Assessing the drivers of connectivity declines for jaguars in the Atlantic Forest

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Abstract

Context.

Habitat loss is a major factor influencing declines in landscape connectivity for many species, but forest patch configuration and changes in matrix permeability can also represent important drivers. To evaluate which of these factors are predominant is key to guiding landscape planning at a regional scale.

Objectives.

We aimed to quantify the loss of jaguar (*Panthera onca*) habitat connectivity throughout 42 years and to analyse the drivers behind this process.

Methods.

We selected the jaguar as a focal species to 1) analyse trends in connectivity between 1973 and 2015 at the Upper Paraná Atlantic Forest eco-region; 2) compare trends in habitat connectivity considering only forest area, considering forest patch configuration, and also considering matrix permeability; and 3) compare trends in connectivity at the scale of each of the three countries of the eco-region over the same period.

Results.

The connectivity trend for jaguars was negative throughout the entire period, losing up to 93% of connectivity. The forest patch configuration was the main driver of this trend, and the effect of decreased matrix permeability was also significant. Both effects had a larger impact on jaguar habitat connectivity compared to the effect of habitat area declines itself. Habitat connectivity trends for the three countries were negative, with the highest loss rates found in Paraguay and Brazil compared to Argentina.

Conclusions.

Analysing landscape dynamics using metrics that go beyond measuring net forest area is key when assessing landscape connectivity. Habitat patch configuration and matrix permeability are important components to evaluate after the habitat loss and fragmentation process.

1. Introduction

Fragmentation and habitat loss are among the main threats to biodiversity conservation, leading to population declines of numerous species on the planet (Haddad et al. 2015; Jetz et al. 2007; Pimm and Raven 2000). Although the amount of habitat has been recognized as a key determinant of the persistence and abundance of many species (Fahrig 2017), the effects of habitat loss are usually magnified by the degree of habitat fragmentation and isolation, and by the spatial configuration of remaining habitat (Betts et al. 2006; Radford et al. 2005; Saura 2020). In this context, maintaining

landscape connectivity is one of the key strategies for biodiversity conservation worldwide (Opdam et al. 2002; Taylor et al. 1993).

Landscape connectivity can be defined as the degree to which the landscape facilitates or impedes the movement of species across it (modified from Taylor et al. 1993). Connectivity can be considered from a structural perspective as a physical continuity of habitat, regardless of any particular species and their dispersal capabilities, or from a functional approach, considering the ability of different species to move across the landscape (Crooks and Sanjayan 2006). In many cases, species cannot cross the matrix due to their low dispersion capabilities or because of the mortality risks involved in crossing it. This is the case of many large carnivore species, for which matrix characteristics are determinant despite their high vagility (Revilla et al. 2004). This suggests that landscape connectivity for these species must be considered primarily from a functional standpoint.

In recent years, the graph-based theory has become a popular method to assess landscape connectivity issues. This approach represents the landscape as a set of nodes (habitat patches) and links (representing the ability of organisms to disperse between two nodes directly) (Urban and Keitt 2001). Graph-based indices can be adapted to different degrees of detail depending on the information available, as they remain operational even when available data are relatively scarce (Calabrese and Fagan 2004). Therefore, graph-based indices are particularly suitable for monitoring connectivity patterns or trends at a regional landscape scale (Saura et al. 2011; Saura and Rubio 2010). Additionally, some of these indices have been developed under the habitat availability concept, integrating the area available within habitat patches and through connections with other habitat patches in the landscape into a single measure (Saura and Pascual-Hortal 2007).

The Atlantic Forest is one of the eco-regions most affected by forest loss and fragmentation in the world, with between 88 and 93% of its original forest cover already lost, making it one of the most threatened biomes on the planet (de Gusmão Câmara 2003; Di Bitetti et al. 2003; Ribeiro et al. 2009). It is South America's second largest forest after the Amazon Forest and one of the world's top eight "biodiversity hotspots" due to its high diversity (Mittermeier et al. 2005; Myers et al. 2000), hence being among the priority regions targeted for conservation efforts (Olson and Dinerstein 2002; WWF 2001). The Upper Paraná Atlantic Forest (UPAF) of Argentina, Brazil and Paraguay, is the largest eco-region of the Atlantic Forest, and it has also suffered a major habitat loss (De Angelo 2009; Di Bitetti et al. 2003; Holz and Placci 2003). The socio-economic development history of the three countries that comprise the UPAF was different and, as a result, the eco-region constitutes a heterogeneous landscape where the remaining forest area and productive uses are unevenly distributed (De Angelo 2009).

