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The jaguar in South America – status review and strategy

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Landscape connectivity analysis and proposition of the main corridor network for the jaguar in South America

Large parts of the formerly continuous jaguar *Panthera onca* range have been lost or fragmented. We performed an analysis with Linkage Mapper to evaluate connectivity between all 92 patches of the 2020 jaguar range in South America. We used two Linkage Mapper tools: (1) the Linkage Paths to calculate the cost-distance values and to select least-cost paths as potential corridors for jaguar movements and (2) the Barrier Mapper to identify barriers along the potential corridors. We derived land-scape resistance values necessary for this analysis from the probabilities of jaguar occurrence estimated with species distribution models. Our analysis indicates that connectivity for jaguars is still good within the central Amazonian and Guiana Shield portions of the jaguar's range. However, outside of this central core, connectivity between the fragmented jaguar populations is generally poor, e.g. in the Andes, Llanos, Atlantic Forest, Caatinga, and Cerrado. Barrier sections cover 21% of the area of potential corridors, and high resistance values were found on 30% of the corridor area. This situation is worsened by high road density around most barrier sections of the potential corridors. The Chocó region of north-western Colombia is likely isolated from the rest of the jaguar range in South America, which means that jaguar populations of Central America have no or minimal connections with the Amazonian populations. Similarly, the connectivity between fragmented jaguar populations in eastern South America (Caatinga, Cerrado, and Atlantic Forest eco-regions) is disrupted at several potential corridors, although some corridors of this region may still retain some potential to facilitate jaguar movement. Only 9% of the area of potential corridors are located within protected areas. Our results can guide planning for jaguar conservation action on a large spatial scale and help focus on sites where such efforts can be most effective and are most needed.

Habitat fragmentation is one of the main drivers of species extinctions on a global scale. Fragmented, small, and isolated populations are vulnerable to demographic and mortality factors and the effects of genetic drift (Sinclair et al. 2006, Crooks et al. 2017). In addition, roads and traffic create additional barriers to animal movement and cause increased animal mortality (Benítez-López et al, 2010, Van Der Ree et al. 2011, Cullen et al. 2016).

Ecological corridors are an important conservation tool that helps mitigate the negative effects of fragmentation on animal populations. These are special areas intended to maintain or restore ecological connectivity, i.e. movement of species and their populations, individuals, and genes (Hilty et al. 2011). The identification of corridors helps in conservation planning, especially in identifying conflicts with existing or planned infrastructure and planning mitigation measures e.g. animal passes (Forman et al. 2003, Glista et al. 2009, González-Gallina 2018), and also helps in directing the efforts of reforestation to restore connectivity (McRae et al. 2012).

The configuration of ecological corridors on the landscape is planned based on a detailed analysis of existing connectivity. Such an analysis usually involves three important steps: (1) determining the core areas, i.e. the areas to be linked; (2) preparation of the resistance map (raster) assessing the potential for movement of individuals through the landscape; and (3) determining the most optimal course of the corridors which ensure the highest probability of animal movements. If the goal is to plan corridors for a threatened species, the selection of core areas should take into account the distribution of all relevant populations of that species, and in particular of those at risk of isolation. Preparing an appropriate resistance raster is a crucial task for proper connectivity analysis. Landscape resistance values can be derived from habitat suitability or species distribution models based on data such as species individual records or movements recorded by GPS telemetry (ref. Keeley et al. 2016, Carroll et al. 2020). It is also essential to consider area protection status in planning ecological corridors. Efforts should be made to ensure that the largest possible part of the corridors is covered by legal area protection or included in spatial management plans (Hilty et al. 2011, Belote et al.2016).

