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Halting the isolation of jaguars: where to act locally to sustain connectivity in their southernmost population

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Abstract

Habitat loss and fragmentation are among the major threats to the conservation of biodiversity. Improvement of landscape connectivity becomes one of the main strategies for alleviating these threats and is an increasingly used target in management policies worldwide. However, implementation of connectivity principles in local management actions often implies great difficulties derived from the different criteria used by connectivity analysts and policy makers. We generated a management tool to incorporate connectivity criteria for large carnivores in landscape conservation planning at a local scale. Focusing on the southernmost population of jaguars *Panthera onca*, we use a graph-based connectivity approach to (1) analyze habitat connectivity and availability in five areas previously identified as *main corridors*; (2) detect priority forest patches for maintaining connectivity, and (3) propose specific management strategies for each area matching the relative importance and role of the forest patches in it. For this purpose, we defined the patches as the local land management units (properties) and used information on land cover and jaguar movement for determining the probabilities of connectivity metric. We identified the key patches that represent 90% of the total contribution to connectivity in the study areas; these patches were less than half of the total number of patches in each corridor. Based on this forest patch prioritization, we identified the most critical areas and specific patches where urgent conservation measures need to be implemented. The percentage of patches and the total area they covered varied among the five analyzed corridors showing contrasting situations for connectivity management and highlighting the importance of the proposed approach to understand the impact of patch-level actions in a broader connectivity context. This approach might serve as a model to account for habitat connectivity for large carnivores in the design of landscape management and land-use plans at a local scale.

Introduction

The intensification of human activities has accelerated habitat loss and fragmentation, becoming major threats for biodiversity conservation (Sanderson *et al.*, 2002*b*; Pimm, 2008; Haddad *et al.*, 2015). Through these processes, natural areas are distributed in small and isolated patches separated by an altered landscape matrix (Saunders, Hobbs & Margules, 1991; Ruediger, 2004). Therefore, the species tend to be restricted to patches with different degrees of isolation, increasing their vulnerability to genetic drift, climate change, and demographic and environmental stochasticity (Frankham, Ballou & Briscoe, 2002; Gaggiotti & Hanski, 2004).

Increasing landscape connectivity, understood as the degree to which the landscape facilitates species movements (Taylor *et al.*, 1993), may contribute to the mitigation of these potentially adverse effects (Opdam, Vos & Foppen, 2002; Araújo & Rahbek, 2006). Improvement of landscape connectivity has consequently become one of the main challenges for biodiversity conservation (Rubio *et al.*, 2014). Connectivity maintenance and restoration is an increasingly important goal in conservation management policies worldwide (Heller & Zavaleta, 2009). However, the implementation of these principles in specific management actions often faces considerable difficulties, caused for example by the different scales, approaches or interests that connectivity planning and the actual implementation of policies have (Knight *et al.*, 2008).

The approaches and indices designed for measuring landscape connectivity are increasingly numerous and varied (Urban *et al.*, 2009; Saura & Rubio, 2010). Graph-based indices, for example, have a good balance between the amount of input data they require and the detail in the information outputs they are able to provide (Calabrese & Fagan, 2004). A graph-based approach represents the landscape as a set of nodes (habitat units) functionally connected by links that join pairs of nodes (Urban & Keitt, 2001; Saura & Pascual-Hortal, 2007). This allows the characterization of the landscape in a spatially explicit manner and the evaluation of the relative importance of habitat patches for maintenance of landscape connectivity. The graph-based prioritization of patches can be incorporated into land management plans, protected area planning or into conservation strategies for threatened species (Minor & Urban, 2008; Saura & Rubio, 2010).

Large carnivores are among the first species to be threatened by habitat loss and fragmentation because they need large territories with good prey availability for survival (Cardillo *et al.*, 2004; Ripple *et al.*, 2014). Large carnivores are often used as umbrella species in the design of conservation landscapes, under the assumption that if they are preserved, other species with less strict spatial and habitat requirements will be also preserved (Ripple *et al.*, 2014). Consequently, these species are particularly suitable for guiding conservation efforts for the maintenance of landscape connectivity (Crooks & Sanjayan, 2006).

The jaguar *Panthera onca* is the largest felid in America and the top predator in the ecosystems where it occurs (Sunquist & Sunquist, 2002). In the last two centuries, its range has undergone a large retraction (>54% of its area) due to habitat loss, depletion of natural prey, and human persecution (Sanderson *et al.*, 2002*a*). This retraction has been especially severe in the northern and southern extremes of its distribution, where surviving populations undergo increasing fragmentation and isolation levels (Rodríguez-Soto *et al.*, 2011; De Angelo *et al.*, 2013; Quiroga *et al.*, 2014). The southernmost population of jaguars survives in the Green Corridor, a region situated in Misiones Province of Argentina and nearby areas of Brazil (De Angelo *et al.*, 2011). This population is estimated to be around 65 individuals and is the greatest of the entire Atlantic Forest of South America (Paviolo *et al.*, 2016). However, habitat loss poses a high risk of subdividing it into several smaller subpopulations with increased isolation levels and extinction risk (Di Bitetti *et al.*, 2016).

In order to ensure jaguar conservation in the Green Corridor, a partnership of institutions developed a management landscape for the species to focus conservation efforts in this area (Schiaffino *et al.*, 2011). This conservation strategy was designed following a regional analysis of jaguar habitat for the entire Upper Paraná Atlantic Forest (De Angelo *et al.*, 2013). The *core areas* in the management landscape for jaguars contain the best habitat for this species. The *main corridors* represent the areas that have the potential to connect the *core areas* in spite of containing lower-quality habitat. However, the *main corridors* are crossed by roads and are subject to increasing human pressure, driving forest conversion into other land uses which likely reduce habitat connectivity for jaguars (De Angelo *et al.*, 2013).