The latest estimates indicate that the remaining forest cover in the UPAF eco-region is 17% (WWF 2017), but this number only represents the total amount of forest without considering its real availability for keystone species from a functional perspective. Accounting for this requires selecting one or more focal species to parameterize landscape use and to understand the degree to which the landscape impedes or favours the movement of these species across the remaining forest. The jaguar (*Panthera onca*) was

selected as one of the umbrella species for designing UPAF conservation strategies (Di Bitetti et al. 2003) and information is now available on the species' dispersal ability in this ecoregion (Crawshaw Jr. 1995; Haag et al. 2010; Morato et al. 2016). In the UPAF, the jaguar shows a clear association with native forest cover, with habitat loss and fragmentation among the main threats to this species (De Angelo et al. 2011; Paviolo et al. 2016). Besides the proportion of native forest, other variables, such as rural population or large-scale agriculture, negatively affect the potential distribution of the species (De Angelo et al. 2013). Some jaguar subpopulations in the UPAF already show signs of loss of genetic variability associated with isolation, although genetic patterns do not necessarily correlate with geographic distance between subpopulations (Haag et al. 2010). This suggests that habitat loss and fragmentation affect jaguars in a more complex way than what can be explained by forest area reduction and structural connectivity loss alone. This species is therefore a keystone species for analysing how changes in the UPAF landscape have affected habitat connectivity, what are the main drivers behind it, and for applying this information to conservation strategies in the region.

Here, we analysed the effect of forest loss and changes in the matrix of productive uses over the last 42 years on jaguar habitat availability and connectivity at the scale of the UPAF. We selected the jaguar as a focal species and used graph-based connectivity models to 1) analyse trends in connectivity between 1973 and 2015 at the scale of the entire UPAF; 2) compare trends in habitat availability and connectivity considering only forest area, considering forest patch configuration, and also considering the effect of the matrix permeability; and 3) analyse and compare trends in connectivity at the scale of each of the three countries that comprise the UPAF over the same period.

2. Material And Methods

2.1 Study area

The UPAF is a subtropical and semi-deciduous forest with an annual precipitation range of 1000–2200 mm and a mean temperature range of 16–22 °C. The history and dynamics of human settlement, land-use change, and fragmentation processes are heterogeneous along the UPAF (De Angelo 2009; Izquierdo et al. 2008; Jacobsen 2003). In the Brazilian UPAF, most of the forest was replaced around the middle of the last century (Ribeiro et al. 2009), while the Paraguayan UPAF has a more recent but accelerated process of forest destruction (Huang et al. 2007). The Argentinean UPAF has a long history of human settlement and forest exploitation but a much lower rate of forest replacement (Izquierdo et al. 2008). For our analysis, we selected an area of 277.000 km² at the border shared by Brazil, Paraguay and Argentina, which includes most of the forest remnants of the UPAF (Fig. 1).

2.2 Connectivity model

We performed a connectivity analysis based on graph-based theory, consisting of several steps (Fig. 1), in which nodes correspond to habitat patches in the landscape and links correspond to functional

connections between habitat units (Saura and Pascual-Hortal 2007). Therefore, we generated the inputs related to a) habitat patches, b) cost surfaces, and c) jaguar dispersal distance in the UPAF (Fig. 1). After generating the inputs we performed a connectivity analysis using Conefor 2.6 (Saura and Torné 2009).

a. Habitat patches

We generated 16 graphs, considering the entire study area and the three countries in the ecoregion for the four periods analysed. To characterise the landscape of the UPAF we used land cover classifications generated by De Angelo (2009) for the years 1973, 1988, and 2004 (UPAF73, UPAF88, UPAF04). These classifications were developed from LANDSAT 1 (MSS) and LANDSAT 5 (TM) images obtained from Global Land Cover Facility (GLCF 2008), Instituto de Pesquisas Espaciales do Brasil (INPE 2008), and from the Comisión Nacional de Asuntos Espaciales de Argentina (www.conae.gov.ar), with a geometric accuracy of at least 330 m. For 2015 (UPAF15), we performed a new classification using LANDSAT 8 imagery obtained from the *United States Geological Survey* server (USGS) (<http://earthexplorer.usgs.gov>) (Table S1, Suppl. Info.). All classifications had a total of 8 land cover classes and a final pixel size of 330 m (10 ha) (Table S2, Suppl. Info.).