Fragmentation of jaguar populations across Central and South America has been increasing recently (Martinez Pardo et al. 2022, Jędrzejewski et al. 2017, 2018, 2023a), mainly driven by deforestation and habitat alteration aimed at increasing areas of cattle production, agricultural plantations, and human settlements (Petracca et al. 2014, Olsoy et al. 2016, Menezes et al. 2021). The development of infrastructure, especially road networks, also leads to fragmentation and a corresponding decline in the number of jaguars (Colchero et al. 2011, Espinosa et al. 2018). Understanding the importance of maintaining ecological connectivity for the persistence of jaguar populations has spawned several initiatives to plan ecological corridors in different parts of the jaguar's range (e.g. Morato et al. 2014, Silveira et al. 2014, Stoner et al. 2015, Martinez Pardo et al. 2017, Thompson and Velilla 2017). Rabinowitz and Zeller (2010) analysed connectivity and proposed the first range-wide network of ecological corridors to connect all jaguar conservation units.

In this paper, we present an analysis of the ecological connectivity for jaguars across South America as a follow-up to the updated analysis of jaguar distribution carried out as a

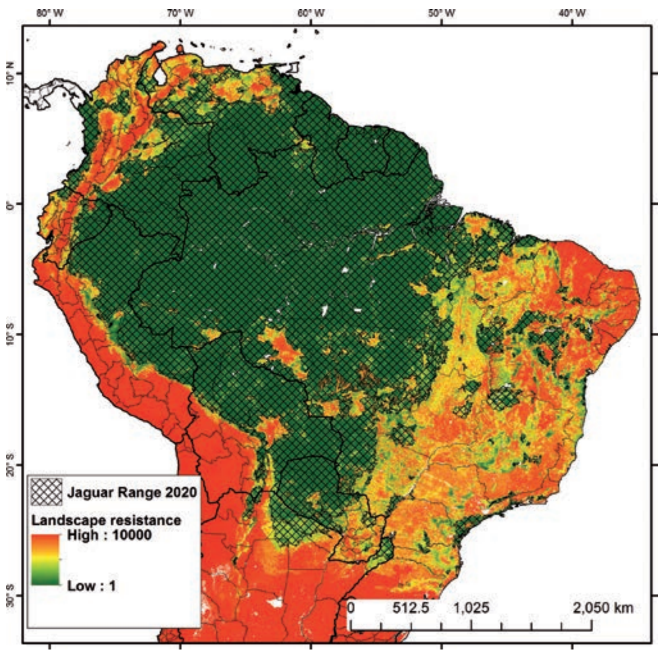

Fig. 1. Jaguar range 2020 in South America shown against the values of landscape resistance for jaguar movements. Jaguar range 2020 (SOM Dataset D1) consists of 92 separate polygons used as core areas in the connectivity analysis. Landscape resistance values (SOM Dataset D2) were calculated as the inverse of the probabilities of jaguar occurrence estimated with species distribution models (Jędrzejewski et al. 2023, see Methods) and they synthesise an impact of several factors important for jaguar populations, such as climate, environmental productivity, water abundance, forest cover, human population density, the share of pastures and agricultural crops, and road density.

