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Modeling the effects of deforestation on the connectivity of jaguar *Panthera onca* populations at the southern extent of the species' range

Jeffrey J. Thompson[1,2,*], Marianela Velilla[1,2]

[1]Guyra Paraguay, Av. Cnel. Carlos Bóveda, Parque Asunción Verde, Viñas Cué, Asunción, Paraguay
[2]Consejo Nacional de Ciencia y Tecnología (CONACYT), Justo Prieto 223 esq. Teófilo del Puerto, Barrio Villa Aurelia, Asunción, Paraguay

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ABSTRACT: We employed least-cost and circuit theory modeling to model the connectivity among previously defined Jaguar Conservation Units (JCUs) at the southern limit of the jaguar's range in Argentina, Bolivia, Brazil and Paraguay, in order to assess the effects of deforestation and land use change between 2000 and 2014. Due to uncertainty about possible limitations to jaguar dispersal, we examined connectivity where linkages were not cost-limited and limited to 1000 km cost-weighted distance. When linkage length was not cost-limited, total linkage area decreased by 9%, and mean least-cost distance and mean effective resistance increased by 6 and 31%, respectively, from 2000 to 2014. Limiting linkages to 1000 km cost-weighted distance indicated that the southern- and eastern-most JCUs were isolated as early as 2000 and that the number of linkages between the other JCUs decreased between 2000 and 2014, causing the linkage area to decrease by 27% while the least-cost distance of the remaining linkages increased by a mean of 4% and effective resistance increased on average by 44%. By limiting linkages to a plausible cost-weighted distance, we demonstrated that JCUs in the Atlantic Forest, Argentine Chaco and the Argentine/Bolivian Yungas have been isolated since at least 2000, and that there has been a loss of connectivity through eastern Bolivia, increased resistance in the remaining linkages and a constriction of all but one linkage to a minimum width of <8 km. Our results are consistent with an observed loss of genetic diversity in jaguar populations within portions of our study area and indicate a need for further research to better quantify jaguar dispersal.

KEY WORDS: Jaguar · *Panthera onca* · Deforestation · Connectivity · Corridors · South America · Circuit theory · Least-cost distance

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INTRODUCTION

Maintaining and restoring ecological connectivity in the face of habitat loss, degradation and fragmentation have become an important component of biodiversity conservation (Crooks & Sanjayan 2006, Beier et al. 2011). Globally, large carnivores have been particularly sensitive to loss of habitat and ecological connectivity (Crooks et al. 2011), which is of concern as these species are important in shaping ecosystem dynamics and function through top-down trophic effects (Estes et al. 2011, Ripple et al. 2014). Moreover, the spatial needs of large carnivores can potentially make them effective umbrella species since, through their conservation, they potentially serve as a surrogate for less spatially demanding species (Ray et al. 2005, Kunkel et al. 2013, Thornton et al. 2016).

The jaguar *Panthera onca* is the largest felid in the Americas, ranging from the southwestern-most United States to northern Argentina (Sanderson et al. 2002, Zeller 2007). However, the species has been extirpated from >50% of its original distribution, >80% of its former distribution outside of the Ama-

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*Corresponding author: jthompson.py@gmail.com

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zon, and is threatened throughout the majority of its range, mainly from habitat loss and persecution (Sanderson et al. 2002, Zeller 2007, de la Torre et al. 2017). Concerns over declining jaguar populations led to the designation of conservation priority areas throughout the species' range (Jaguar Conservation Units, JCUs) based upon expert opinion (Sanderson et al. 2002, Zeller 2007). Further concerns over the viability of populations within the JCUs, reduced genetic exchange and drift-induced differentiation among populations led to the Jaguar Corridor Initiative, which identified least-cost connectivity corridors among JCUs at a range-wide scale as part of a conservation plan to maintain the ecological and genetic integrity of the jaguar throughout its range (Rabinowitz & Zeller 2010, Zeller et al. 2013).

Continuing agricultural expansion and habitat loss have been shown to threaten connectivity between JCUs (Zeller et al. 2011, Petracca et al. 2014a,b, Olsoy et al. 2016); a threat that is particularly acute at the northern and southern limits of the jaguar's distribution and in northwestern South America, where connectivity corridors are considered vulnerable due to their narrowness (Rabinowitz & Zeller 2010). At the southern extent of the jaguar's range, an important region-wide threat to maintaining connectivity among JCUs stems from deforestation and land-use changes that have been occurring during the last 15 yr, particularly in the Gran Chaco, which has been subjected to some of the highest deforestation rates in the world (Hansen et al. 2013, Caldas et al. 2015, Vallejos et al. 2015).

The effects of forest loss and fragmentation within the corridors defined by Rabinowitz & Zeller (2010) are substantial throughout the jaguar's range (Olsoy et al. 2016). However, the potential effects of deforestation on the size and location of the linkages among JCUs have not been evaluated. The previous delineation of least-cost corridors connecting JCUs was undertaken using range-wide data on vegetative cover and land use from 2000 (Rabinowitz & Zeller 2010), and given the rapid and extensive deforestation and the subsequent changes in land use that have occurred at the southern limit of the jaguar's range, we reevaluated connectivity among JCUs in that region to quantify how the process of deforestation and land use change has affected connectivity within the context of the overall conservation vision for the jaguar.

We analyzed the effect of deforestation and land-use change on connectivity among 9 JCUs in Argentina, Bolivia, Brazil and Paraguay, at the southern range of the jaguar, by incorporating updated geographical data including high-resolution forest cover data from 2000 and 2014 (Hansen et al. 2013). We employed a hybrid approach that combined least-cost modeling and circuit analysis, which has previously been applied to connectivity modeling for multiple species, including large carnivores (Castilho et al. 2015, Dutta et al. 2016, WHCWG 2010). We utilized the movement costs and assumptions from the analysis of Rabinowitz & Zeller (2010) to conduct a least-cost analysis (Adriaensen et al. 2003) in order to delineate connectivity corridors among these JCUs at the regional level, incorporating the circuit theory-based analysis to measure effective resistance of linkages and define pinch points (i.e. areas where landscape resistance disproportionally restricts movement as measured by current density; McRae et al. 2008). Using this analysis, we quantified the effects of deforestation and changes in land use on the connectivity of jaguar populations in our study region and defined their conservation implications for maintaining connectivity among JCUs.