We obtained the nodes from the forest cover fragments generated from the land cover maps described above. We split fragments traversed by main roads, to consider the "dissection" effect of the main routes on the fragmentation of the landscape (Bogaert et al. 2004). Then we measured the area in hectares as the attribute selected for node characterization. Considering that forest patches smaller than 235 ha have a low probability of being occupied by jaguars in the UPAF (De Angelo 2009), we selected as nodes only the patches larger than this area to facilitate computing processing.

To analyse each country separately, we used the nodes generated previously for all the UPAF and selected the ones distributed within the boundaries of each country (national nodes). Subsequently, for taking into account the possible role of patches in the neighbour area of each country as connectors (Herrera et al. 2017), we selected the nodes outside the national boundaries (transnational) in a buffer of 86 km, which represents twice the median dispersal distance of the jaguar in this region. To those transnational patches, we assigned an attribute equal to 0 (surface area measured in ha= 0) so it does not count for their area when quantifying the surface of habitat within the country. For all the previous steps, we used the software ArcGIS 10.5.

b. Cost surfaces

Links represent the probability for direct movement between each pair of nodes, usually obtained as a function of the distance between nodes (Pascual-Hortal and Saura 2006). This distance can be calculated as a Euclidean distance (straight line) or an effective distance, which considers variations in the dispersal capacity and mortality risk of a given species or process across different land cover types present in the landscape matrix (Adriaensen et al. 2003; McRae and Beier 2007).

To measure the changes in global connectivity due only to changes in forest patches rather than changes in matrix permeability, we created a cost surface (CS1, Table S3, Suppl. Inf.) with all pixels distributed among the forest patches with the minimum friction value (1), except for the most important natural water bodies (large rivers), where each pixel was assigned a value of 1000 (more details in the next section).

To characterise the matrix and relative costs for jaguar movement we used the inverse of habitat suitability models. This approach assumes that animal movements are influenced by the same variables as habitat selection (Mateo-Sánchez et al. 2015). We replicated the habitat suitability model developed by De Angelo et al. (2013) for jaguars in the UPAF, using Maxent 3.4.1 (Phillips et al. 2017; Phillips et al. 2006) and extrapolating the model to the four periods analysed (Fig. 1). From these models, we applied the following formula to calculate the inverse:

$$R' / R'_{min}$$

where $R'=1$ - "habitat model". From this inverse, we generated five cost surfaces with different friction values corresponding to the periods analysed (Table S3, Suppl. Inf.).

We then set the costs of cities and roads over the period proportionally to the increase in the total population of the region, starting from the values given for the 1973 surface (cities = 2000; roads = 1000; Table S3, cost surface CS2; Gurrutxaga et al. 2011). This increase was 18% for the period 1973-1988, 7% between 1988-2004, and 26% between 2004 and 2015 (Table S3, CS3, CS4 and CS5 respectively). Once the friction surfaces were generated, we estimated the least-cost paths among nodes using Linkage Mapper 0.9 software (McRae and Kavanagh 2011). The least-cost path distances constituted the values of the effective distances between each pair of adjacent nodes for each period and the different cost surfaces.

c. Jaguar dispersal distance in the UPAF

We used the dispersal data available for the species in this region, including genetic data (Haag et al. 2010), data from individuals with VHF collars (Crawshaw Jr. 1995), and camera-trap records from Yaguareté Project (A. Paviolo, unpublished). We estimated dispersal distance by measuring the distance between the centroids of the locations of the dispersal movements of each individual from the different records: centroid of the initial area to the centroid of the dispersal area (Table 2, Fig. 1). To calculate these distances in cost units, we calculated the least-cost path between the centroids using the cost surfaces described in the previous section. We selected the median dispersal values to include in the analyses of the connectivity indices.

The connectivity indices used in this study were calculated on weighted graphs and a probabilistic model of connectivity, in which each connection between two patches is characterised by a certain probability of movement or dispersion between them. According to this model, the probability of direct movement

between each pair of patches (p_{ij}) is obtained by a negative exponential curve as a function of the Euclidean/effective distance between nodes (distance from edge to edge of the nodes). To estimate the direct probability of jaguar movement between nodes, we fit the negative exponential curve to the value of the median effective distance of movement estimated for jaguars in the UPAF (350,575 cost units equivalent to a value of $p_{ij} = 0.5$ on the curve), with 1 being the probability p_{ij} when the distance between patches equals 0.

d. Connectivity indices

The probability of connectivity (PC) is a network-based habitat availability index that quantifies functional connectivity. It is defined as the probability that two points randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected) given a set of n habitat patches and the links (direct connections) among them (Saura and Pascual-Hortal 2007; Saura and Rubio 2010). PC varies with the spatial arrangement and attributes of the habitat patches, and with the dispersal abilities of the species, and has a bounded range of variation from 0 to 1. It is given by:

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

where a_i and a_j are the areas of habitat patches i and j , the attribute considered for the analysis. A_L is the maximum landscape attribute; when the patch attribute is habitat area (as we will assume hereafter), A_L corresponds to the total landscape area (i.e., area of the study region, comprising both habitat and non-habitat patches). The strength of each link is characterized by p_{ij} , which is the probability of direct dispersal between patches i and j (without passing through any other intermediate habitat patch). This index relies on the habitat availability concept, in which a patch itself is considered as a space where connectivity exists (Saura and Pascual-Hortal 2007).

