a functional landscape model. Landsc. Urban Plan. 64, 233–247. https://doi.org/10.1016/S0169-2046(02)00242-6.

Albert, C.H., Rayfield, B., Dumitru, M., Gonzalez, A., 2017. Applying network theory to prioritize multispecies habitat networks that are robust to climate and land-use change. Conserv. Biol. 31, 1383–1396. https://doi.org/10.1111/cobi.12943.

Beca, G., Vancine, M.H., Carvalho, C.S., Pedrosa, F., Alves, R.S.C., Buscariol, D., Galetti, M., 2017. High mammal species turnover in forest patches immersed in biofuel plantations. Biological Conservation 210, 352–359. https://doi.org/10.1016/j.biocon.2017.02.033.

Beier, P., Majka, D.R., Newell, S.L., 2009. Uncertainty analysis of least-cost wildlife modeling for designing linkages. America (NY) 19, 2067–2077.

Beier, P., Majka, D.R., Spencer, W.D., 2008. Forks in the road: choices in procedures for designing wildland linkages. Conserv. Biol. 22, 836–851. https://doi.org/10.1111/j.1523-1739.2008.00942.x.

Benítez-López, A., Alkemade, R., Schipper, A.M., Ingram, D.J., Verweij, P.A., Eikelboom, J.A.J., Huijbregts, M.A.J., 2017. The impact of hunting on tropical mammal and bird populations. Science 356, 180–183. https://doi.org/10.1126/science.aaj1891.

Bennett, A.F., Saunders, D.A., 2010. Habitat fragmentation and landscape change. In: Sodhi, N.S., Ehrlich, P. (Eds.), Conservation Biology for All. Oxford University Press, pp. 88–106.

Bodin, Ö., Saura, S., 2010. Ranking individual habitat patches as connectivity providers: integrating network analysis and patch removal experiments. Ecol. Model. 221, 2393–2405. https://doi.org/10.1016/j.ecolmodel.2010.06.017.

Bogoni, J.A., Peres, C.A., Ferraz, K.M.P.M.B., 2020. Extent, intensity and drivers of mammal defaunation: a continental-scale analysis across the Neotropics. Sci. Rep. 10, 1–17. https://doi.org/10.1038/s41598-020-72010-w.

Brodie, J.F., Giordano, A.J., Dickson, B., Hebblewhite, M., Bernard, H., Mohd-Azlan, J., Ambu, L., 2015. Evaluating multispecies landscape connectivity in a threatened tropical mammal community. Conserv. Biol. 29, 122–132. https://doi.org/10.1111/cobi.12337.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, USA.

Cáceres, N.C., 2003. Use of the space by the opossum Didelphis aurita Wied-Newied (Mammalia, Marsupialia) in a mixed forest fragment of southern Brazil. Rev. Bras. Zool. 20, 315–322. https://doi.org/10.1590/S0101-81752003000200023.

Cassano, C.R., Barlow, J., Pardini, R., 2012. Large mammals in an agroforestry mosaic in the Brazilian Atlantic Forest. Biotropica 44, 818–825. https://doi.org/10.1111/j.1744-7429.2012.00870.x.

Cruz, P., De Angelo, C., Martínez Pardo, J., Iezzi, M.E., Varela, D., Di Bitetti, M.S., Paviolo, A., 2019c. Cats under cover: habitat models indicate a high dependency on woodlands by Atlantic Forest felids. Biotropica 51. https://doi.org/10.1111/btp.12635.

Cruz, P., Iezzi, M.E., De Angelo, C., Varela, D., Di Bitetti, M.S., 2019b. Landscape use by two opossums is shaped by habitat preferences rather than by competitive interactions. J. Mammal. 1–13. https://doi.org/10.1093/jmammal/gyz133.

Cruz, P., Iezzi, M.E., De Angelo, C., Varela, D., Di Bitetti, M.S., Paviolo, A., 2018. Effects of human impacts on habitat use, activity patterns and ecological relationships among medium and small felids of the Atlantic Forest. PLoS One 13, e0200806. https://doi.org/10.1371/journal.pone.0200806.

Cruz, P., Varela, D., Di Bitetti, M.S., Paviolo, A., Quiroga, V.A., Angelo, De, Arrabal, J.P., 2019a. Leopardus pardalis. In: Categorización 2019 de Los Mamíferos de Argentina Según Su Riesgo de Extinción. Lista Roja de Los Mamíferos de Argentina. Secretaría de Ambiente y Desarrollo Sustentable de la Nación y Sociedad Argentina para el Estudio de los Mamíferos. http://cma.sarem.org.ar.