MATERIALS AND METHODS

Study area and land-use history

We modeled connectivity among 9 JCUs within Argentina, Bolivia, Brazil and Paraguay, representing mainly Atlantic Forest, Central Andean Yungas, Chaco dry forest, Southwestern Amazonia forest, Chiquitano dry forest and the Pantanal, covering an area of approximately 2 450 000 km^2 (Table 1, Fig. 1, see Fig. A1 in the Appendix). Of the JCUs included, 4 (Noel Kempff Mercado, Pantanal, Gran Chaco, Misiones) are categorized as highest priority for jaguar conservation (Zeller 2007). Previous least-cost modeling of connectivity identified a network of corridors among the JCUs in the study area, of which >80% were designated as vulnerable due to their narrowness and the relative ease that connectivity could be disrupted (Rabinowitz & Zeller 2010).

More than 20% of the forest cover in the study area was lost between 2000 and 2014, with focal areas of deforestation in the Dry Chaco of Argentina, Bolivia and Paraguay (Killeen et al. 2007, Hansen et al. 2013, Vallejos et al. 2015), Chiquitano Forest in eastern Bolivia (Killeen et al. 2007) and the Humid Chaco and Pantanal in Paraguay (Caldas et al. 2015). The most extensive and rapid deforestation occurred in the Dry Chaco of western Paraguay (Hansen et al. 2013, Caldas et al. 2015, Vallejos et al. 2015) where, for example, from 2000 to 2012, >3.2 million ha were

Table 1. Jaguar Conservation Units (Zeller 2007) included in the analysis and their corresponding jaguar geographic region (Zeller 2007) and global ecoregions (Olson et al. 2001, Zeller 2007)

Jaguar Conservation Unit	Jaguar geographic region	Global ecoregion
Noel Kempff Mercado	Upper Amazon: tropical moist lowland forest; Cerrado: tropical dry forest	Southwestern Amazonian moist forest, Chiquitano dry forest
Isiboro-Secure	Upper Amazon: tropical moist lowland forest; tropical Andes: tropical moist lowland forest	Southwestern Amazonian moist forest, central Andean Yungas
Carrasco/Amboro	Tropical Andes: tropical moist lowland forest	Central Andean Yungas
Pantanal	Cerrado: tropical dry forest; Pantanal: herbaceous lowland grassland	Pantanal flooded Savanna
Gran Chaco	Chaco: tropical dry forest; Pantanal: herbaceous lowland grassland	Dry Chaco
Baritú-Calilegua	Tropical Andes: tropical moist lowland forest; Puna: herbaceous montane grassland	Central Andean Yungas
Upper Rio Paraná	Atlantic: tropical moist lowland forest; Cerrado: tropical dry forest	Atlantic Forest
Chaco	Chaco: tropical dry forest	Dry Chaco
Misiones	Atlantic: tropical moist lowland forest; Pampas: herbaceous lowland grassland; Brazilian araucaria: temperate forest	Atlantic Forest

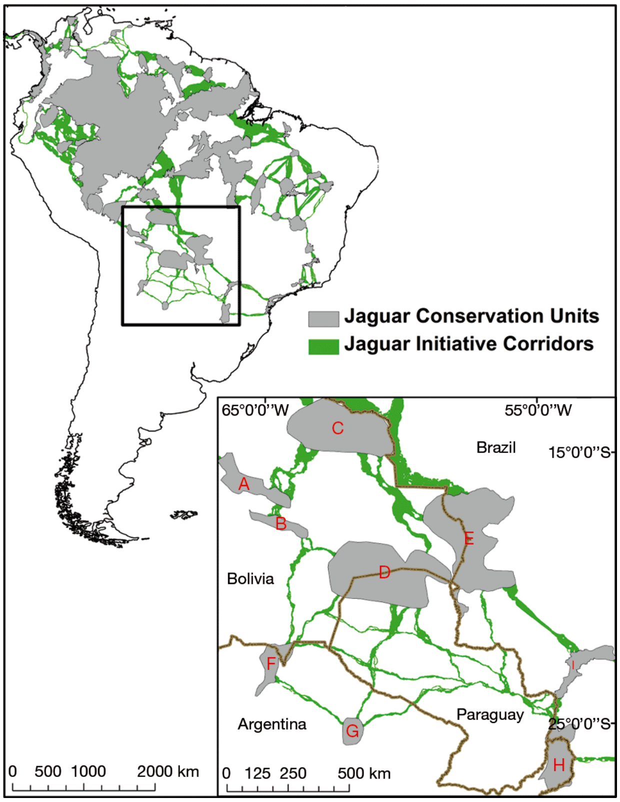

Fig. 1. Study area in South America showing the range-wide location of Jaguar Conservation Units (JCUs) and Jaguar Initiative Corridors; inset shows those within the study area. Letters correspond to JCUs within the study area: (A) Isiboro-Secure, (B) Carrasco/Amboro, (C) Noel Kempff Mercado, (D) Gran Chaco, (E) Pantanal, (F) Baritú-Calilegua, (G) Chaco, (H) Misiones and (I) Upper Rio Paraná

deforested, equal to 19% of the forest area in 2000. As a result, 26% of the region had been deforested by 2012, with the deforestation from 2000–2012 constituting 70% of all deforested land in the Paraguayan Dry Chaco region (Vallejos et al. 2015).