To evaluate overall changes in connectivity over time in the UPAF, we used the ECA index (Saura et al. 2011), which is based directly on the PC index, preserving the same properties but allowing to evaluate the connectivity in the complete landscape. ECA is defined as the size of a single habitat patch (maximally connected) that would provide the same value of the probability of connectivity as the actual habitat pattern in the landscape. It is calculated as the square root of the numerator of the PC index as follows:

$$ECA = \sqrt{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*}$$

ECA is a network-based index that takes into account the connected area existing within the habitat patches, the estimated dispersal flux between different habitat patches in the landscape (corresponding

to the product $a_i a_j p_{ij}$ when $i \neq j$ and i and j are the starting or ending points of those fluxes), and the contribution of patches and links as stepping stones or connecting elements that uphold the connectivity between other habitat areas (Saura and Rubio, 2010).

The ECA index has area units while maintaining at the same time the good properties and appropriate reaction to spatial changes that it inherits from PC and the habitat availability indices in general (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007; Saura and Rubio 2010). Then, the relative variation in ECA after a particular spatial change (or set of changes) in the landscape (dECA, defined as the difference between the ECA value after and before the spatial change, divided by the ECA value before that change) can be directly compared with the variation in the total amount of habitat area in the landscape after the same change (dA). This enables an easy interpretation and additional insights that can be gained about the degree to which areas of forest that were lost (or gained), in terms of area, are important for the maintenance of connectivity and the maintenance of ecological flows (Saura et al. 2011). In addition, changes in ECA may occur due to changes in the permeability of the matrix between habitat patches (e.g., road construction, intensification of agricultural areas, etc.). When these types of changes are taken into consideration, the effect of variations in ECA due to changes in the permeability of the matrix, considered in this case by the dECAMatrix index, will be added to the effect of variations due to changes in the distribution of habitat patches (dECA) (Saura et al. 2011).

Comparison of these three parameters (dA, dECA and dECAMatrix) provides insight into the predominant drivers of change in the landscape following habitat loss (or gain):

- $dECA > dA \Rightarrow$ changes in the configuration of forest patches (fragmentation) have an effect on habitat connectivity and availability that is larger than the one due only to changes in the total forest area.
- $dECAMatrix > dECA \Rightarrow$ changes in matrix permeability have a significant and additional effect on habitat connectivity compared to changes given by forest patch configuration or area alone.

Comparison of these parameters is always done in absolute values. To assess which processes are dominating the changes in connectivity (changes in total forest area, changes in forest patch configuration or matrix permeability), the difference between (a) dECA vs dA and (b) dECA vs dECAMatrix is analysed. If the differences in *a* are larger than the differences in *b*, the process dominating the changes in connectivity is mostly related to changes in forest patch configuration, either by a loss of patch area, an increase in the distance between patches, or the loss of connecting patches. In the opposite case, $b > a$, although there may be an effect due to changes in forest patches configuration, the predominant process is mostly related to a decrease or an increase in the permeability of the landscape matrix (Saura et al. 2011). To meet the objectives proposed in this study, we analysed the differences between these three parameters over time that occurred in the entire UPAF region and in the three countries separately. We used Conefor 2.6 (Saura and Torné 2009) to perform the entire connectivity analysis.

3. Results

Connectivity trends in UPAF (1973-2015) were always negative, even those measured by only the forest area (dA), and those driven by changes in forest patch configuration (dECA) and matrix permeability (dECA_{matrix}) (Table 1; Fig. 2). The highest connectivity losses occurred between 1973 and 1988 (dECA_{matrix} = -65%), although in the other two analysed periods the losses were also very high (Table 1). Changes in connectivity and habitat availability given by dECA were greater than changes in forest area (dA) by 17% between 1973 and 2015 (Table 1). Additionally, the difference between dECA and dECA_{matrix} was 6%, with dECA_{matrix} being greater, indicating that the effect of decreased matrix permeability was also a significant driver in the loss of connectivity and habitat availability for the jaguar (Table 1).