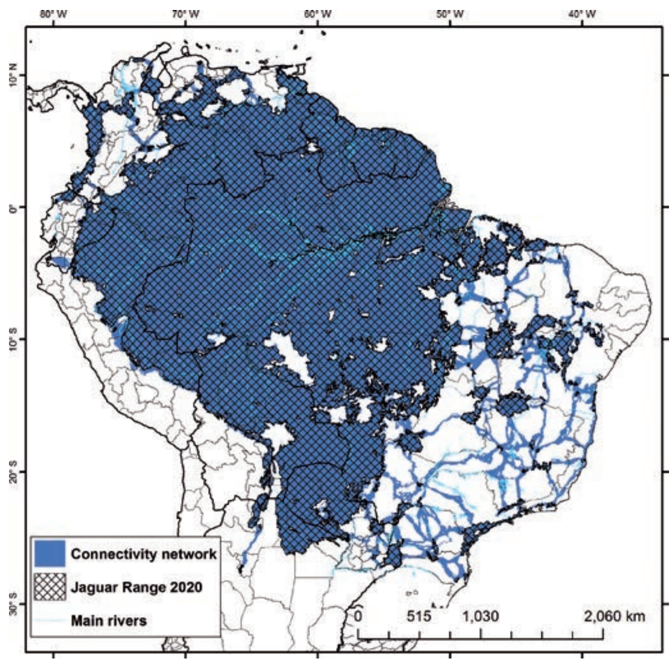

Fig. 2. Jaguar connectivity network selected with the Linkage Mapper as the areas with the lowest cost distance values (see Methods). This network includes: (1) the 92 pathes of the current (2020) jaguar range (SOM Dataset D1); and (2) the principal ecological corridors (SOM Dataset D3), connecting patches of the jaguar range. Banks of rivers and water reservoirs may provide additional linkages between fragmented jaguar populations, as indicated on this map. Numeration of the corridors is provided in the attribute table of the shape file in SOM Dataset D3. The network of the principal jaguar corridors proposed here can be farther developed at the regional or local levels.

part of the IUCN jaguar conservation strategy (Berzins et al. 2023, Jędrzejewski et al. 2023 a,b, Thompson et al. 2023). The main objectives of this analysis were: (1) to assess the overall degree of connectivity between jaguar populations in South America; (2) to determine which populations are most isolated; (3) to propose a network of ecological corridors for jaguars; (4) identify the most important barriers within this network; and (5) to estimate the role of existing protected areas and indigenous territories in maintaining connectivity throughout the jaguar range.

Methods

We estimated connectivity for jaguar populations in South America using two tools in Linkage Mapper v.3.0: Linkage Pathways and Barrier Mapper (McRae and Kavanagh 2011, McRae 2012, McRae et al. 2012). Linkage Pathways identifies least-cost linkages between core areas based on landscape resistance values and calculates the cost-weighted distance values. Barrier Mapper identifies critical barriers within the least-cost corridors.

As core areas, we used all 92 separate polygons representing the updated jaguar range in 2020 (Jędrzejewski et al. 2023a, Supplementary Online Material SOM Dataset D1). The landscape resistance values (SOM Dataset D2) were calculated as the inverse (subtracting from 1 and multiplying by 100) to the probability of jaguar occurrence estimated with the models presented in Jędrzejewski et al. 2023a. These models included several predictive variables reflecting the effect of natural and anthropogenic factors, such as precipitation, mean temperature, habitat productivity indices, water abundance, forest cover, human population density, the proportion of pastures and agriculture in the landscape, and road density. Models were run separately for each of the eight main ecoregions of South America to account for recently discovered genetic differences between jaguar populations (Roques et al. 2016, Lorenzana et al. 2020) and potential variation in responses to habitat features unique to each ecoregion. To increase the effect of barriers on the cost-distance values in the analysis in Linkage Mapper, we squared resistance values (McRae 2012a, Keeley et al. 2016) which resulted in the final cell values from 1 to 10,000.

We trimmed the mosaic normalised cost-distance ("corridor") map generated by Linkage Pathways to the values equal to or less than 50,000,000, and we presented the result as a map of potential connectivity network that included all patches of the jaguar range and connecting corridors. We supplemented this map with the network of main rivers (https://www.esri.com/arcgis-blog/products/product/mapping/esri-data-maps/) to indicate that water courses are important for jaguar movements and may provide additional movement opportunities (Silveira et al. 2014, Castilho et al. 2015, Azevedo et al. 2021, Eriksson et al. 2022). Corridors connecting individual fragments of the jaguar range were identified, separated from the entire connectivity network, and transformed into polygons, treating them as a network of principal ecological corridors (SOM Dataset D3).

To assess the quality (permeability) of corridors indicated by Linkage Pathways, we ran the Barrier Mapper and plotted the resulting barrier values along the corridors (SOM