The eastern portion of the study region was subjected to extensive land conversion prior to 2000, particularly in the Atlantic forest, where only 7.8% of the original forest area remained by 2003 (Di Bitetti et al. 2003). In Brazil, only 2.7% of the Atlantic forest remained by 2003 (Di Bitetti et al. 2003), making connectivity between the JCUs in the Atlantic Forest and those adjacent to them highly dependent upon the remaining forest in eastern Paraguay (Fig. 1) (Rabinowitz & Zeller 2010). However by 2000, 75% of the Atlantic forest in eastern Paraguay had been converted to other land uses (Huang et al. 2009), and from 2000 to 2014 an additional ~7730 km^2 (equivalent to 35% of the remaining Atlantic forest) had been lost in Paraguay, despite national legislation guaranteeing zero forest loss (Hansen et al. 2013).

Connectivity modeling

We modeled connectivity using a combination of least-cost modeling (Adriaensen et al. 2003) and circuit theory (McRae et al. 2008), utilizing the landscape characteristics and cost values to movement from Rabinowitz & Zeller (2010) derived from expert opinion. To produce a landscape permeability matrix for 2000 and 2014, we developed a geographic information system using ArcGIS 10.0 software (ESRI) consisting of 9 raster data layers of landscape characteristics: distance from principal roads, distance from human settlements (2000 and 2014), human population density, elevation, land cover (2000 and 2014), and percent forest cover (2000 and 2014) based upon 8 spatial data sets (Table 2).

In our modeling, we took advantage of recent spatial data so that only distance from roads, land cover in 2000, and elevation were (or were based upon) the same data sets used by Rabinowitz & Zeller (2010). We derived 2014 forest cover by using Global Forest Watch data on forest loss for 2000 to 2014 to modify data on 2000 forest cover (Hansen et al. 2013). The derived 2014 forest cover was used to update the layer of 2000 land use (see below), while the layers of distance from roads and from human settlements were derived from road and settlement base layers (CIESIN & ITOS 2013, Open Street Map 2015) using the 'Euclidean distance' function in ArcGIS.

Although the layer of human settlements included most settlements in the study area, it did not include some small rural settlements, nor did it provide the geographic extent of towns or cities, which we considered important to include, as human presence at a local scale has been shown to negatively determine the occurrence of jaguars within the study area (Cuyckens et al. 2014, Thompson & Martinez 2015). Consequently, we modified the layer of human settlements by including data from images of lights at night for 2000 and 2014 (NOAA 2015; Table 2), which identified small rural settlements not included in the layer of human settlements, as well as the extent of larger settled areas.

We produced the 2014 layer of land cover by overlaying the map of 2000 to 2014 forest loss upon the 2000 land cover layer (Table 2), classifying all deforested areas from 2000 to 2014 as mosaic agriculture. Although most of the deforested area was converted to mosaic agriculture (mainly for intensive cattle production), a portion of the converted area was known to be used for intensive agriculture (Müller et al. 2012, Gasparri et al. 2013, Caldas et al. 2015). For this reason, we conducted a sensitivity analysis to evaluate the effect of assigning deforested areas as either mosaic or intensive agriculture and found no relevant effects on connectivity. Therefore, we maintained the classification of mosaic agriculture for the areas deforested during 2000–2014.

We standardized all layers to the same projection and re-sampled them to a 1 km^2 resolution. Using the same cost values and methodology used by Rabinowitz & Zeller (2010) (Table 3), we developed resistance layers for 2000 and 2014 by adding the values of each map cell across the 6 layers, to produce a layer of the cumulative costs of movement in the study area for both years. Costs ranged from 1 to 47 km in cost-weighted distance and, to remain consistent with the parameters used by Rabinowitz & Zeller (2010), areas with a cost of >25 km in cost-weighted distance were defined as barriers to dispersal. Consequently, the cost-weighted distance through a map cell with the lowest cost (1) was equal to the Euclidean distance of 1 km, while the highest cost-weighted distance for a map cell that was traversable was 25 km.

To map the least-cost linkages among the JCUs in the study area, we utilized the 'Linkage Mapper' 1.0 toolkit for ArcGIS 10.0 (McRae & Kavanagh 2011) to calculate the cost-weighted distance and least-cost

Table 2. Geographic data used in the connectivity modeling

Data layer	Time period	Resolution	Source
Forest cover	2000	30 × 30 m	Tree cover extent (Hansen et al. 2013)
Tree cover loss	2001–2014	30 × 30 m	Hansen/UMD/Google/USGS/NASA tree cover loss and gain area (Hansen et al. 2013)
Land cover	2000	1 × 1 km	Global land cover 2000 (Global Land Cover 2000 Database 2003)
Elevation	1996	30 arc seconds	Global 30 arc-second elevation (GTOPO30) (US Geological Survey 1996)
Human density	2010	3 arc seconds	WorldPop project (www.worldpop.org.uk)
Roads	1980s–2010	1:250000 scale	Global roads open access data set (gROADS), v1 (1980–2010) (CIESIN & ITOS 2013)
Settlements	2014	1:250000 scale	Open street map (Open Street Map 2015)
Lights at night	2000, 2014	30 arc seconds	Version 4 DMSP-OLS nighttime lights time series (NOAA 2015)

Table 3. Classification of data layers and associated cost values for jaguar movement from Rabinowitz & Zeller (2010) utilized in the analysis. N/A: barrier to movement

Land cover type		% Forest cover		Elevation (m)		Distance from settlements (km)		Distance from roads (km)		Human population density (people km^{-2})	
Class	Cost value	Class	Cost value	Class	Cost value	Class	Cost value	Class	Cost value	Class	Cost value
Broadleaved/deciduous forest	0	0–10	9	0–1000	0	0–2	8	0–2	7	0–20	1
Regularly flooded forest	2	10–20	7	1000–2000	2	2–4	5	2–4	4	20–40	5
Shrubland	2	20–40	5	2000–3000	7	4–8	4	4–8	2	40–80	7
Flooded savanna	5	40–60	2	3000–5000	10	8–16	1	8–16	1	80–160	9
Mixed agriculture/degraded forest	5	60–100	0	>5000	N/A	>16	0	>16	0	160–320	10
Water	6									>320	N/A
Grassland/savanna	7										
Mixed agriculture/tree cover	7										
Cultivated/managed areas	8										
Urban areas	10										
Permanent snow/ice	N/A										

paths between adjacent JCUs for 2000 and 2014, for which we used the most current delineations of JCUs (Panthera 2015, Olsoy et al. 2016, Thornton et al. 2016). Least-cost corridors were defined by Linkage Mapper by normalizing the summed cost-weighted distances between adjacent JCUs and then subtracting the least-cost path distance, which gave the deviation for each raster cell from the least-cost path in least-cost distance units. Then the normalized corridors were combined into a composite linkage layer using the ArcGIS 'Mosaic' function, where each raster cell is represented by the minimum cost value among all of the normalized corridor layers.