Cushman, S.A., Landguth, E.L., 2012. Multi-taxa population connectivity in the Northern Rocky Mountains. Ecol. Model. 231, 101–112. https://doi.org/10.1016/j.ecolmodel.2012.02.011.

da Silva, L.G., Ribeiro, M.C., Hasui, É., Aparecida, C., 2015. Patch size, functional isolation, visibility and matrix permeability influences neotropical primate occurrence within highly fragmented landscapes. PLoS One 10, 1–20. https://doi.org/10.1371/journal.pone.0114025.

de Bustos, S., Varela, D., Lizárraga, L., Cirignoli, S., Quiroga, V.A., Chalukián, S., Albanesi, S., 2019. Tapirus terrestris. In: Categorización 2019 de Los Mamíferos de Argentina Según Su Riesgo de Extinción. Lista Roja de Los Mamíferos de Argentina. Secretaría de Ambiente y Desarrollo Sustentable de la Nación y Sociedad Argentina para el Estudio de los Mamíferos. http://cma.sarem.org.ar.

Di Bitetti, M.S., Paviolo, A., De Angelo, C.D., 2014. Camera trap photographic rates on roads vs. off roads: location does matter. Mastozool. Neotropical 21, 37–46.

Di Bitetti, M.S., Paviolo, A., Ferrari, C.A., De Angelo, C., Di Blanco, Y., 2008. Differential responses to hunting in two sympatric species of brocket deer (Mazama americana and M. nana). Biotropica 40, 636–645. https://doi.org/10.1111/j.1744-7429.2008.00413.x.

Engelhard, S.L., Huijbers, C.M., Stewart-Koster, B., Olds, A.D., Schlacher, T.A., Connolly, R.M., 2017. Prioritising seascape connectivity in conservation using network analysis. J. Appl. Ecol. 54, 1130–1141. https://doi.org/10.1111/1365-2664.12824.

Ferreguetti, Á.C., Pereira-Ribeiro, J., Prevedello, J.A., Tomás, W.M., Rocha, C.F.D., Bergallo, H.G., 2018. One step ahead to predict potential poaching hotspots: modeling occupancy and detectability of poachers in a neotropical rainforest. Biol. Conserv. 227, 133–140. https://doi.org/10.1016/j.biocon.2018.09.009.

FSC, 2015. Forest Stewardship Council. Plan estratégico Global 2015-2020. Trabajando en pos de tener bosques para todos para siempre. FSC International, Germany.

<collab>Fundación Vida Silvestre Argentina, W.W.F.collab, 2017. State of the Atlantic Forest: Three Countries, 148 Million People, One of the Richest Forest on Earth. Puerto Iguazú, Argentina.

Gaggiotti, O.E., Hanski, Ilkka, 2004. Mechanisms of extinction. In: Hanski, I., Gaggiotti, O. (Eds.), Ecology, Genetics, and Evolution in Metapopulations. Academic Press, pp. 337–366.

Giraudo, A.R., Abramson, R.R., 2000. Diversidad cultural y usos de la fauna silvestre por los pobladores de la selva misionera: ¿Una alternativa de conservación? In: Bertonati, C., Corucuera, J. (Eds.), La Situación Ambiental Argentina 2000. Fundación Vida Silvestre Argentina, Buenos Aires, Argentina, pp. 233–243.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Appl. Ecol. 1–9. https://doi.org/10.1126/sciadv.1500052.

Hartfelder, J., Fletcher, R.J., Reynolds, C., Stanton, R.A., 2020. The allometry of movement and the connectivity of communities. PNAS 1–25.

Iezzi, M.E., Cruz, P., Varela, D., De Angelo, C., Di Bitetti, M.S., 2018. Tree monocultures in a biodiversity hotspot: impact of pine plantations on mammal and bird assemblages in the Atlantic Forest. For. Ecol. Manag. 424, 216–227. https://doi.org/10.1016/j.foreco.2018.04.049.

Iezzi, M.E., Cruz, P., Varela, D., Di Bitetti, M.S., De Angelo, C.D., 2019. Fragment configuration or environmental quality? Understanding what really matters for native mammals conservation in the Atlantic Forest of Argentina. J. Nat. Conserv. 52 https://doi.org/10.1016/j.jnc.2019.125751.

Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? Glob. Ecol. Biogeogr. 24, 52–63. https://doi.org/10.1111/geb.12233.

