Received: 30 April 2018 | Revised: 6 July 2018 | Accepted: 3 August 2018

DOI: 10.1111/ddi.12843

BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

Habitat loss and overhunting synergistically drive the extirpation of jaguars from the Gran Chaco

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Funding information
German Ministry of Education and Research, Grant/Award Number: 031B0034A; German Research Foundation, Grant/Award Number: KU 2458/5-1

Editor: George Stevens

Abstract

Aim: Understanding how habitat loss and overhunting impact large carnivores is important for broad-scale conservation planning. We aimed to assess how these threats interacted to affect jaguar habitat (*Panthera onca*) between 1985–2013 in the Gran Chaco, a deforestation hotspot.

Location: Gran Chaco ecoregion in Argentina, Paraguay and Bolivia.

Methods: We modelled jaguar habitat change from 1985–2013 using a time-calibrated species distribution model that uses all occurrence data available for that period. We modelled habitat as a function of resource availability and hunting threats, which allowed us to separate core (high resource availability and low hunting threat), refuge (low resources but safe), attractive sink (high resources but risky) and sink (low resources and risky) habitat for 1985, 2000 and 2013.

Results: Jaguar core areas contracted by 33% (82,400 km^2) from 1985–2013, mainly due to an expansion of hunting threats. Sink and attractive sink habitat covered 58% of the jaguar range in 2013 and most confirmed jaguar kill sites occurred in these

A Spanish version of this paper is available as Supporting Information.

areas. Furthermore, habitat loss and hunting threats co-occurred in 29% of jaguars' range in 2013. Hunting threats also deteriorated core areas within protected areas, but 95% of all core areas loss occurred outside protected lands. About 68% of the remaining core areas in 2013 remained unprotected, mostly close to international borders.

Main conclusions: Our study highlights the synergistic effects that habitat loss and hunting threats exert on large carnivores, even inside protected areas, emphasizing the need to consider the geography of threats in conservation planning. Our results also point to the importance of areas along international borders as havens for wildlife and thus the urgent need for cross-border planning to prevent the imminent extinction of jaguars from the Chaco. Opportunities lie in reducing jaguar mortality over the widespread attractive sinks, particularly in corridors connecting core areas.

KEYWORDS

human–wildlife conflicts, land use change, large carnivores, persecution, poaching, protected areas, resource deterioration, retaliation hunting, source/sink habitats, species distribution models

1 | INTRODUCTION

Global biodiversity is in decline, mainly due to habitat loss and overhunting (Maxwell, Fuller, Brooks, & Watson, 2016). Regarding habitat loss, agricultural land use change, driven by increasing demand for food, livestock feed and biofuel, is the main driver (Foley et al., 2005; Machovina, Feeley, & Ripple, 2015), affecting wildlife populations through diminishing resources available as well as population fragmentation (Bradshaw, Sodhi, & Brook, 2009). Overhunting is a second major threat (Dirzo et al., 2014; Woodroffe & Ginsberg, 1998) and can quickly deplete populations even in otherwise intact habitats, turning such areas into population sinks (Benitez-Lopez et al., 2017; Delibes, Gaona, & Ferrerast, 2001; Dirzo et al., 2014; Redford, 1992). Habitat loss and overhunting often co-occur, yet neither their relative importance nor their interactions are well understood (Brook, Sodhi, & Bradshaw, 2008).

Where habitat loss and overhunting co-occur, they can produce strong synergistic effects that are larger than their additive sum (Brook et al., 2008; Mora, Metzger, Rollo, & Myers, 2007). For instance, habitat loss not only reduces and isolates populations, but also increases hunter accessibility in remaining habitat patches (Brook et al., 2008; Peres, 2001). Habitat loss and hunting are rarely studied simultaneously though, which hampers our ability to understand their interactions, and thus to propose effective conservation strategies (Brook et al., 2008; Mora et al., 2007).

One way to understand the interaction between these threats is to depict a species' habitat in a two-dimensional conceptual space, where one axis corresponds to resource availability and a second axis corresponds to hunting threats by humans (Bleyhl et al., 2015; De Angelo, Paviolo, Wiegand, Kanagaraj, & Di Bitetti, 2013; Naves, Wiegand, Revilla, & Delibes, 2003). This expands on traditional source–sink modelling (Pulliam, 1988), to allow separating core areas (high resource availability and low mortality risk from humans) from attractive sinks (high resources but risky), refuges (low resources but safe) and sinks (low resources and risky). Because most human-induced mortality likely occurs in attractive sinks and sinks, mapping them can guide management interventions more effectively than traditional habitat suitability models. This is especially relevant for large predators, which are highly susceptible to both threats, but for which different management interventions might be needed in response to these threats (De Angelo et al., 2013; Naves et al., 2003; Ripple et al., 2014).