We did not initially limit the cost-weighted distance of linkages between JCUs in order to fully quantify the change in movement costs throughout the study area stemming from changes in landscape characteristics, as well as due to uncertainty over cost limitations to dispersal. Despite uncertainty over limits to jaguar dispersal, which is exacerbated by potential age and sex-specific differences in dispersal ability exhibited by large carnivores (Elliot et al. 2014), we expected that there is a cost limit to dispersal. To account for this uncertainty over dispersal limits we also evaluated linkages by applying a 1000 km cost-weighted distance limit as an optimistic maximum dispersal distance for jaguars between JCUs, which we chose based upon several criteria.

The mean ratio of cost-weighted distance to least-cost path length from our analysis was 4:1 km; consequently, a 1000 km cost-weighted distance equates to a path length of 250 km based upon the mean resistance value. Since jaguars disperse into the southwestern United States from the nearest core population in northern Mexico over a linear distance of ~300 km (Jaguar Observation Database, http://jaguardata.info/), across a less than optimal landscape matrix, a path length of 250 km seems plausible. Furthermore, jaguars are capable of moving more than 20 km d^{-1} in human-altered systems (Morato et al. 2016, McBride & Thompson preprint doi:10.1101/119412), which also suggests that crossing a distance of up to 250 km through a landscape with the mean resistance of our study area is plausible.

Our modeling takes a more formalized approach to estimating corridor width than Rabinowitz & Zeller (2010), who defined corridor width as the area of least-cost linkages represented by the lower 0.1 % of least-cost values. Our approach makes an assumption that the normalized least-cost paths allow for movements between JCUs, and the linkage area is defined as a least-cost distance from those paths. To define linkage area, we assumed that dispersal was limited to areas with a cost-weighted distance from the least-cost paths of ≤25 km, based upon the assumed cost value applied as a dispersal barrier used by Rabinowitz & Zeller (2010).

We complemented the least-cost analysis by incorporating a hybrid analysis employing circuit theory (McRae et al. 2008). We used Circuitscape (McRae et al. 2013), incorporated into Pinchpoint Mapper (McRae 2012) within the Linkage Mapper toolkit (McRae & Kavanagh 2011), conducting a pairwise circuit analysis between JCU pairs confined to the least-cost linkages in order to measure current flow throughout the linkage network. Circuit theory exploits the analogies between random walk and electricity passing through a circuit (Snell & Doyle 2000); the less resistant an area is, the less restrictive the flow of current is through those areas and consequently current densities (amps per grid cell) are lower. By mapping current densities, areas where increased resistance has disproportionately large effects on connectivity (pinch points), as indicated by higher current densities, can be identified (McRae et al. 2008).

RESULTS

The least-cost modeling defined linkages that did not differ much in their general location between 2000 and 2014, with the exception of a large eastward shift in the linkage between the Chaco and Misiones JCUs and the loss of a direct linkage between the Isiboro-Secure and Gran Chaco JCUs (Fig. 2). The total area of the linkage network decreased from 99 106 km^2 in 2000 to 85 241 km^2 in 2014, a 14 % reduction (Fig. 2), while the movement cost through the entire linkage network increased on average by 6 %, and least-cost distances between JCUs increased between 0 and 11 % (Table 4).

Limiting linkages to a maximum cost-weighted distance of 1000 km reduced the number of linkages to 6 in 2000 and to 5 in 2014, all between JCUs in the northeastern portion of the study area (Fig. 2). With the loss of a direct linkage between the Noel Kempff Mercado and the Gran Chaco JCUs from 2000 to 2014, the total linkage area decreased by 27 % (Fig. 2) and the least-cost distance of the linkages present in both 2000 and 2014 increased by 0 to 7 %