Although the management landscape for jaguars has identified these areas as important for preserving habitat connectivity (Schiaffino *et al.*, 2011), the conservation of all the forest fragments remaining in those areas is very unlikely. The National Government of Argentina and the local government in the area of the Green Corridor developed laws for forest preservation and restoration, including in their fundamentals the preservation of large carnivores (National Law N°26.331 and Provincial Law XVI N°105). However, territorial planning policies of forest conducted by the government are applied at a property scale, which is a very local scale in relation to the management landscape developed for jaguars. For this reason, it is essential to adjust the information from the management landscape for jaguars to the scale and demands of the forest protection laws, prioritizing specific areas to focus the government's conservation efforts.

Our main objective was to incorporate connectivity criteria of large carnivores' species in local landscape conservation planning. We focus on the jaguar at the southern limit of the species' distribution in the Green Corridor. We use graph theory as the analytical approach with the aim of: (1) analyzing habitat connectivity and availability in the areas identified as *main corridors* for the jaguar; (2) detecting priority forest patches for maintaining connectivity of the species, and (3) proposing specific management strategies for each area matching the relative importance and role of the forest patches in it. By doing so, we also demonstrate the applicability of this approach in territorial planning and conservation of large and endangered carnivores in other landscapes and regions with similar pressures on connectivity.

Materials and methods

Study area

The Atlantic Forest ecoregion extends across Brazil, Argentina and Paraguay, and is considered one of the world's 'biodiversity hotspots' (Myers *et al.*, 2000). The region has undergone a severe transformation process, with only around 12% of the original native forest cover remaining (Galindo-Leal & De Gusmão Câmara, 2003; Ribeiro *et al.*, 2009). Our study was conducted in the Green Corridor, located in the southern portion of the Atlantic Forest (Fig. 1). The dominant vegetation in the region is subtropical semi-deciduous forest with subtropical humid climate. The Green Corridor comprises the largest remaining area of continuous Atlantic Forest in the world (approximately 1 000 000 ha) and is one of the few areas with potential to preserve populations of large mammals in this ecoregion (Paviolo *et al.*, 2008).

This region is mainly covered by protected areas, native forest in private lands, subsistence agriculture, plantations and grasslands (Izquierdo, De Angelo & Aide, 2008). We focused our work on the five most important areas classified as *main corridors* in the management landscape for jaguars (Fig. 1; Schiaffino *et al.*, 2011). Forest cover and proportion of different land-uses vary among these areas, providing different scenarios and challenges for the maintenance of habitat connectivity for the species.