Habitat assessments typically use predictors gathered at a single point in time (e.g., a land cover map) and match them with available occurrence data. Such static approaches are problematic in regions where land use is highly dynamic, such as active deforestation frontiers, and might lead to underestimating threat levels and ultimately misguided conservation effort (Elith, Kearney, & Phillips, 2010; Nogués-Bravo, 2009; Sieber et al., 2015). One solution is to pair occurrence data gathered over longer periods with corresponding environmental conditions. Such "time-calibrated" habitat models have multiple advantages, including a better description of how species select habitat, a mitigation of problems related to sampling bias or non-equilibrium populations, and the ability to reconstruct habitat dynamics consistently over time (Kuemmerle, Hickler, Olofsson, Schurgers, & Radeloff, 2012; Nogués-Bravo, 2009; Sieber et al., 2015). Combining time-calibrated habitat models with the core/sink framework described above would allow to reconstruct core/sink dynamics over time. Yet, to our knowledge, no study has done this so far.

Large predators are particularly vulnerable to habitat loss and overhunting because they are naturally rare, reproduce slowly, roam widely and are persecuted over livestock predation (Cardillo et al., 2005; Woodroffe, Thirgood, & Rabinowitz, 2005). As a result, large

predators are declining at alarming rates across the globe, especially in the tropics, triggering cascading ecosystem-level impacts (Ripple et al., 2014; Terborgh, 2015). Given the vulnerability and ecological importance of large predators, their decline is among the most worrisome aspects of the ongoing biodiversity crisis (Ripple et al., 2014; Terborgh, 2015). Understanding the relative effects of habitat loss and hunting on predator populations is therefore critical (De Angelo et al., 2013; Kanagaraj, Wiegand, Kramer-Schadt, Anwar, & Goyal, 2011; Naves et al., 2003). This is arguably most challenging in ecoregions that extend across national borders, requiring transnational cooperation given the wide-ranging nature of large carnivores (Bleyhl et al., 2017; Paviolo et al., 2016).

The Gran Chaco ecoregion is such a region and a particularly relevant area to assess the effects of habitat loss and hunting threats on large predators. The 1.1 million km² ecoregion extends over three countries (Argentina, Bolivia and Paraguay) and is a global deforestation hotspot (Baumann et al., 2017; Hansen et al., 2013; Kuemmerle et al., 2017), experiencing widespread defaunation (Altrichter, 2005; Noss, Oetting, & Cuéllar, 2005; Periago, Chillo, & Ojeda, 2014). The top predator in the Chaco, the jaguar (*Panthera onca*), occurs in low densities there (<1 individual/km^2) and depends on very large home range areas (400–2,900 km^2; Giordano, 2015; McBride & Thompson, 2018; Noss et al., 2012; Romero-Muñoz, Noss, Maffei, & Montaño, 2007). The Chaco contains some of the most southern jaguar populations, but these have declined in many areas of the Chaco recently and the species is facing widespread extirpation from the Chaco (Altrichter, Boaglio, & Perovic, 2006; Cuyckens, Perovic, & Herrán, 2017; Giordano, 2015; Quiroga, Boaglio, Noss, & Di Bitetti, 2014; Rumiz, Polisar, & Maffei, 2011). However, a high-resolution, Chaco-wide assessment of where core jaguar habitat remains, which factors threaten jaguars in these areas and whether remaining core areas are protected or not is missing. Understanding how core/sink habitats dynamics have contributed to the ongoing decline of the jaguar would be important to develop ecoregional strategies to safeguard jaguar populations in the Chaco and in other ecoregions facing similar threats.

Our overall goal was to assess how jaguar habitat has changed across the Gran Chaco since 1985, a period covering most of