Trends for the three countries that compose the UPAF eco-region were also negative, with the highest loss rates found in Paraguay and Brazil (Fig. 3). Argentina, despite being the country that retained the most habitat connectivity for the jaguar, also showed a negative trend (Fig. 3). Particularly at the end of the period, Argentina suffered a high loss of connectivity relative to the loss of forest area, with dECA being much higher than dA (55%) (Fig. 3). Unlike Brazil and Paraguay, this was the only country where dECA was greater than dECA_{matrix} (4.3%) and, in addition, dECA was much greater than dA (47%). In Paraguay, between 85 and 95% of connectivity was lost, given by dECA and dECA_{matrix}, respectively (Fig. 3). In this case, dECA_{matrix} was higher than dECA by 10%, and dECA was higher than dA by 5% at the end of the period. In Brazil, between 87 and 89% of connectivity was lost (Fig. 3). The changes given by dECA were 11% greater than the changes given by dA, and, in addition, the difference between dECA_{matrix} and dECA was 2%. Between 2004 and 2015, we found a positive dA in this country, i.e., there was a recovery of forest area. However, both dECA and dECA_{matrix} remained negative, so connectivity continued to decline, although at lower rates than in previous periods (Fig. 3).

4. Discussion

The analysis at the scale of the entire UPAF revealed that the loss of habitat connectivity for the jaguar over the last 40 years has been dramatic, with reductions up to 90% of the area of functionally connected forest for the species. This trend is mainly due to changes in the spatial configuration and area of forest patches and, to a lesser degree, to changes in the permeability of the matrix that separates them. The loss of forest cover was a determining factor in the changes that occurred in the availability and connectivity of jaguar habitat in the UPAF. The magnitude of this loss is, however, much greater when considering its functional components, i.e., the distribution and spatial configuration of these remnant forests and the composition of the matrix that separates them. Thus, the processes of habitat connectivity losses in the UPAF are complex, dynamic spatially and temporally, and with impacts on species habitat availability beyond those given by the loss of habitat area alone.

When evaluating the entire period, we found that the rate of connectivity loss remained relatively constant throughout time, although the dominant spatial processes varied through time. Between 1973 and 1988, although the loss of forest was the greatest in the whole period, there was a clear effect of the decrease in the permeability of the matrix ($dECA_{\text{matrix}} \text{ vs } dECA > dECA \text{ vs } dA$) and this was primarily due to the conversion of native forest to small-scale agriculture and, secondarily, to the conversion of forest to pasture for cattle ranching (De Angelo 2009). Between 1988 and 2004, this situation shifted. The matrix configuration was similar to the previous period (De Angelo 2009) and the effect of changes in matrix permeability was smaller than the effect of changes in forest patch configuration ($dECA_{\text{matrix}} < dECA$). The loss of forest area (dA) remained very high at almost 40%, but the loss of connectivity ($dECA$) was 51%, indicating that the forest patches that were lost played a key role in maintaining connectivity (Saura et al. 2011). Thus, changes in the configuration of forest patches had the greatest effect on connectivity loss in the second period analysed. In the latter period, the loss of forest area was much smaller ($dA = -13\%$), although connectivity still declined sharply ($dECA = -50\%$). By far the largest impact on this loss was due to changes in forest patch configuration ($dECA \text{ vs } dA \gg dECA_{\text{matrix}} \text{ vs } dECA$). This strong decrease maybe because, after decades of changes in forest patch configuration and area loss, a threshold was reached at which subsequent changes and losses in the UPAF landscape would have a much greater impact on the maintenance of connectivity than in previous periods (Pardini et al. 2010; Saura et al. 2011). In addition to this effect, the patches that were lost in this last period may be regarded as highly relevant connecting elements. Changes in matrix permeability again had a negative effect on connectivity ($dECA_{\text{matrix}} > dECA$) and, on this occasion, it was the conversion to large-scale agriculture that dominated the changes in the UPAF landscape (Da Ponte et al. 2017; MapBiomass 2021).