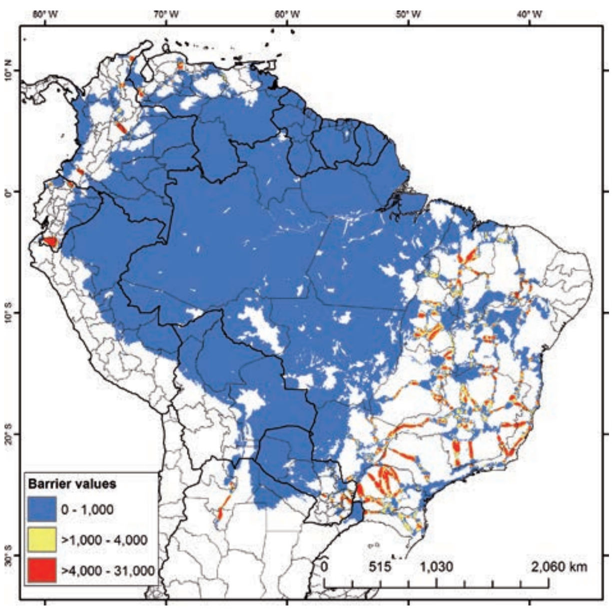

Fig. 3. Barriers for jaguar movements within the connectivity network, as indicated by the analysis with the Barrier Mapper tool in the Linkage Mapper (SOM Dataset 4).

Dataset D4). To the final map, we also added main and secondary roads (Meijer et al. 2018, https://www.globio.info/download-grip-dataset) to indicate which potential corridors between jaguar populations are most threatened by existing high-density infrastructure. To obtain another indicator of the quality of potential corridors, we transferred the values from the resistance raster to each corridor and presented the results on a separate map. To estimate the proportion of the connectivity network that is under legal protection, we laid maps of protected areas and indigenous territories over the obtained connectivity network and calculated the percentage of the overlapping area (http://www.protectedplanet.net, Amazonia Socioambiental RAISG 2019; https://www.amazoniasocioambiental.org/es/mapas/#!/areas).

Results

In general, the overlay of the 2020 jaguar range and the resistance map indicated that connectivity for jaguars is still good within the core of its range (central Amazonia & the Guiana Shield), while outside, it is relatively poor (Fig. 1, SOM Datasets D1 & D2). Also, the normalised cost-distance values calculated with Linkage Mapper within all persisting patches of jaguar distribution were low, indicating remaining good connectivity within the areas inhabited by jaguars.

Linkage Mapper selected the best possible connections (least-cost paths with the lowest cost-distance values) between and within the 92 patches of the jaguar range, producing a potential connectivity network. This network is complemented by the main rivers (Fig. 2). However, the analysis performed with Barrier Mapper revealed that outside the core jaguar's range, connectivity was disrupted along the least cost paths (principal corridors) at many points. In addition, most of the corridors had some sections with high barrier values (Fig. 3). Overall, 45% of the area of corridors indicated by Linkage Mapper had low barrier values (high permeability), 34% medium values, and 21% high barrier values (Fig. 3). The superimposition of the values obtained from the resistance raster in the corridor network showed, in general, a similar situation along the corridors outside the patches of jaguar range (Fig. 4), with 26% of the corridor area with low resistance values (high permeability), 43% medium, and 30% high values (low permeability). In contrast, within the jaguar's range patches, the connectivity was generally high, with 95% of the area with low resistance values, 4% medium, and 1% high values (Fig. 4).

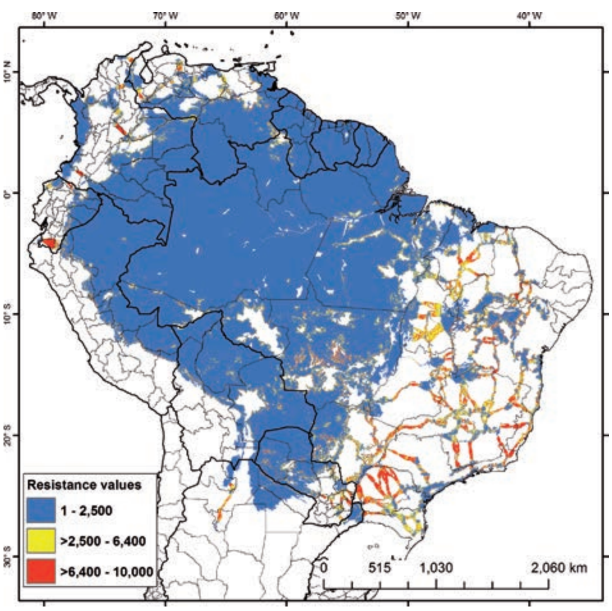

Fig. 4. Permeability within the jaguar connectivity network indicated by the direct superimposition of the resistance values (as in Fig. 1). Lower resistance values indicate higher permeability for jaguar movements.