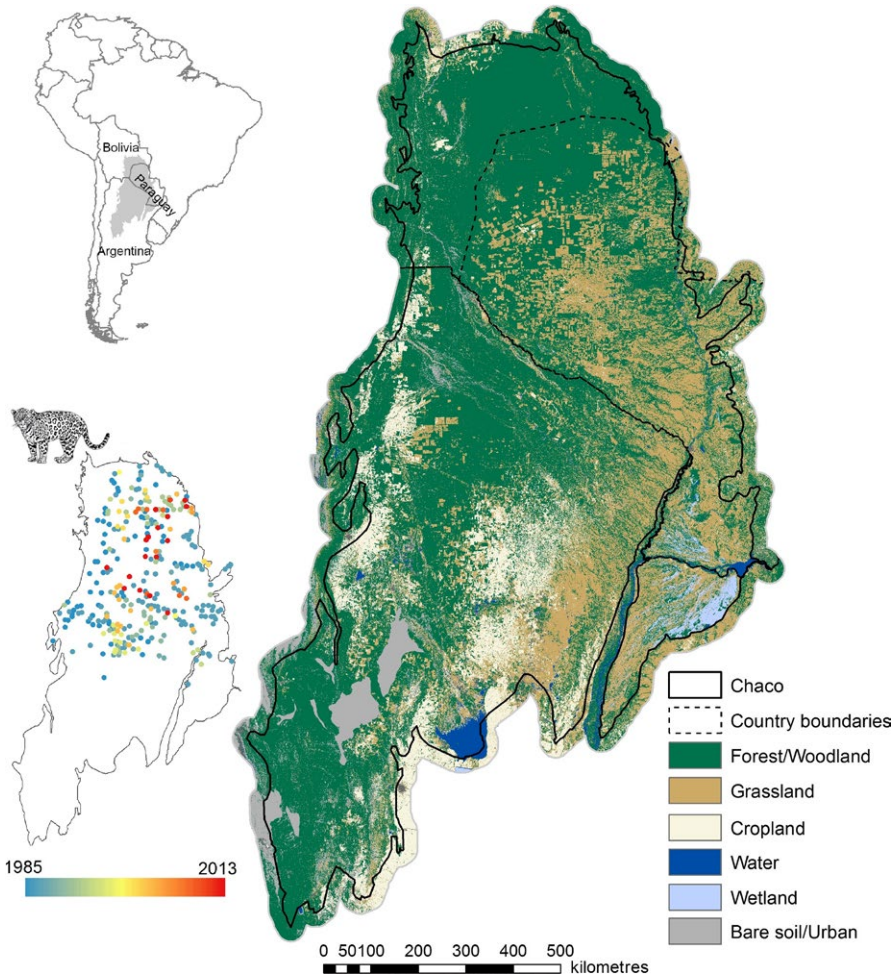

FIGURE 1 Gran Chaco ecoregion (plus a 30-km buffer) with the land use/cover categories of forest/woodland, grazing lands and croplands for the year 2013 (based on Baumann et al., 2017). "Grasslands" include natural grasslands and savannahs and planted pastures. The lower left panel shows colour-coded occurrence records for jaguar to indicate the year of recording

TABLE 1 Predictor variables for the two-dimensional habitat modelling for jaguar in the Chaco

Variable	Description	Source	Temporal resolution [b]	Expected effect	Explanation
Resource-related variables					
%Forest [a]	% forest and open woodland around target cell	Landsat Archive	Yearly	+	Provides resources for food, cover and reproduction for jaguar
%Cropland [a]	% of cropland around target cell	Landsat Archive	Yearly	–	Indicates lack of resources for predators in given habitat modification
Water_Dist	Distance to water	Landsat Archive	Once	–	Indicates accessibility to water which is an important resource (Hatten, Averill-Murray, & Van Pelt, 2005).
%Edge_Forest	% of edge forest around target cell	Landsat Archive	Yearly	–	Indicates potential suboptimal resource availability due to edge effects
Annual_Temp	Annual average temperature	ClimateSA v1.12 http://tinyurl.com/ClimateSA	Period average	–	Temperature is a physical limiting factor for several elements of biodiversity, which may include resources for jaguars, and varies widely in the Chaco
Annual_Prec	Annual precipitation	ClimateSA v1.12	Period average	+	Indicates productivity of the system and water availability
Hunting-related variables					
Dens_2ryRoads	Secondary road density at 30 km radius	OpenStreetMap and digitalization	1985, 2000, 2013	–	Indicates concentration of secondary roads, which indicates accessibility to remote areas, while less affected by higher detectability of jaguars
Dist_ForestBorder	Distance to forest border from inside the forest	Landsat Archive	Yearly	+	Indicates both accessibility to the forest by hunters from outside and likelihood of contact of predators with humans as predators approach the forest edge
Cost_dist	Cost distance surface from all cells to towns through primary roads	OpenStreetMap and digitalization for roads, SEDAC for towns	1985, 2000, 2013	+	Indicates the lowest cumulative travel cost from any given cell in the study area to the nearest town. A higher cost distance means less accessibility and presumably less hunting risk. The cost distance analysis weights Euclidean distance by a cost surface. As the input cost surface, we assigned values of 1, 2 and 3 to three categories of primary roads ("motorway," '"trunk" and "primary," respectively) and 10 to all the remaining cells. The output values are in cost units, rather than geographic units
Dist_2ryRoads	Euclidean distance to secondary roads	OpenStreetMap	1985, 2000, 2013	–	Indicates accessibility to relatively remote areas by hunters, but secondary roads are also used by jaguars for travelling, which may increase their detectability
Dist_Grass	Euclidean distance to grasslands	Landsat Archive	Yearly	+	Indicates accessibility of larger numbers of people to the surrounding predators' habitat
%Grassland [a]	% of grasslands around target cell	Landsat Archive	Yearly	–	Indicates likelihood or hunting by persecution due to perceived or actual risks of livestock loses to predators