As observed at the scale of the entire UPAF, both $dECA$ and $dECA_{\text{matrix}}$ were negative throughout the entire period in the three countries comprising the ecoregion. Although Argentina is the country that conserved the highest proportion of forest in the study area, in the last 11 years analysed, changes in the configuration and area of remnant forest patches ($dECA$) had a very large impact on the availability and connectivity of jaguar habitat. Between 1973 and 1988, this country retained much of its connectivity (97.6%) and changes in jaguar habitat connectivity were mainly due to a decrease in matrix permeability ($dECA_{\text{matrix}} \text{ vs } dECA > dECA \text{ vs } dA$). In this period, there was a considerable increase in rural population density in much of the Argentine portion of the UPAF (Izquierdo et al. 2008). This variable has negative effects on the jaguar habitat in the UPAF (De Angelo et al. 2013), so that the decrease in matrix permeability is probably due to this human population increase and its associated landscape changes and pressures. In the second period, although connectivity continued to decline (between -11 and -13%), it did not reach the high rates of loss as in Brazil and Paraguay. Despite this relative maintenance of habitat availability, the jaguar subpopulation of the Argentine UPAF showed a rapid decline during these years probably caused by the lack of prey as a result of poaching and due to direct jaguar persecution (Paviolo et al. 2008). Between 2004 and 2015, the connectivity dropped by 65% with changes in forest patches being the major cause of this loss ($dECA \text{ vs } dA \gg dECA_{\text{matrix}} \text{ vs } dECA$). De Angelo (2009) pointed out that despite being Argentina the UPAF country with the highest proportion of protected native forest, the advance of the anthropogenic use frontier and the rapid increase in road construction

were threatening connectivity in this region as early as 2004. A connectivity analysis focused on jaguar movements in key corridors inside the Argentine UPAF observed that the patches of forest that support the connectivity of the largest forest blocks in the east and south of the region were in a critical situation (Martinez Pardo et al. 2017). Although the large forest blocks in this country are legally protected, they are intersected by several main roads. In addition, large tracts of rural and cattle-ranching areas surround these protected areas (Izquierdo et al. 2008). Despite large patches of forest have been maintained in this region, advancing human pressures outside protected area boundaries may be reducing the area of functionally connected jaguar habitat.

Paraguay represented the most critical situation in the entire region, as total connectivity losses were higher than in Brazil and Argentina. In the first and third periods, in addition to changes in forest patch configuration, decreased matrix permeability played a key role in jaguar habitat connectivity. Between 1973 and 1988 this decrease in matrix permeability was driven by the conversion of native forest to small-scale agriculture (De Angelo 2009). However, although $dECA_{matrix}$ was higher than $dECA$, $dECA$ values were also very high (-43%), which could be because this period experienced the highest rate of deforestation in the country (Huang et al. 2007). This was also reflected in the abrupt drop in the forest area given by dA (-41%). In the second period, the connectivity trend was even more negative and both factors had the same weight ($dECA$ vs $dA=6\%$; $dECA_{matrix}$ vs $dECA=6\%$). Again, we found a very high deforestation rate (1190 km²/year) and a matrix dominated by small-scale agriculture (De Angelo 2009). In the last period, the pattern of land-use changes and small-scale agriculture is replaced by large-scale agriculture, which dominated the Paraguayan landscape and doubled its surface area compared to 2004 (MapBiomass 2021; Martinez Pardo 2020). This resulted in a sharp decrease in matrix permeability, with $dECA_{matrix}$ values much higher than those of $dECA$.

Brazil's socio-economic development history was very different from that of its neighbouring countries and, as far as jaguar habitat connectivity is concerned, it presents a rather critical landscape from the beginning of the period analysed, although with the particularity that the trends observed were significantly reduced over time. The first period registered the highest annual deforestation rate of the three countries that comprise the UPAF. The native forest was converted mainly to small-scale agriculture and, secondarily, to pasture for cattle ranching (De Angelo 2009). This resulted in an enormous loss of connectivity, with values of up to -78%, and both processes were equally weighted ($dECA$ vs $dA=5\%$; $dECA_{matrix}$ vs $dECA=5\%$). Between 1988 and 2004, the proportion of land uses was very similar to the previous period and, while the rate of deforestation decreased significantly between 1988 and 2004 (De Angelo 2009), connectivity decreased by 45% ($dECA$). This time, changes in forest patches were the most relevant factor for connectivity loss ($dECA$ vs $dA > dECA_{matrix}$ vs $dECA$). The forest patches that were lost probably played a very important role as connecting elements or habitat reservoirs for the jaguar. Haag et al. (2010), showed that the genetic isolation of the jaguar subpopulations of the Brazilian UPAF was already very pronounced by the end of the last century and that the genetic differences among these subpopulations were not explained by their geographic distance, indicating a potential great effect of the matrix that surrounds the remnant forest in determining jaguar dispersal. This isolation even between