Keeley, A.T.H., Beier, P., Gagnon, J.W., 2016. Estimating landscape resistance from habitat suitability: effects of data source and nonlinearities. Landsc. Ecol. 31, 2151–2162. https://doi.org/10.1007/s10980-016-0387-5.

Liu, C., Newell, G., White, M., Bennett, A.F., 2018. Identifying wildlife corridors for the restoration of regional habitat connectivity: a multispecies approach and comparison of resistance surfaces. PLoS One 13, 1–14. https://doi.org/10.1371/journal.pone.0206071.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, E.J., 2006. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press, San Diego, USA.

Magioli, M., Setz, E.Z.F., Percequillo, A.R., Ferraz, K.M.P.M.de B., Rondon, M.V.de S.S., Kuhnen, V.V., Rodrigues, M.G., 2016. Connectivity maintain mammal assemblages functional diversity within agricultural and fragmented landscapes. European Journal of Wildlife Research 62, 431–446. https://doi.org/10.1007/s10344-016-1017-x.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253.

Martínez Pardo, J., 2020. Modelado de las amenazas antrópicas para el jaguar (panthera onca) en la selva paranaense: uso de modelos espaciales para comprender sus determinantes primarios y formular estrategias para la conservación de un depredador tope. University of Córdoba, Argentina. Doctoral dissertation.

Martínez Pardo et al., under review J. Martínez Pardo P. Cruz S. Moya E. Pizzio F. Foletto F. Robino … C. De Angelo under review. Predicting poaching hotspots on the largest remnant of the Atlantic Forest by combining passive acoustic monitoring and occupancy models. Sent to Biol. Conserv.

Martínez Pardo, J., Paviolo, A., Saura, S., De Angelo, C., 2017. Halting the isolation of jaguars: where to act locally to sustain connectivity in their southernmost population. Anim. Conserv. 1–12 https://doi.org/10.1111/acv.12354.

McRae, B.H., Kavanagh, D.M., 2011. Linkage Mapper Connectivity Analysis Software. The Nature Conservancy, Seattle, WA. Available from linkagemapper.

Mendes, C.P., Carreira, D., Pedrosa, F., Beca, G., Lautenschlager, L., Akkawi, P., Galetti, M., 2020. Landscape of human fear in Neotropical rainforest mammals. Biological Conservation 241, 108257. https://doi.org/10.1016/j.biocon.2019.108257.

Mesquita, C.A.B., Holvorcem, C.G.D., Reverberi Tambosi, L., Costa Da Silva, S., 2012. Mosaicos florestai sustentáveis: monitoramento integrado da biodiversidade e diretrizes para restauração florestal. Conservation International, Belo Horizonte, Brazil.

Meurant, M., Gonzalez, A., Doxa, A., Albert, C.H., 2018. Selecting surrogate species for connectivity conservation. Biol. Conserv. 227, 326–334. https://doi.org/10.1016/j.biocon.2018.09.028.

Meyer, N.F.V., Moreno, R., Reyna-Hurtado, R., Signer, J., Balkenhol, N., 2020. Towards the restoration of the Mesoamerican Biological Corridor for large mammals in Panama: comparing multi-species occupancy to movement models. Mov. Ecol. 8, 1–14. https://doi.org/10.1186/s40462-019-0186-0.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Nagy-Reis, M.B., Estevo, C.A., Setz, E.Z.F., Ribeiro, M.C., Chiarello, A.G., Nichols, J.D., 2017. Relative importance of anthropogenic landscape characteristics for Neotropical frugivores at multiple scales. Anim. Conserv. 1–12 https://doi.org/10.1111/acv.12346.

Pardini, R., de Arruda Bueno, A., Gardner, T.A., Prado, P.I., Metzger, J.P., 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. PLoS ONE 5, e13666. https://doi.org/10.1371/journal.pone.0013666.

Pardini, R., Marques de Souza, S., Braga-Neto, R., Metzger, J.P., 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. Biol. Conserv. 124, 253–266. https://doi.org/10.1016/j.biocon.2005.01.033.

Pascual-Hortal, L., Saura, S., 2006. In: Brief Note Comparison and Development of New Graph-based Landscape Connectivity Indices: Towards the Priorization of Habitat Patches and Corridors for Conservation, pp. 959–967. https://doi.org/10.1007/s10980-006-0013-z. Puerto Iguazú, Argentina.

Paviolo, A., Cruz, P., Iezzi, M.E., Martínez Pardo, J., Varela, D., De Angelo, C., Di Bitetti, M.S., 2018. 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. For. Ecol. Manage. 430, 576–586. https://doi.org/10.1016/j.foreco.2018.08.029.