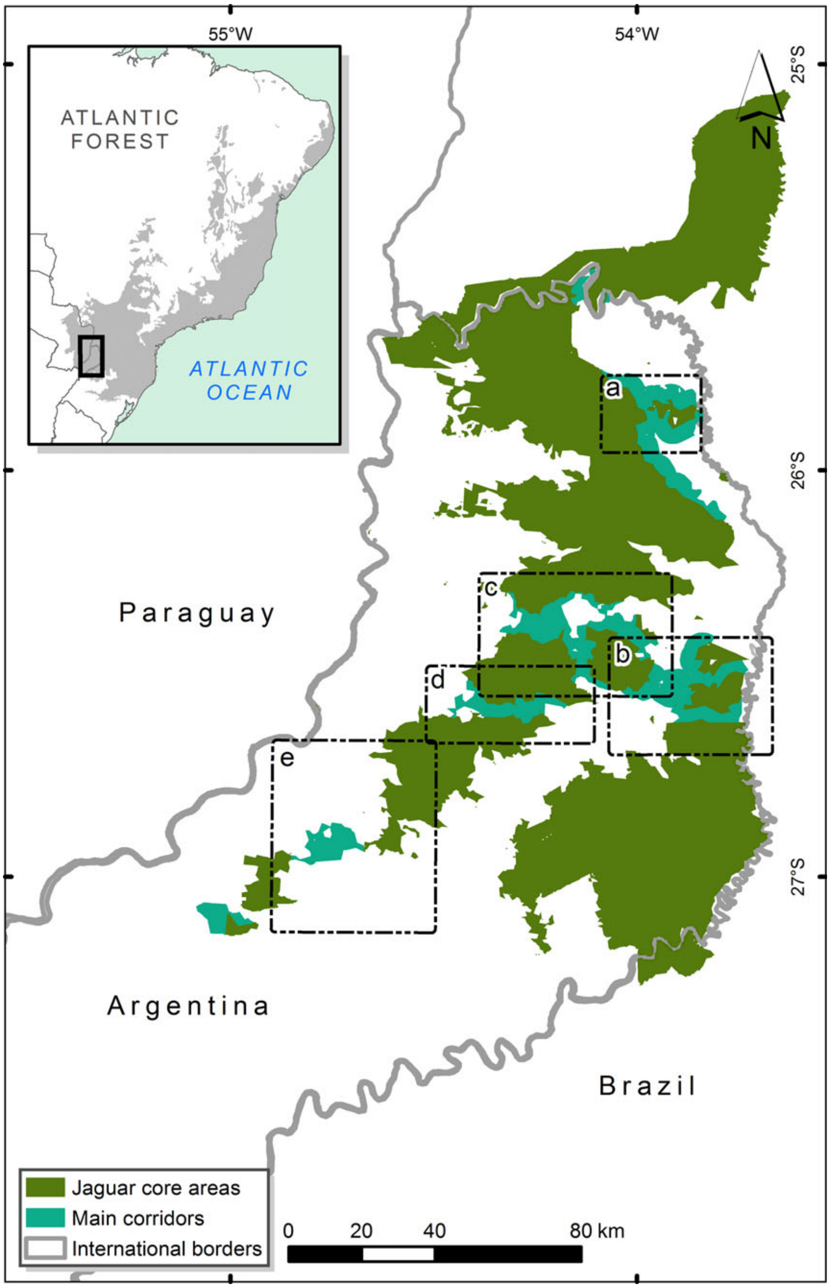

Figure 1 The jaguar management landscape in the Green Corridor of the Atlantic Forest. The main map shows the five corridors analyzed: (a) Foerster-Urugua-í; (b) Yabotí; (c) North; (d) Central and (e) South corridor. The upper left inset shows the location of the study area in South America representing the Atlantic Forest in grey. [Colour figure can be viewed at wileyonlinelibrary.com]

Definition of forest habitat patches

First of all, we identified habitat patches and represented them as nodes in the graph. We adapted the analysis to the administrative scale used by the provincial government to apply the Forest Law, selecting as nodes the properties with native forest located in the five *main corridors*. Information about forest cover was obtained from aerial photographs taken in 2009 and digitized by the Subsecretaría de Ordenamiento Territorial of the Ministry of Ecology of Misiones (MEyRNR). The property limits were obtained from a vector layer containing cadastral information from the MEyRNR. We used the property layer to divide forest fragments artificially and then measured the area in hectares as the attribute selected for node characterization.

Links among habitat patches

Graph links represent the probability of direct movement between each pair of nodes, which is obtained as a function of the distance between them (Pascual-Hortal & Saura, 2006). We calculated this distance as an effective distance, which is the accumulated cost of moving through the least-cost path between each pair of adjacent nodes (Adriaensen *et al.*, 2003). This approach considers variations in movement capacity and risk of mortality of a given species across the different land uses occurring in the landscape matrix (Adriaensen *et al.*, 2003). For this calculation, we first constructed the friction surface. We developed land-cover layers for each corridor based on Landsat 5 TM images obtained from the National Institute for Space Research of Brazil (INPE; see details in Supporting Information Appendix S1). The resulting land-cover layers were transformed into friction surfaces by assigning cost values to the different land uses and covers present in the matrix separating forest patches in each corridor. Connectivity analyses are sensitive to the uncertainties and quality of the information used for determining the friction values (Zeller, Mcgarigal & Whitele, 2012). Although our analysis is not free from the potential impacts of those uncertainties, we used the best available information for the species. Values were assigned based on records in the literature (Fu *et al.*, 2010; Rabinowitz & Zeller, 2010; Gurrutxaga, Rubio & Saura, 2011; Saura *et al.*, 2011) and expert opinions from researchers that have been working with jaguars in this region for over 13 years (J. Martinez Pardo, A. Paviolo, S. Saura & C. De Angelo, pers. comm.). The lowest friction values were assigned to those land covers that had the best conditions for movement and/or survival for the species and the highest values to the least favorable land covers (Table AII in Supporting Information Appendix S1). Roads were incorporated into the friction surface since they pose an immediate mortality threat (road kills), but also because they involve human presence, provide access to hunting of jaguar or its prey, and the expansion of the agricultural frontier (De Angelo *et al.*, 2013). The cell size used for all the raster layers was 100 m. Data processing was developed using ArcGIS 10.1 (ESRI, Redlands, CA, USA).

We used the friction surface to calculate effective distances among all the habitat units (nodes) of the five areas analyzed. We obtained the effective distance values between each pair of nodes using Linkage Mapper 0.9 (Mcrae & Kavanagh, 2011).

The effective distances were transformed into probabilities of movement for jaguars, which provided information on the connectivity levels for the species as given by its home-range movements. In particular, we focused on evaluating functional connectivity for (1) the species daily activities rather than during occasional dispersal events, and for (2) females, since their capacities for movement and dispersal are more limited than those of males, and they are more relevant to species population viability than males (Eizirik, Indrusiak & Johnson, 2002). We selected telemetry data of the three adult females obtained from different studies conducted in the Green Corridor (Crawshaw Jr, 1995; Morato *et al.*, 2016). We used the value of the mean distance of locations to the arithmetic center (MDLAC), which is the average of distances between locations and the center of the home range of each individual (Crawshaw Jr, 1995) and provides information about the distances moved by individuals within their home range. To convert this distance (Euclidean) to an effective distance (cost units), we calculated the mean value of friction of the matrix within the home ranges of the studied jaguar females and multiplied it by MDLAC. In that way, we obtained an estimation of the mean effective distance moved by jaguar females within their home range, which was equal to 58 225 cost units.

According to this, the probability of jaguar movement between two patches was obtained from a negative exponential function of the effective distance separating those patches. The decay parameter of this negative exponential function gives the mean dispersal distance of the species under consideration and was hence made equal to 58 225 cost units. The negative exponential function gives a probability of movement equal to 1 when the distance between patches is equal to zero, with decreasing probability values for larger distances separating the patches under consideration (Saura & Pascual-Hortal, 2007; Saura & Rubio, 2010).