nearby subpopulations was also observed when Cullen et al. (2013) analysed jaguar movements in the first decade of this millennium in the Brazilian Upper-Paraná – Paranapanema region in the north of Brazilian UPAF. In the most recent period, we found positive dA values (8%), i.e., there was an increase in forest area, especially in forest patches corresponding to the selected threshold (> 235 ha). However, when looking at the changes in dECA and dECA_{matrix}, these were still negative, although with much lower values than in previous periods (-13 and -16%, respectively). The difference between dA and dECA indicates that the area of forest gained in this landscape provided structural but not functional connectivity. This highlights the importance of incorporating criteria to identify those areas where it is more necessary to implement native forest restoration plans that positively impact habitat connectivity. The reported increase in forest cover may correspond to patches adjacent to existing patches or to patches too isolated from the rest to importantly contribute to habitat connectivity for the jaguar. This would explain why the increase in forest area had no net impact on connectivity and the trend remains negative (Saura et al. 2011).

The scenario concerning connectivity and habitat availability described in the three countries is consistent with the current critical situation of the jaguar population in the UPAF. The latest estimates indicate that subpopulations of the species in this region are small, highly isolated, and occur mainly in the largest forest fragments (Paviolo et al. 2016). Habitat loss and fragmentation have had a major impact on the persistence of the jaguar in the UPAF and, together with poaching and prey scarcity, represent a major threat to the survival of the species in this landscape in a short period of time (Paviolo et al. 2016). This dramatic situation is similar to that faced by endangered large carnivore species in other regions of the World (Ripple et al. 2014) and it requires urgent efforts to prevent their extinction.

5. Conclusion And Implications

Given the current rates of deforestation worldwide, it is crucial to quantify losses of connectivity and habitat availability that go beyond the structural loss of forest cover, especially for those species that are particularly threatened by the advance of the anthropogenic frontier, such as the jaguar. In this study, we analysed the impact of forest cover loss and land-use change on jaguar habitat connectivity, finding different patterns over the analysed period and between the three countries comprising the UPAF eco-region. Although there were variations in the different connectivity measures over the period, the fact that the trend was always negative indicates that, under the change scenarios that occurred in this landscape, jaguar habitat connectivity in the UPAF tends to decrease sharply and sometimes independently of the amount of forest loss.

Separate analyses in each country allowed us to assess which changes in land use most negatively affected jaguar habitat connectivity. While Brazil and Paraguay suffered a huge loss of jaguar habitat connectivity, in Argentina, where the process of the native forest conversion to productive land uses was less pronounced, the connectivity decline was smaller. Despite being the country comprising the smallest portion of the UPAF, from 1988 it presented the highest values of functional habitat connectivity compared to the other two countries. Possibly, the early policies of creating large protected areas

implemented in this country in the late 1980s may have contributed to slowing down the loss of connectivity (De Angelo 2009). However, our results showed that Argentina may have reached a threshold where future changes in remaining forest patches would have a devastating effect on jaguar habitat connectivity, and the conservation of the main protected areas is currently not sufficient to halt this process. In this context, there is an urgent need for the correct implementation of the land-use planning established by the National Law on Minimum Requirements for the Environmental Protection of Native Forests (Law No. 26.331), which allows for the prioritisation of the conservation of forest patches that play a key role in maintaining jaguar habitat connectivity (Martínez Pardo et al. 2017). Meanwhile, in Paraguay, the few remaining forest fragments that sustain connectivity are immersed in a matrix of intensive use, mainly for large-scale agriculture such as soya (Da Ponte et al. 2017). According to our results, this is the worst scenario of change for the jaguar habitat connectivity and is even worse for species with lower dispersal capacities (de la Sancha et al. 2021). Although there are laws in this country focused on conserving Paraguay's remaining forest (Zero Deforestation Law No. 2524/04; Law on Valuation and Retribution of Environmental Services No. 3001/06), the difficulty in implementing them may explain why the annual deforestation rate has not decreased as expected in this region. The predominant production model in Paraguay was promoted by the creation of the Itaipú dam in 1978 and the associated infrastructure development, which together with the social differences that led landless farmers to occupy new territories paint a bleak picture in this region (Macedo and Cartes 2003; Matteucci et al. 2004). It is essential to effectively implement conservation of natural protected areas that support the last remaining habitat reservoirs for the jaguar, to strengthen policies to stop deforestation and to promote native forest restoration projects between the main protected areas. As for Brazil, it showed the lowest functional connectivity values of the three countries in the UPAF from 1988 onwards. The starting scenario was not at all favourable for jaguar habitat connectivity, since the UPAF in Brazil is one of the most developed agricultural and cattle-raising regions in the country (de Gusmão Câmara 2003). This is why, as early as the 1970s, the forest patches were relatively isolated and immersed in an agricultural matrix (De Angelo 2009). This process of agricultural expansion continued throughout the 1970s and 1980s, promoted by different economic and political incentives, which, together with the construction of important infrastructure projects, favoured the intensification of agriculture and the growth of cities in this region (De Angelo 2009; Frickmann Young 2003). This scenario worked against the conservation of jaguar habitat connectivity, which explains the very negative trends between 1973 and 2004 found in our study. Our results described that this trend becomes less pronounced between 2004 and 2015, showing an increase in forest area and smaller functional connectivity losses. In addition to effectively enforcing the conservation status of the protected areas in Brazil, it would be essential to encourage and direct the development of native forest restoration plans in areas that can effectively improve connectivity between them. It is also worth mentioning that, in this country, the government is planning to add nearly 129,000 km to the existing 1.7 million kilometres of roads in the next 20 years (DNIT 2013; Teixeira et al. 2016). These plans to expand the network of roads in Brazil may damage jaguar habitat connectivity since the construction of roads implies forest conversion to other land covers (Cerqueira et al. 2021) and because they facilitate human access to remote areas (Barber et al. 2014). This issue urgently requires an