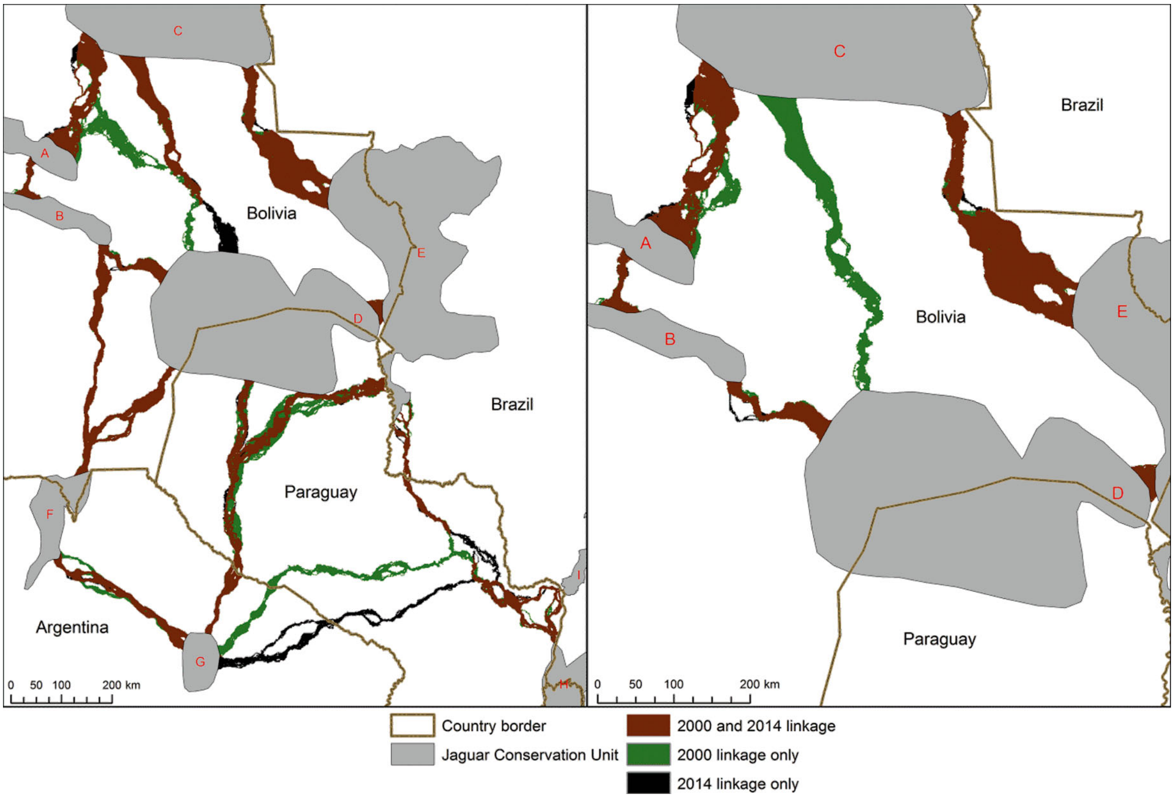

Fig. 2. Least-cost connectivity linkages and paths among Jaguar Conservation Units (JCUs) for 2000 and 2014. Shown are the linkage network without limits to cost-weighted distance movement between JCUs (left) and linkages limited to 1000 km cost-weighted distance movement between JCUs (right). Linkages are displayed for 25 km cost-weighted distance from the least-cost paths. Letters correspond to JCUs shown in Fig. 1

Table 4. Cost-weighted distance and percent change in cost-weighted distance and effective resistance between adjacent Jaguar Conservation Units (JCUs) from 2000 to 2014. Linkages with a cost-weighted distance of ≤1000 km in both 2000 and 2014 are listed separately. The linkage between the Isiboro-Secure and Gran Chaco JCUs was not present in 2014

Linkages between JCUs		Cost-weighted distance		% Change in cost-weighted distance from 2000–2014	% Change in effective resistance from 2000–2014
		2000	2014		
Chaco	Misiones	4660	4957	6	24
Pantanal	Upper Rio Paraná	3979	4324	9	5
Pantanal	Misiones	3519	3816	8	31
Pantanal	Chaco	3412	3612	6	65
Gran Chaco	Chaco	2847	2979	5	41
Baritu-Calilegua	Chaco	2108	2150	2	56
Carrasco/Amboro	Baritú-Calilegua	1867	1884	1	6
Gran Chaco	Baritú-Calilegua	1683	1684	0	17
Isiboro-Secure	Gran Chaco	1161	–	–	–
Misiones	Upper Rio Paraná	1141	1186	4	8
Noel Kempff Mercado	Gran Chaco	991	1099	11	–9
Linkages with ≤1000 km cost-weighted distance in 2000 and 2014					
Noel Kempff Mercado	Pantanal	921	953	3	47
Carrasco/Amboro	Gran Chaco	735	783	7	23
Isiboro-Secure	Noel Kempff Mercado	504	525	4	103
Isiboro-Secure	Carrasco/Amboro	258	277	7	43
Gran Chaco	Pantanal	11	11	0	5

(Table 4). The shortest of these linkages, and the only one not to increase in cost between 2000 and 2014, was between the Gran Chaco and Pantanal JCUs, at 11 km cost-weighted distance. All remaining linkages were considerably higher in costs, with the linkage between the JCUs in the Bolivian Yungas (Isiboro-Secure and Carrasco/Amboro) having the next lowest value at 277 km cost-weighted distance in 2014 (Table 4).

The circuit theory-based analysis demonstrated the greatest proportional increases in effective resistance in the linkages between the Noel Kempff Mercado JCU and the Isiboro-Secure and Pantanal JCUs (103 and 47 %, respectively), between the Chaco JCU and the Pantanal, Gran Chaco and Baritú-Calilegua JCUs (65, 41 and 56 %, respectively), and between the Isiboro-Secure and Carrasco/Amboro JCUs (43 %) (Table 4). For the other linkages in the cost-limited linkage network, there was a 23 and 5 % increase in effective resistance between 2000 and 2014 in the linkages between the Gran Chaco and Carrasco/Amboro JCUs and between the Gran Chaco and Pantanal JCUs, respectively, while effective resistance decreased 9 % in the linkage between the Gran Chaco and Noel Kempff Mercado JCUs (Table 4).

Within the unlimited cost network, the areas with high current densities in 2000 generally expanded by 2014, particularly in the connections between the Argentine Yungas and the Argentine Chaco and the Bolivian Yungas, throughout the eastern portion of the study area, and in western Paraguay through the linkage between the Chaco and Gran Chaco JCUs (Fig. 3). The most notable increases in current density occurred in the linkages from the Noel Kempff Mercado JCU to the Isiboro-Secure and Gran Chaco JCUs in Bolivia, and in the linkages from the Chaco JCU in northern Argentina to the Baritú-Calilegua, Gran Chaco and Pantanal JCUs (Fig. 4). An expansion of areas of high current density was evident throughout the linkage network limited to 1000 km cost-weighted distance (Fig. 3), although the largest increases in current density occurred between the Noel Kempff Mercado and the Isiboro-Secure JCUs (Fig. 4).

DISCUSSION

Despite uncertainty over the dispersal ability of jaguars, we demonstrated that between 2000 and 2014, habitat loss and other anthropic factors reduced connectivity among JCUs for the species, by reducing the number of direct linkages and linkage area and by increasing cost-weighted distance, effective resistance and current density of linkages. We further demonstrated that it is likely that many of the JCUs in our study area are not effectively connected to other JCUs.