Connectivity analysis: relative importance of forest patches

We used the probability of connectivity index (PC) to analyze connectivity of jaguar's habitat in the corridor areas. This index is defined as the probability that two randomly located points within the landscape are situated in connected habitat units, for a given set of nodes (habitat patches) and links (functional connections). This may occur if these two points either fall within the same habitat patch or in two different patches that have a strong functional connection (Saura & Pascual-Hortal, 2007). PC is based on the concept of habitat availability, which considers a habitat patch itself as an area where there is connectivity, and integrates the intrapatch connectivity with the direct and indirect connections between different patches in a single measure (Pascual-Hortal & Saura, 2006). PC is calculated via weighted graphs and a probabilistic model of connectivity in which each connection between two patches is characterized by a given probability of dispersal or movement. In our case, we used the jaguar movement analysis explained in the previous section to estimate the interpatch connectivity for the PC calculation.

We prioritized forest patches by measuring the percentage of variation in the PC index (*dPC*), that is the per cent decrease in habitat connectivity and availability caused by the loss of a given patch in the landscape, according to the following formula:

$$dPC = 100 \cdot \frac{\mathrm{PC} \;\; - PC_{\mathrm{elim}}}{\mathrm{PC}},$$

where *dPC* is the importance of a given patch in maintaining habitat connectivity and availability according to this index, PC is the index value in the original landscape (before removing any patch), and PC_{elim} is the index value after removing the given patch (Saura & Pascual-Hortal, 2007).

We compared the values of the three fractions of *dPC* for each corridor: dPC_{flux}, dPC_{intra} and $dPC_{connector}$. dPC_{intra} evaluates the contribution of a given patch in terms of area connected within it, regardless of its position in the landscape network. dPC_{flux} evaluates how well a given patch is connected with the rest of the habitat patches in the landscape. $dPC_{connector}$ evaluates how irreplaceable a given patch is as a connecting element or stepping stone between the rest of the habitat patches in the landscape (Saura & Rubio, 2010). We decided to focus on the latter fraction ($dPC_{connector}$) for the analyses in the *main corridors* given that the areas of the analyzed patches are too small for jaguars to maintain individual territories and that the main aim of this work was to prioritize the patches that served as stepping stones to other suitable lands.

Additionally, we estimated the BC(PC) centrality index, which was developed using the same probabilistic model as that used for PC (Bodin & Saura, 2010). Both $dPC_{connector}$ and BC(PC) indices quantify the importance of patches as connecting elements by measuring the degree of involvement of a given patch in the movements between the remaining patches of the landscape. However, BC(PC) index quantifies this aspect in the intact landscape, without making patch removal experiments, allowing to identify those patches that play a role as stepping stones in the current landscape. In contrast, $dPC_{connector}$ quantifies the impact that the loss of a patch would have on the maintenance of connectivity between the remaining patches (Bodin & Saura, 2010). We performed all connectivity analyses using the software Conefor 2.6 (www.conefor.org; Saura & Torné, 2009), which computes the values of the PC and BC(PC), and the *dPC* fractions: dPC_{flux}, dPC_{intra} and $dPC_{connector}$ (see Saura & Torné, 2009 for more details about the procedures to obtain these indices and fractions).

Finally, with the aim of facilitating the interpretation of the results obtained from those indices and of summarizing this information for management recommendations, we identified the patches with the highest contribution to habitat connectivity (hereafter, key patches). We ranked all the patches according to their contribution in maintaining the connectivity in each corridor, doing that independently for the different indices: the fraction $dPC_{connector}$, BC(PC) and *dPC*. Then, for each index we used the corresponding ranking to select the minimum number of patches (MNPC) needed to maintain the 90% of the connectivity: the MNPC according to $dPC_{connector}$, the MNPC according to BC(PC) and the MNPC according to *dPC*. All the patches included at least in one MNPC was considered a 'key patch', but we classified them into three conservation categories: 'maximum priority' were those key patches included in the group of MNPC for the $dPC_{connector}$ (i.e. irreplaceable connecting patches); 'high priority', were those key patches not classified as maximum priority but that were included in the MNPC for BC(PC) index (i.e. other important stepping-stone patches), and 'medium priority' were those key patches not classified as maximum or high priority (i.e. other important patches according to their impact in the probability of connectivity – *dPC*). 'Low priority' patches were those that were not included in the MNPC for none of the mentioned indices, and consequently were not considered as key patches.

Results

For the five areas analyzed, the resulting number of nodes ranged between 478 (Foerster-Urugua-í corridor) and 1281 (South corridor). On average, the Central corridor showed the largest patches followed by the North corridor, with the most permeable matrix found in the Yabotí corridor but with a very high variation (i.e. the lowest mean CWD/ED ratio ± SD, Table 1). The Foerster-Urugua-í corridor presented the smallest patches which were separated by the less permeable matrix (Table 1).