evaluation of all the potential environmental impacts to properly balance development and conservation (Kaszta et al. 2020).

Understanding the effects of spatial dynamics and changes in these dynamics is key to understanding ecological processes and improving landscape management planning (Martensen et al. 2017). Landscapes in developing countries, such as the UPAF ecoregion, are highly susceptible to abrupt changes, making it critical to analyse landscape dynamics at a spatiotemporal scale using metrics that go beyond measuring net forest area (Auffret et al. 2015). Our results highlight that the impact of native forest loss on the UPAF landscape is even greater than expected and show the serious consequences it is having on the functional connectivity of the jaguar habitat. The cases reported here, such as those for Brazil or Argentina, also show the importance of including landscape connectivity criteria in land-use planning at a regional scale. We generated detailed information on the status of jaguar habitat connectivity in the landscapes of the UPAF and at the regional scale of each country. A jaguar conservation strategy in this landscape should aim at reducing threats in the protected areas that conserve the main forest fragments and to generate information on habitat connectivity at the scale of jaguar subpopulations, which will allow to effectively incorporate conservation criteria at the level of jaguar management units.

Declaration

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Competing interests

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Author contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Julia Martínez Pardo, Carlos de Angelo and Ariel Insaurrealde. The first draft of the manuscript was written by Julia Martínez Pardo and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Compliance with Ethical Standards

The authors have no competing interests to declare that are relevant to the content of this article. The research has not involved Human Participants or Animals. Due to the subject of this work, it is not necessary to report any Informed consent.

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Tables

Table 1. Variations expressed as a percentage in dA (determined only by changes in forest area), dECA (determined only by changes in forest patches area and configuration), and dECAmatrix (determined by changes in forest patches area, configuration and matrix permeability) between the periods 1973-1988, 1988-2004, 2004-2015 and the entire period 1973-2015 for the Upper Paraná Atlantic Forest ecoregion of Argentina, Brazil and Paraguay.

Index	1973-1988 (%)	1988-2004 (%)	2004-2015 (%)	1973-2015 (%)
<i>dA</i>	-44	-38	-13	-70
<i>dECA</i>	-47	-51	-50	-87
<i>dECA_{matrix}</i>	-65	-49	-60	-93

Figures

Figure 1

Connectivity analysis and study area. 1) The study area comprises most of the Upper Paraná Atlantic Forest (UPAF), a highly fragmented eco-region distributed along the east coast of Brazil, eastern Paraguay, and northeastern Argentina. The study was performed over 42 years (1973-2015), a period in which the native forest was converted to different productive uses. 2) Model inputs used by Conefor 2.6: I. Suitable patches; II) Cost surfaces and III) Dispersal distance of the focal species (*Panthera onca*). 3) Connectivity analysis: a graph-based analysis where the landscape is modelled as a graph (nodes=forest

patches; links=connections between habitat patches). 4) Model outputs were obtained for the entire landscape and for the three countries that comprise the UPAF eco-region.

Figure 2

Changes in habitat connectivity for jaguar in the UPAF ecoregion between 1973 and 2015 as measured by the ECAmatrix index, which considers variations in matrix permeability.

Figure 3

Total area (either forest area or effective connected area) estimated by the different indices for each country over time measured in thousands of hectares.

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