Given the uncertainty over the dispersal ability of jaguars, and for comparison to previous range-wide

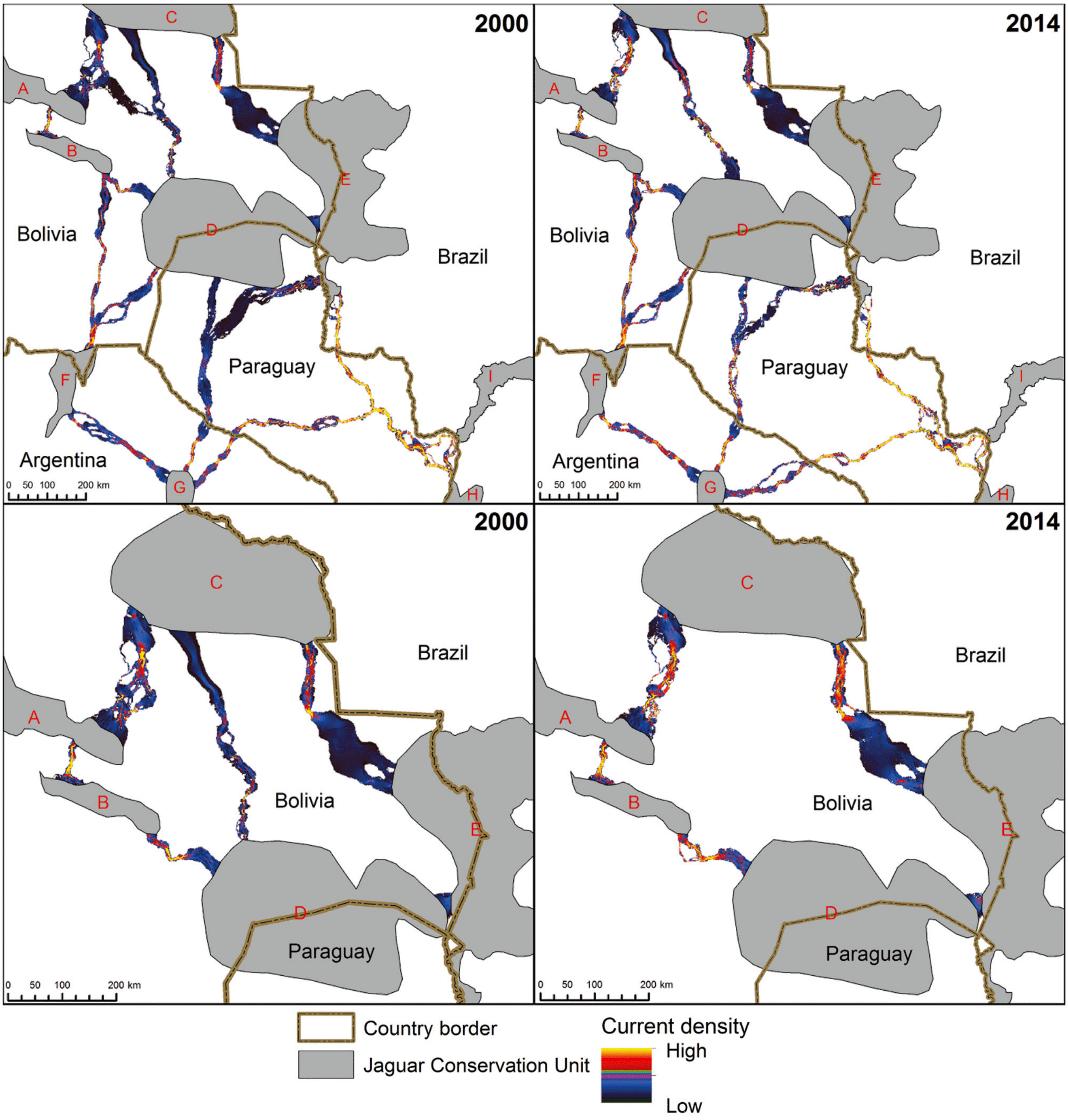

Fig. 3. Current density within the least-cost linkage networks between Jaguar Conservation Units (JCUs) for 2000 and 2014 displayed for 25 km cost-weighted distance from the least-cost paths. Shown are the linkage network without limits to cost-weighted distance movement between JCUs (top panels) and linkages limited to 1000 km cost-weighted distance (bottom panels). Maps are displayed using a histogram equalized stretch with units ranging from 0 to 8.5 amps per grid cell for the cost-unlimited linkage network and from 0 to 2.7 amps per grid cell for the cost-limited network. Letters correspond to JCUs shown in Fig. 1

corridor delineations (Rabinowitz & Zeller 2010), we presented all linkages regardless of movement costs. However, applying an optimistic cost-weighted limit to movements of 1000 km indicated that as early as 2000, the JCUs in the Atlantic forest, the Argentine Chaco and the Yungas in Argentina and Bolivia had been effectively isolated from each other and from other JCUs. This interpretation is supported by the distribution and population genetics of jaguars in these systems (Altrichter et al. 2006, Haag et al. 2010,