Paviolo, A., De Angelo, C., Di Blanco, Y., Agostini, I., Melzew, R., Ferrari, C., Di Bitetti, M.S., 2009. Efecto de la caza y el nivel de protección en la abundancia de los grandes mamíferos del Bosque Atlántico de Misiones. In: Carpinetti, B., Carciarena, M. (Eds.), Contribuciones para la conservación y manejo en el Parque Nacional Iguazú. Administración de Parques Nacionales, Buenos Aires, Argentina, pp. 237–254.

Paviolo, A., De Angelo, C., Ferraz, K.M.P.M.B., Morato, R.G., Martinez Pardo, J., Srbek-Araujo, A.C., Azevedo, F., 2016. A biodiversity hotspot losing its top predator: the challenge of jaguar conservation in the Atlantic Forest of South America. Sci. Rep. 6, 1–16. https://doi.org/10.1038/srep37147.

Pereira, M., Segurado, P., Neves, N., 2011. Using spatial network structure in landscape management and planning: a case study with pond turtles. Landsc. Urban Plan. 100, 67–76. https://doi.org/10.1016/j.landurbplan.2010.11.009.

Peres, C.A., Lake, I.R., 2003. Extent of nontimber resource extraction in tropical forests: accessibility to game vertebrates by hunters in the Amazon basin. Conserv. Biol. 17, 521–535. https://doi.org/10.1046/j.1523-1739.2003.01413.x.

Peres, C.A., Palacios, E., 2007. Basin wide effects of game harvest on vertebrate population densities in Amazonian Forests: implications for animal mediated seed dispersal. Biotropica 39, 304–315. https://doi.org/10.1111/j.1744-7429.2007.00272.x.

Poli, C., Hightower, J., Fletcher, R.J., 2020. Validating network connectivity with observed movement in experimental landscapes undergoing habitat destruction. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.13624.

Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. Am. Nat. 158, 87–99. https://doi.org/10.1086/320863.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science 343. https://doi.org/10.1126/science.1241484.

Saura, S., Pascual-Hortal, L., 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. Landsc. Urban Plan. 83, 91–103. https://doi.org/10.1016/j.landurbplan.2007.03.005.

Saura, S., Rubio, L., 2010. A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. Ecography (Cop.) 33, 523–537. https://doi.org/10.1111/j.1600-0587.2009.05760.x.

Saura, S., Vogt, P., Velázquez, J., Hernando, A., Tejera, R., 2011. Key structural forest connectors can be identified by combining landscape spatial pattern and network analyses. For. Ecol. Manag. 262, 150–160. https://doi.org/10.1016/j.foreco.2011.03.017.

Sutherland, G.D., Harestad, A.S., Price, K., Lertzaman, K.P., 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. Conserv. Ecol. 4, 16. https://doi.org/10.1111/j.1469-8137.1991.tb00984.x.

Trainor, A.M., Walters, J.R., Morris, W.F., Sexton, J., Moody, A., 2013. Empirical estimation of dispersal resistance surfaces: a case study with red-cockaded woodpeckers. Landsc. Ecol. 28, 755–767. https://doi.org/10.1007/s10980-013-9861-5.

Urban, D., Keitt, T., 2001. Landscape connectivity: a graph-theoretic perspective. Ecology 82, 1205–1218. https://doi.org/10.1002/app.32629.

Urban, D.L., Minor, E.S., Treml, E.A., Schick, R.S., 2009. Graph models of habitat mosaics. Ecol. Lett. 12, 260–273. https://doi.org/10.1111/j.1461-0248.2008.01271.x.

Wickham, H., 2014. An implementation of the Grammar of Graphics. "ggplot2" R Package.

Zeller, K.A., Jennings, M.K., Vickers, T.W., Ernest, H.B., Cushman, S.A., Boyce, W.M., 2018. Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. Divers. Distrib. 24, 868–879. https://doi.org/10.1111/ddi.12742.

Zuleta, G.A., Gauto, O.A., Varela, D.M., De Angelo, C., Johnson, B.G., Lorán, D., Zurita, A.A., 2015. Evaluaciones Ambientales Estratégicas y Programa de Monitoreo de la Biodiversidad en las Regiones de Mesopotamia y Delta del Paraná. Proyecto de Conservación de la Biodiversidad en Paisajes Productivos Forestales (GEF TF 090118). Technical report. Buenos Aires, Argentina.