Connectivity between jaguar range patches was further worsened by the high density of roads, especially in trans-Andean corridors (e.g. in Colombia) as well as in the Atlantic Forest and Cerrado (eastern Brazil, Fig. 5). Some areas within the core of the jaguar range also had high road density, e.g. in Mato Grosso in Brazil and in Paraguay (Fig. 5).

Frequent barrier sections along the potential corridors and high road density cut off several fragments of the jaguar range from the main central core. Among them was the Choco region in western Colombia and Ecuador and various patches of the jaguar range in eastern Brazil, Argentina, and Venezuela.

Protected areas and indigenous territories covered 49% (29% and 20%, respectively) of the total area inside the jaguar range patches (Fig. 6). However, only 9% of the area of the least-cost paths (principal corridors) was covered by protected areas or indigenous territories (8% and 1% respectively, Fig. 6).

Discussion

In this paper, we show the current connectivity status within and between jaguar populations in South America and propose a network of potential principal ecological corridors that may facilitate continued jaguar movement between existing patches. Our analyses demonstrate that the central core of the jaguar's range, located mainly in the Amazon basin and Guiana Shield, retains good connectivity. In contrast, the connectivity between the fragmented parts of the former jaguar range has largely been lost due to habitat transformations and transportation infrastructure development. Furthermore, most of the ecological corridors selected by Linkage Mapper as the best options (least-cost paths) are interrupted by frequent barriers that prevent or hinder jaguar movements and may lead to the isolation of some jaguar populations.

Our results indicate that among those likely to become isolated from the central core is the jaguar population of the Choco region in Colombia and Ecuador, which is an extension of jaguar populations in Central America. This means there is likely no longer any or very limited gene flow between the jaguar populations in the Amazon and Central America. Similarly, jaguar movement and genetic exchange may currently be disrupted in the east of the continent, within the Caatinga, Cerrado, and Atlantic Forest ecoregions. However, not all of the corridors identified by our analysis are of equally poor quality. Some corridors have relatively few barriers along their course, which may still offer favourable conditions for jaguar movement. Narrow bands of gallery and riverine forests, river valleys, and the banks of other bodies of water may offer additional linkages between fragmented populations (Silveira et al. 2014, Castilho et al. 2015), and it would be advisable to conduct a more detailed analysis of their potential to serve as additional corridors. Several local or regional connectivity analyses for various parts of the jaguar range have already been performed, e.g. for Argentina, Paraguay, Bolivia, and Brazil (Morato et al. 2014, Silveira et al. 2014, Castilho et al. 2015, Paviolo et al. 2016, Portugal et al 2019, Thompson & Velilla 2017, Diniz et al. 2018, Wallace et al. 2020), and their results can be combined or compared with ours for a better understanding of jaguar connectivity.

In our analysis, the landscape resistance values were derived from jaguar distribution models based on a large set of presence and absence points across South America and a broad set of predictive variables that included environmental and anthropogenic factors known to affect jaguars (Jędrzejewski et al. 2023a). Moreover, these models were conducted separately for eight main ecoregions of South America to account for the genetic differences between jaguar populations (Roques et al. 2016, Lorenzana et al. 2020) and possible adaptations to the unique ecological factors of each ecoregion. We believe this approach also increases the probability of correctly estimating the resistance values, resulting in improved connectivity assessment.