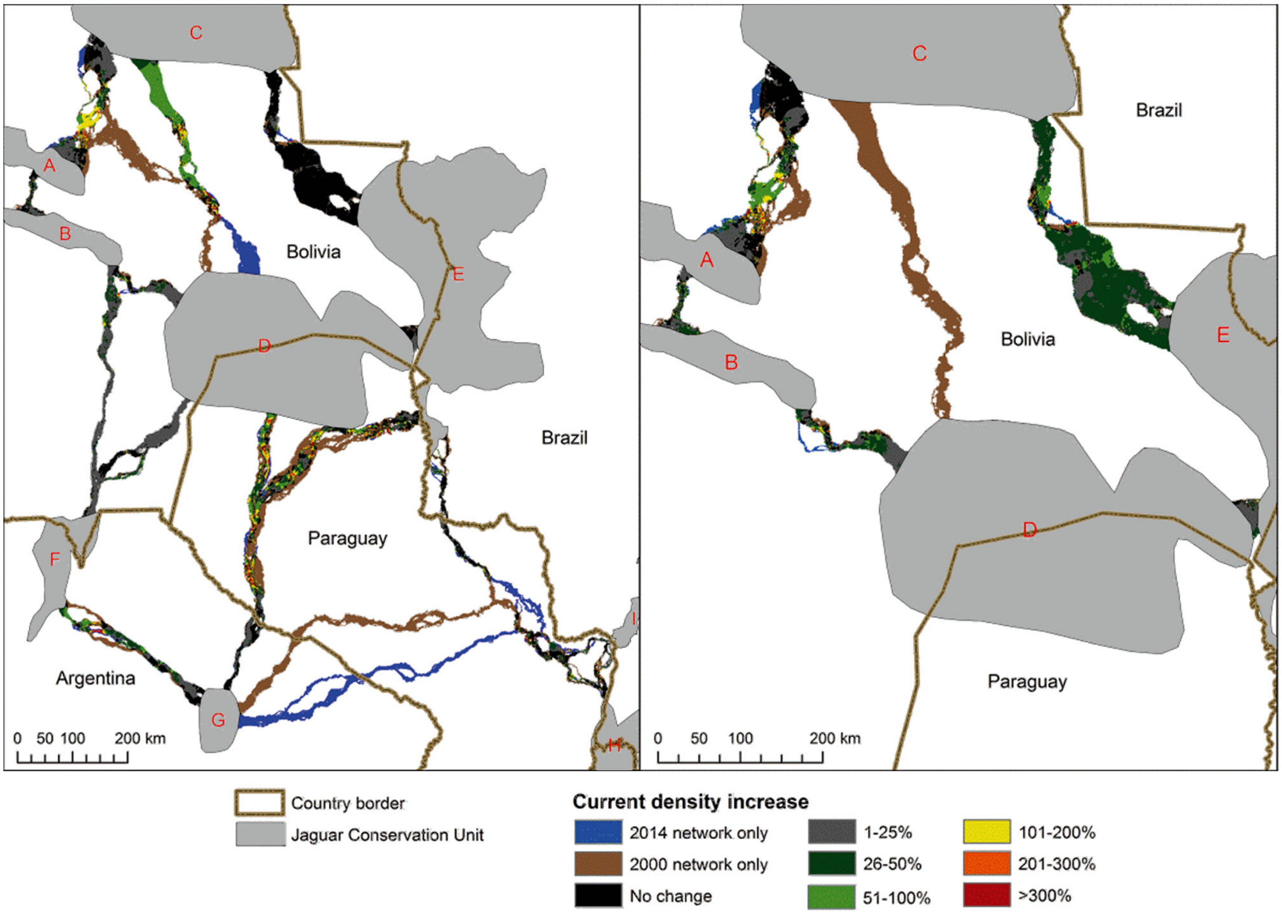

Fig. 4. Percent increase in current density within the least-cost linkage networks (displayed for 25 km cost-weighted distance from the least-cost paths) between Jaguar Conservation Units (JCUs) for 2000 and 2014, without (left) and with (right) a 1000 km cost-weighted distance limit between JCUs. Letters correspond to JCUs shown in Fig. 1

De Angelo et al. 2011, 2013, Quiroga et al. 2014, Thompson & Martinez 2015, Paviolo et al. 2016), and consequently is of particular concern for the conservation of the species at the regional scale, and for range-wide efforts for the integrated management of the species.

The loss of connectivity among the eastern- and southern-most JCUs in the study area suggested by our modeling is supported for the Atlantic forest, where connectivity of jaguar populations is considered to be greatly compromised due to historic deforestation (Haag et al. 2010, Paviolo et al. 2016). Although jaguars still persist in the Atlantic forest of Argentina, Brazil and Paraguay, our modeling illustrates that continuing land conversion has exacerbated an already tenuous connectivity or completely isolated the Upper Paraná and Misiones JCUs so that if dispersal is still possible between these JCUs the most plausible movement pathway is through eastern Paraguay. This finding is consistent with previous Atlantic forest-specific connectivity modeling (De Angelo et al. 2013, Paviolo et al. 2016).

We also demonstrated reduced linkage area and increased cost and resistance to potential movement from the Baritú-Calilegua and Chaco JCUs in the Argentine Yungas and Chaco, respectively, through the Chaco of Bolivia and Paraguay and through the Bolivian Yungas, when assuming no cost limits to movements between JCUs. The use by jaguars of defined corridors between the Baritú-Calilegua, Chaco and Gran Chaco JCUs has, however, been demonstrated to be extremely limited in the Bolivian Yungas and the Bolivian and Argentine Chaco (Thompson & Martinez 2015). This supports the validity of our approach to cost-limit linkages between JCUs, which is further reinforced by the critically endangered status of the jaguar population in the Argentine Chaco (Altrichter et al. 2006, Quiroga et al. 2014).

Focusing upon the cost-limited linkage network demonstrates how ongoing land use change in eastern Bolivia has resulted in the loss of direct connectivity between the southwest Amazon and Chiquitano forest (Noel Kempff Mercado JCU) and the Bolivian and Paraguayan Chaco (Gran Chaco JCU), in addition to the isolation of the southern and easternmost JCUs. Aside from increases in movement costs through linkages, there were general overall increases in effective resistance and current density which further indicate how the potential for movement by jaguars has been reduced. Furthermore, all the linkages, with the exception of that between the Gran Chaco and Pantanal JCUs, consisted of large areas with high current densities and restricted to widths of <8 km at their narrowest points.

Disparities in the spatial patterns of the change in current density between the cost-limited and cost-unlimited linkage networks stem from the effects on current flow which are due to the differences in the number of linkages and nodes (i.e. JCUs) in the 2 networks. The effect of the loss of the linkage from the Noel Kempff Mercado JCU to the Gran Chaco JCU from 2000 to 2014 in the cost-limited network is evident in the increase in current density in the linkage from the Noel Kempff Mercado JCU to the Pantanal JCU (Fig. 4). Similarly, in the cost-unlimited network, the loss of a direct linkage from the Isiboro-Secure JCU to the Gran Chaco JCU from 2000 to 2014, which partially overlapped the linkage from the Noel Kempff Mercado JCU to the Gran Chaco JCU, affected the current flow and led to the decrease in effective resistance observed in 2014 in the latter linkage.