Overall, we found a wide variation in the relative importance to maintain the connectivity of the patches in each corridor according to the PC index, with patches showing different relevance in relation to each component of the index (Fig. 2 and see more details in Supporting Information Appendix S2). The relevance of the three components also varied among the analyzed corridors (Table 1). The dPC_{flux} fraction of the PC index had a higher share in the habitat availability than the other two fractions (Table 1), with this fraction being more important in the corridors with larger

Table 1 Characterization of the analyzed corridors regarding their patches (number and mean area), the matrix (mean ratio among the cost weighted distance -CWD- and the Euclidean distance -ED- separating each pair of nodes), the connectivity and habitat availability analyses (percentage contributions of the three components of the *dPC* index; Saura & Rubio, 2010), and the minimum number of patches (expressed as percentages of the total number of patches in each corridor) which together comprise 90% of the connectivity evaluated by *dPC*, BC(PC) and $dPC_{connector}$

Corridor	Number of patches	Mean patch area ± SD (ha)	Mean CWD/ED ratio (±SD)	dPC_{intra} (%)	dPC_{flux} (%)	$dPC_{connector}$ (%)	dPC (90%)	BC(PC) (90%)	$dPC_{connector}$ (90%)
Foerster-Urugua-í	478	8 (±13)	108.1 (±278.4)	0.04	81.70	18.70	46.0	8.7	3.8
Yabotí	937	69 (±503)	30.3 (±2091.4)	3.00	82.60	14.40	18.0	3.7	2.3
North	685	101 (±390)	66.6 (±250.2)	0.80	80.30	19.00	9.0	4.0	0.8
Central	789	136 (±601)	33.9 (±128.4)	0.70	96.70	2.60	19.0	5.5	3.0
South	1281	28 (±88)	36.4 (±186.7)	0.10	71.00	29.00	35.0	6.3	2.3

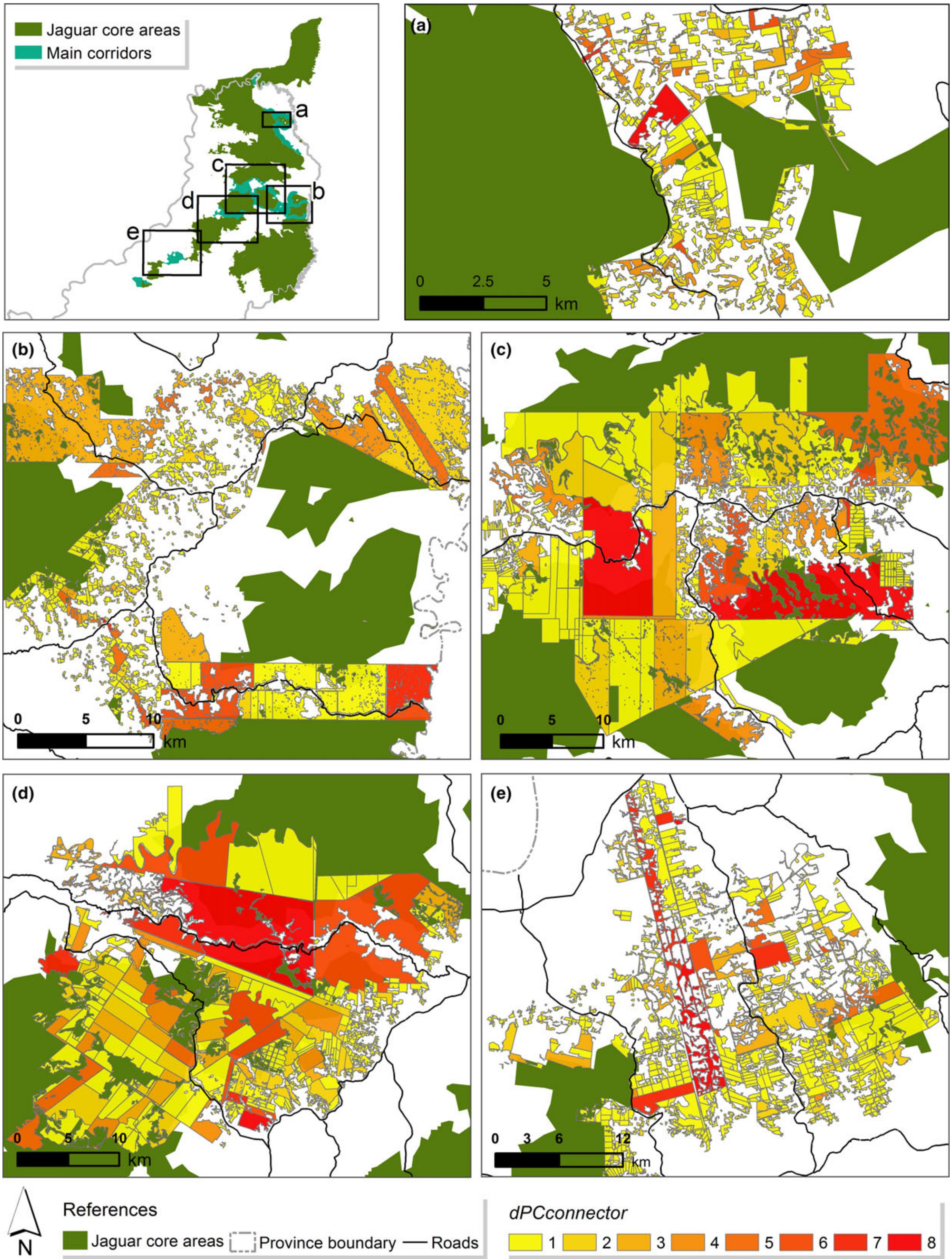

Figure 2 Importance of each habitat patch in the five corridors analyzed in terms of its individual contribution to the maintenance of overall landscape connectivity as measured by $dPC_{\mathrm{connector}}$. The colors in the legend represent the differences in relative importance from the highest (dark red = 8) to the lowest (light yellow = 1).

patches (e.g. Central corridor). The $dPC_{\mathrm{connector}}$ fraction showed, however, relatively high contributions to global connectivity (Table 1). It was most important in areas with the highest number of patches of relatively small size (South corridor, Fig. 2e), and it contributed the least in the Central corridor (Table 1; Fig. 2d). Regarding dPC_{intra}, it showed a low weight in all the corridors (Table 1).