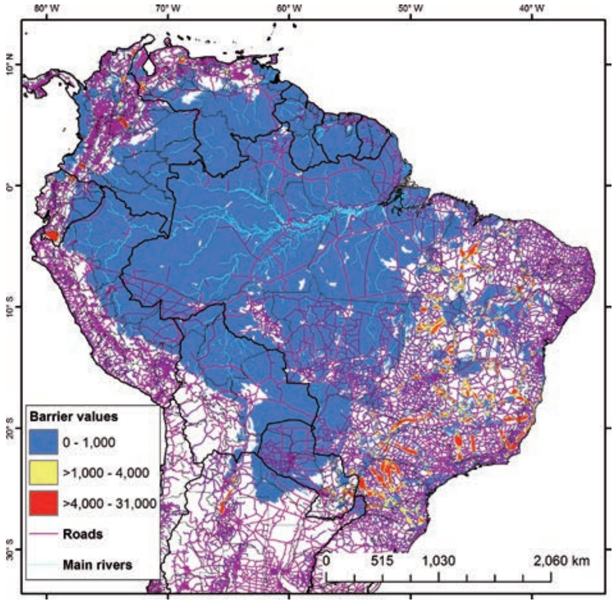

Fig. 5. South America's major and minor road network as an additional factor in the fragmentation of the jaguar population in addition to the barriers within the connectivity network identified by the Barrier Mapper analysis.

The loss and fragmentation of jaguar habitats are increasing (Menezes et al. 2021, Martinez et al. 2022), causing declines in jaguar population size and genetic diversity (Haag et al. 2010, Srbek-Araujo et al. 2018). Therefore, it is important to support conservation and management efforts that halt further fragmentation of jaguar habitat and increase connectivity between habitat areas that have already been fragmented. In addition, restoration of some habitat patches within corridors (e.g. reforestation) could reduce barriers and increase the permeability of some corridors (McRae et al. 2012, Banks-Leite et al. 2020, Hilty et al. 2020). This recommendation coincides with the Decade on Ecosystem Restoration proclaimed by UN Environmental Program to promote Global Ecosystem Restoration (UNEP 2021).

Additionally, nominating important corridor fragments for legal protection is important (Hilty et al. 2020), as only 9% of the corridor areas are currently legally protected. Another critical action is the construction of animal passes wherever conflict between potential jaguar movements and existing or planned highways or other heavy traffic roads exist, both inside the jaguar inhabited areas or between them (Forman et al. 2003, Glista et al. 2009, Jędrzejewski et al. 2009, Matthews et al. 2015, González-Gallina et al. 2018). The results of our work can guide the planning of any of these conservation actions at a large scale and help focus on sites where such actions can be most effective and are most needed.

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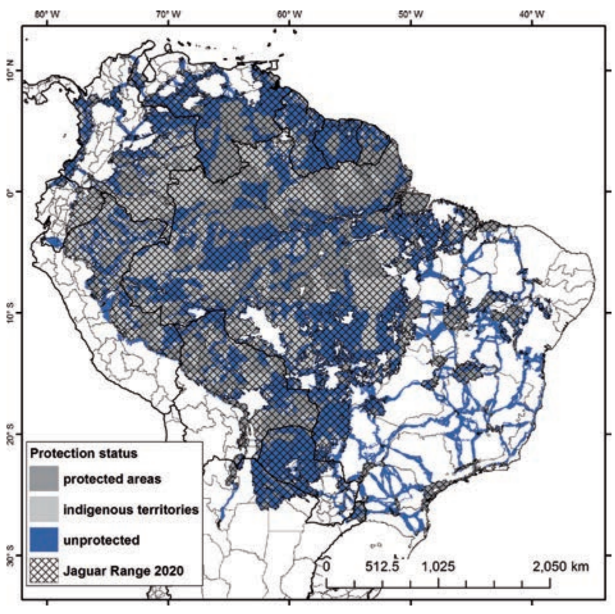

Fig. 6. Role of protected areas and indigenous territories in the protection status of the jaguar connectivity network.

collaboration leading to this article. We also thank everyone who provided the data that resulted in jaguar distribution models for South America and enabled the analysis of connectivity for jaguars.

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We dedicate this work to colleagues - scientists from Ukraine who had to abandon their research in order to fight for freedom and all human values that lie at the basis of noble scientific work.

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Supporting Online Material SOM Datasets D1–D4 available at www.catsg.org.

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