The uncertainties over the dispersal ability of jaguars, and the extent of use of defined corridors in the context of continuing deforestation within corridors highlight the need for further ground-truthing and the incorporation of data on jaguar occurrence to refine and alter corridor delineation (Rabinowitz & Zeller 2010, De Angelo et al. 2013, Zeller et al. 2013, Morato et al. 2014, Petracca et al. 2014a,b, Thompson & Martinez 2015, Olsoy et al. 2016). Although we believe that our assumptions are valid and allow for comparison with other range-wide connectivity modeling, there is the possibility that habitat-based resistance may underestimate landscape permeability when compared to genetically based resistance models (Mateo-Sánchez et al. 2015).

We recognize that our choice of the limitation to jaguar dispersion is arguably optimistic, which, if it is, indicates that the potential for movement by jaguars among JCUs in our study area is even more restricted than what we present. For example, if the upper limit for dispersal cost was reduced to 500 km of cost-weighted distance, the model estimates that all but 2 linkages between 2 pairs of JCUs (Gran Chaco–Pantanal, Isiboro-Secure–Carrasco/Amboro) would be viable.

This uncertainty over jaguar movement ecology and landscape genetics emphasizes the critical need for GPS-based telemetry that addresses age and sex-specific differences in habitat use and movements (Elliot et al. 2014) and regional-scale genetics research (Haag et al. 2010, Roques et al. 2014, 2016, Valdez et al. 2015, Wultsch et al. 2016), to better quantify jaguar movement, dispersal behavior and genetic diversity in the context of anthropogenic factors. Moreover, the need for data-based reassessments of the delineation of JCUs (such as that by De Angelo et al. 2013) is evident in the face of the rapid and extensive changes in land use that are occurring in the region, and in the updated delineations of JCUs that we used in this analysis. There is also a need for robust population estimates and evaluations of habitat quality and connectivity within JCUs (Cuyckens et al. 2014, Paviolo et al. 2016, de la Torre et al. 2017).

Given the extensive deforestation that occurred in the study area, our results are not surprising. The implications for the isolation of jaguar populations are supported by several recent studies of jaguar genetic diversity, which demonstrate drift-induced loss of genetic heterogeneity within populations — particularly the smaller, more isolated ones — resulting from habitat loss and fragmentation (Haag et al. 2010, Valdez et al. 2015, Roques et al. 2014, 2016). The expected continuation of habitat conversion, combined with the precarious status of jaguar populations throughout much of the study area, indicates an urgent need to address habitat loss, reductions in connectivity and other conservation threats (i.e. persecution) to jaguars. Given the trajectories in habitat conversion, the dominance of private lands and increasing opportunity costs, conservation and research efforts need to address the value of agricultural, grazing and forestry lands in maintaining connectivity towards ensuring the long-term persistence of jaguar populations throughout the southern extent of the species' range.

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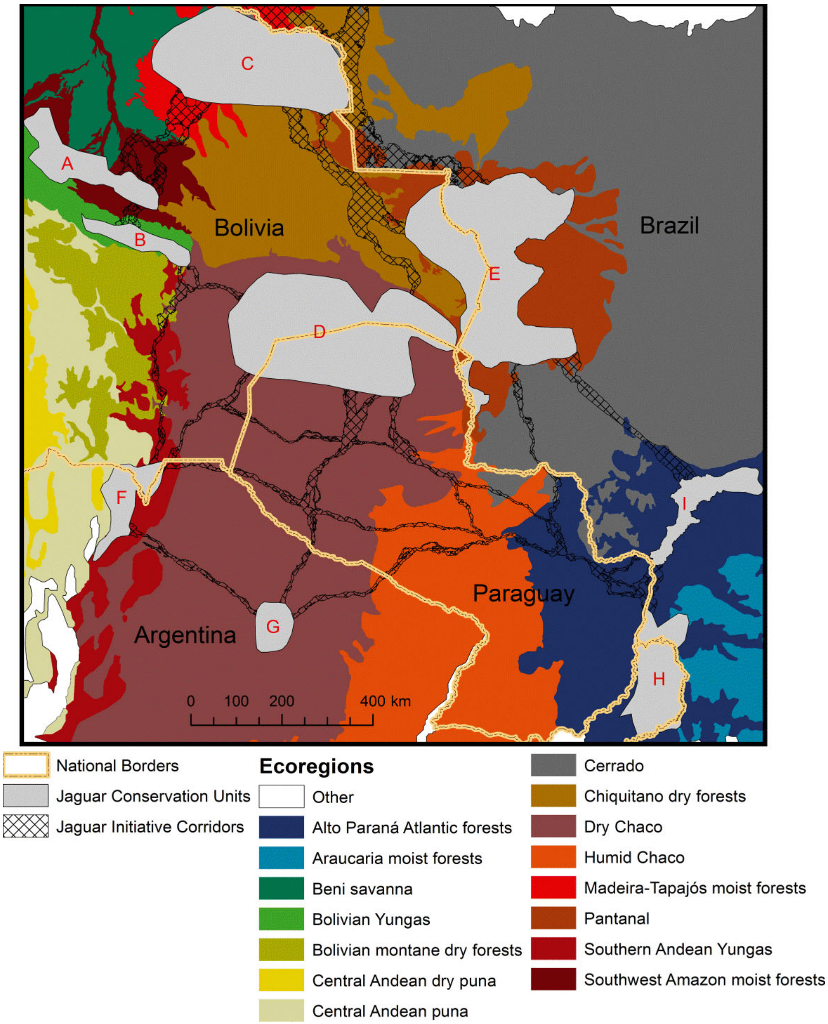
Appendix.

Fig. A1. Global ecoregions in the study area. The locations of Jaguar Conservation Units (JCUs) and jaguar initiative corridors are shown in relation to global ecoregions (Olson et al. 2001). Letters correspond to JCUs shown in Fig. 1



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