We found a number of key patches that represent 90% of connectivity according to the different indices, but that constitute a relatively low percentage (<50%) out of the total number of patches in each corridor (Table 1). According to the BC(PC) index or the $dPC_{\mathrm{connector}}$ fraction, the number of key patches was even lower, and in general proportion of key patches was larger in the corridors with smaller patches (Table 1).

Based on forest patch prioritization and classification we found that from the total area comprised with the patches of all corridors, 47% was categorized as *high* or *maximum priority* (Table 2). However, patch percentage and area for the three conservation categories varied among corridors showing contrasting situations (Table 3; Fig. 3 and see more details in Supporting Information Appendix S3). In the North corridor, for example, the highest priority patches were large patches belonging to large properties (Table 3), with two main potential connection pathways linking the main core areas of this region (Fig. 3a). Interestingly, in Yabotí corridor the small or medium-sized properties (Table 3) were mostly those that established the main connection of *high priority* patches between Yabotí Biosphere Reserve and the central zone of the main forest block of the Green Corridor (Fig. 3b). The situation of the three remaining corridors was very variable, with areas where connectivity was highly threatened, such as the South corridor and Foerster-Urugua-í and others where remnant forest cover was greater, such as the Central corridor (see more details in Supporting Information Appendix S3).

Discussion

Using the jaguar as focal species and a graph-based connectivity analysis, we characterized the situation in five corridors in terms of habitat availability and connectivity and identified the priority areas where management and conservation actions should be implemented at a scale relevant to the local application authority. Our results show that the five analyzed areas present different conditions and need distinct management actions in order to maintain habitat connectivity for the jaguar. These dissimilarities are due to the variability in the configuration and

Table 2 Description of the prioritization categories of forest patches to preserve jaguar habitat connectivity, including the main management recommendations, the percentage of patches and total area covered by each category summing the patches from the five corridors analyzed

Prioritization category	Percentage	Total area (ha)	Description	Main management recommendation
Maximum	20.86	172 262	Forest patches that play a key role as irreplaceable connecting patches whose loss cannot be compensated by others	Preserve all forest coverage. Reduce all sources of jaguar mortality and poaching of prey. Livestock activities should not be allowed. Implement road effects mitigation. Urgently promote habitat restoration in adjacent patches.
High	25.82	213 224	Forest patches that play a key role as stepping stones in the current landscape	Preserve all forest coverage. Reduce all sources of jaguar mortality and poaching of prey. Reduce the conflict with livestock owners. It is desirable to implement road effects mitigation. Promote habitat restoration in adjacent patches.
Medium	26.70	220 551	Forest patches that play a key role as reservoirs of habitat	Logging activities should be carried out following low-impact techniques. Reduce all sources of jaguar mortality and poaching prey. Reduce the conflict with livestock owners.
Low	26.63	219 921	Forest patches that are not within the group of patches that comprise 90% of corridor connectivity	It would be advisable to maintain as much forest cover as possible. Reduce sources of jaguar mortality and poaching of prey. Reduce the conflict with livestock owners.

Table 3 Mean patch area and number of patches (expressed as a percentage of the total number of patches) for the four categories of forest patches based on their priority for conservation in each of the corridors

	Maximum priority		High priority		Medium priority		Low priority	
Corridor	Mean patch area (ha)	Patches (%)	Mean patch area (ha)	Patches (%)	Mean patch area (ha)	Patches (%)	Mean patch area (ha)	Patches (%)
Foerster-Urugua-í	8. 7 (±14.3)	3.85	8.6 (±14.2)	5.98	8.0 (±13.3)	37.82	8.2 (±13.3)	52.35
Yabotí	27.5 (±182.3)	2.5	26.9 (±212.0)	1.79	31.3 (±204.5)	12.17	30.1 (±199.7)	83.59
North	264.4 (±907.7)	0.73	143.7 (±630.1)	3.22	209.4 (±745.9)	6.14	136.1 (±602.1)	89.91
Central	90.5 (±308.4)	2.59	105.4 (±406.3)	3.54	101.6 (±392.3)	14.99	100.8 (±390.8)	78.88
South	60.6 (±129.6)	3.75	29.6 (±94.3)	3.91	48.1 (±56.2)	28.05	18.4 (±41.7)	63.83

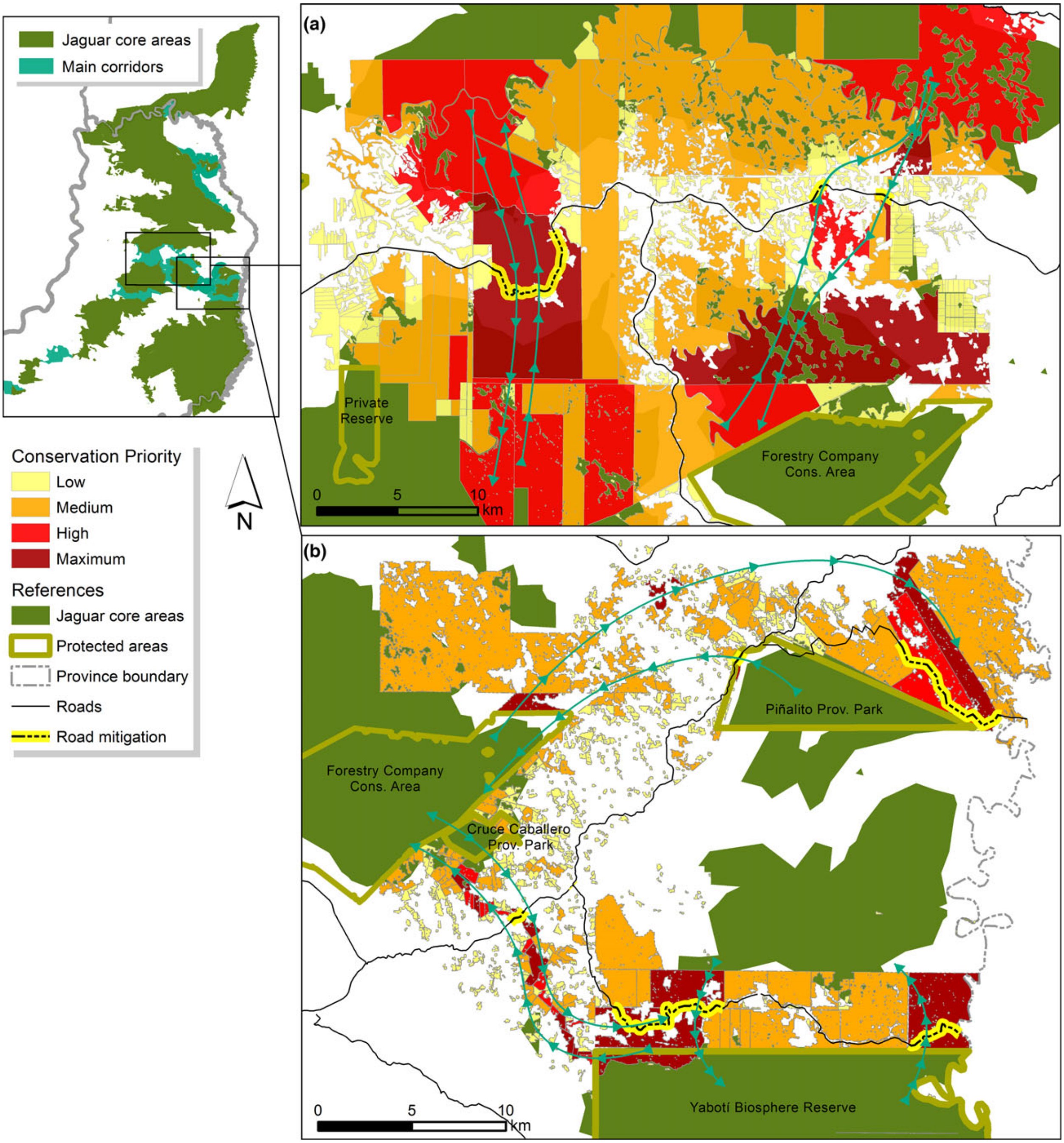

Figure 3 Importance of each habitat patch in North corridor (a) and Yabotí corridor (b) according to their prioritization category. The turquoise arrows indicate the potential jaguar movements.

number of patches, the patch area and the matrix heterogeneity of each corridor, which is typical of highly human-modified landscapes, such as the Atlantic Forest (De Gusmão Câmara, 2003). These findings highlight the importance of conducting detailed analyses, as those performed in this work, in order to target management actions efficiently according to the specific situation in each area.

In a graph-based view of our corridors, we found that the PC was dominated by the dPC_{flux} fraction. This is an expected result since the analysis was conducted in relatively small areas (distance between patches <30 km) and we focused our analysis on a species of large movement capacities (Crawshaw Jr, 1995). For large movement capacities species, the loss of a single patch is unlikely to completely hinder the possibility of moving using other patches or alternative paths (Hodgson *et al.*, 2009; Saura & Rubio, 2010), which results in high dPC_{flux} values. Stepping-stone patches were, however, significantly important for jaguar habitat connectivity in the area; jaguar movements between the core habitat areas depended to some extent, even if not completely, on individual forest patches that could be used as intermediate connectors along the way. Indeed, the comparison of our $dPC_{connector}$ values with those reported elsewhere (Saura & Rubio, 2010; Gurrutxaga *et al.*, 2011) shows that our values are relatively high in all the corridors, except for the Central corridor, which has a greater proportion of forest and larger patches. These results suggest that connectivity in the Central corridor should be less limited and less dependent on the possible loss of small habitat patches, thereby explaining the lower $dPC_{connector}$ values. Conversely, values of dPC_{intra} were lower than those of the two mentioned fractions for all corridors, suggesting that patch connectivity plays a fundamental role in maintaining total habitat availability for jaguars in the study region, and that partial or total loss of connections would have a great impact on the populations living in this region (Saura & Rubio, 2010).

We also detected that a great part of the connectivity (90%) is concentrated in a low percentage of key forest patches. This result is especially useful for territorial and conservation planning since it allows decision makers to concentrate conservation efforts in the areas of the greatest importance in maintaining habitat connectivity for this species. Likewise, our results highlight that some patches are of higher priority than others in a given area, and the loss of those key patches would have a greater impact on the functioning of the network of all the remaining patches.

The observed variability in the percentage and mean size of key patches may serve as a first approximation to establish the most suitable management strategies. On one hand, there are corridors with a low percentage of *maximum* or *high priority* patches, but with those patches having large areas, such as in the North corridor, where most of the land belongs to forestry companies. These patches should be designated as protected areas, preferably with high protection levels. If that would not be possible, an alternative would be that they are declared as 'areas of high conservation value' by the companies that run them. Such designation has already been used by some forestry companies working in the area and it is promoted by the principles of the Forest Stewardship Council (FSC, 1996). On the other hand, in areas such as Yabotí corridor, where the percentage of key patches is considerably higher and their mean patch area is smaller, corridors should be implemented preserving the set of stepping-stone patches by a regional program promoting jaguar habitat conservation through economic incentives provided by the government (Trainor *et al.*, 2013). This initiative could easily be included in the current National and Provincial legislation, which already considers this type of incentives in native forest areas of great importance for conservation (Laws N°26.331 and XVI N°105, respectively).

Two of the analyzed areas deserve special attention since they maintain key connections for jaguar habitat conservation not only in this region of the Atlantic Forest but also throughout its distribution range. These areas are the South and Yabotí corridors, which maintain connections with the protected areas that form the southernmost distribution of the jaguar (De Angelo *et al.*, 2011). In both cases, connectivity is seriously threatened. In Yabotí area, the estimated jaguar densities are the lowest values detected for the region, with only 10 individuals persisting (Paviolo *et al.*, 2008). This estimation indicates that, despite its large area (more than 200 000 ha), Yabotí can hardly maintain by itself a viable jaguar population and, therefore, maintaining connectivity between this area and the rest of the Green Corridor is crucial for jaguar survival. Implementing measures to mitigate the barrier effect of the road extending across this area is urgent. In addition, it would be necessary to promote restoration projects of native forest in areas adjacent to *maximum* or *high priority* patches.

The South corridor connects a protected area of 13 000 ha in the south-west extreme of the Green Corridor. Considering the large territories of jaguars, the size of this area is relatively small and therefore, only a few individuals can survive in this region and possibly their home ranges include the analyzed area. The main land use in this corridor is pine plantations and, therefore, as proposed for the North corridor, actions should be conveyed with the companies that exploit these areas. Big companies or pools of companies that exploit large areas can use these prioritization strategies for regional planning. The Sustainable Forest Mosaics Initiative is an example of the implementation of such strategies in other regions of the Atlantic Forest (Mesquita *et al.*, 2012).

A common challenge in animal conservation research is to develop results that can be easily adapted and incorporated into decision-making and management strategies. For our analysis, we divided remnant forest patches 'artificially' using property limits; this procedure is of great advantage since by linking the nodes directly with the land ownership we gave priority to the units that can (or cannot) be truly influenced by management actions. However, this procedure also implies that most patches were adjacent to one another, evidenced complex shapes resulting from cadastral errors, and had much smaller areas than those of the patches defined exclusively based on the continuity of forest cover. The adopted graph-based approach is able to reduce the potential impacts on the spatial prioritization resulting from using land properties, rather than forest continuity when defining the patches (nodes) for the analyses. On one hand, Saura & Pascual-Hortal (2007) showed that the landscape-level value of the PC index is not affected by the presence of adjacent habitat patches imposed by ownership, administrative or management limits (property 13 of the PC index as described in that paper). On the other hand, Blazquez-Cabrera, Bodin & Saura (2014) showed that the spatial prioritization of connectivity areas provided by the PC index is robust against different scales or hierarchical levels used in defining the habitat patches. While it is important to take into account the aspects related to the patch definition and scale of analysis when interpreting the results, we could here address a specific management need at the real working scale of the government or local organizations by defining patches based on land properties. This is a fundamental issue that facilitates the implementation of recommendations that emerge from our analysis as viable management and conservation measures, reducing the gap that often exists between the generated knowledge and planning and implementation on the ground (Opdam *et al.*, 2002).

Maintaining habitat connectivity is one of the main strategies proposed for large carnivores conservation at the global level (Ripple *et al.*, 2014) and, indeed, some conservation plans have already included this action (e.g. Global Tiger Initiative, Paseo Pantera, etc.). There are initiatives promoting connectivity improvement for the jaguar throughout its distribution range that have identified potential corridors among the main populations of the species (Rabinowitz & Zeller, 2010). Following the same objective, some works have been conducted at the scale of the entire Atlantic Forest (Paviolo *et al.*, 2016) and in the southern part of this region (De Angelo *et al.*, 2013). Given the resolution and the aims of those works, connectivity analyses were of structural type and did not consider the functional aspect related to the movement capacity of jaguars. Here, we incorporated this aspect and provided detailed information to improve connectivity for the jaguar in specific and strategic portions of its habitat.

In broad terms, the actions we suggest for preserving habitat connectivity for the jaguar in this region (Table 2) agree with recommendations proposed for other large carnivorous species (Chapron *et al.*, 2014; Ripple *et al.*, 2014) but they are prioritized spatially and indicated in land management units. We hope that the specific approach we adopted for applying the graph-based methodology might serve as an example for other cases in which large carnivores and land-use planning are involved and where it is necessary to bring the analytical results closer to the scale and needs of the actual implementation of conservation management measures on the ground.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Land-use analysis.
Appendix S2. Importance of each habitat patch in the five corridors analyzed in terms of its individual contribution to the maintenance of overall landscape connectivity as measured by BC(PC), dPC, dPC_{flux} and dPC_{intra}.
Appendix S3. Importance of each habitat patch in the Foerster-Urugua-í corridor (a), Central corridor (b) and South corridor (c) according to its prioritization category.