[a]Variables were calculated for different scales (3, 7, 11 km radius). [b]Yearly means layers for 1985 and for each year from 2000 to 2013.

the drastic expansion of industrialized agriculture in the region. Specifically, we explored the following research questions:

1. How has the extent and distribution of core and sink jaguar habitat changed between 1985 and 2013 across the Chaco?
2. Which factors, habitat loss or threat of hunting, were more important in driving jaguar habitat change in the Chaco?
3. How are remaining core habitat areas distributed among the three Chaco countries and inside vs. outside protected areas?

2 | METHODS

2.1 | Study region

The Gran Chaco (Figure 1) is the largest continuous tropical dry forest ecoregion in the world, at 1.1 million km² (Grau, Gasparri, & Aide, 2008; Olson et al., 2001), extending across Argentina (60%), Paraguay (28%) and Bolivia (11%). Temperature decreases with latitude, with tropical climate in the north and subtropical climate in the south (annual temperature: 22°C, min: <0°C, max: >50°C). Rainfall ranges from >1,200 mm/year in the eastern wet Chaco to <400 mm/year in the western dry Chaco, with >70% of rainfall concentrated during the summer months (Prado, 1993). The Chaco harbours high biodiversity, containing more than 50 distinct vegetation types and more than 150 mammal species, as well as 500 birds, 120 reptiles, 100 amphibians and 3,400 plant species (Nori et al., 2016; TNC, FVS, FDSC & WCS, 2005). However, only 9.1% of the Chaco is currently under protection (43.1% in Argentina, 40.6% in Bolivia and 16.2% in Paraguay; Nori et al., 2016).

Land use change in the Chaco has been rampant over the last two decades, due to the expansion of large-scale cattle ranches and agri-business crops (Baumann et al., 2017). Between 1985 and 2013, >20% of the Chaco forests (142,000 km^2) were converted to grasslands and croplands, with deforestation rates increasing across the Chaco countries, especially since 2000 (Baumann et al., 2017), reducing biodiversity over wide areas (Torres, Gasparri, Blendinger, & Grau, 2014). Additionally, overhunting is causing widespread defaunation, particularly of larger mammals (Altrichter, 2005; Periago et al., 2014). The Chaco's large predators, especially the jaguar and puma (*Puma concolor*), are often killed, mainly by subsistence and commercial ranchers due to real or perceived risk of attacks on livestock (Altrichter et al., 2006; Arispe, Rumiz, Venegas, & Noss, 2009; Quiroga et al., 2014). Jaguars historically occupied the entire Chaco, but their range has declined significantly during the last century (Altrichter et al., 2006; Cuyckens et al., 2017; Rumiz et al., 2011). Two Jaguar Conservation Units (JCU), the Gran Chaco JCU in the north and the Chaco JCU in the centre, and corridors to connect them, have been proposed for the Chaco to protect important jaguar populations, (Rabinowitz & Zeller, 2010; Zeller, 2007). Land use change, however, is increasingly reducing habitat inside and connectivity among them (Piquer-Rodríguez et al., 2015; Thompson & Velilla, 2017).

2.2 | Habitat modelling

To model habitat suitability, we used maximum entropy modelling, using MAXENT version 3.4.1 (Phillips, Anderson, Dudik, Schapire, & Blair, 2017). This machine-learning approach typically outperforms parametric algorithms (Elith & Leathwick, 2009; Elith et al., 2011) and has been used successfully both for developing time-calibrated habitat models (Kuemmerle et al., 2012; Sieber et al., 2015) and core/sink habitat models (Bleyhl et al., 2015). To prevent overfitting, we only used quadratic and hinge features and a regularization multiplier of 1 (Elith et al., 2011; Kuemmerle et al., 2012; Merow, Smith, & Silander, 2013). To assess the robustness of our models, we ran 10-fold cross-validation and assessed variable importance through a jackknife estimation of variable contribution (Phillips & Dudík, 2008). We compared alternative habitat models using area under the curve (AUC) values.

Maxent requires occurrence and background data. As occurrence data, we used 741 confirmed jaguar records from across the Chaco from 1985 to 2013 from the authors' own published and unpublished work, and other databases (Supporting Information Table S1). To reduce potential sampling bias, we applied spatial filtering by randomly selecting one occurrence record within a radius of 12 km (i.e., 452 km^2), representing average female jaguar home range sizes in the region (Giordano, 2015; McBride & Thompson, 2018). We assigned each record to the closest focal year (1985, 2000 or 2013). This left 386 records for our analysis, 79, 189 and 118 records for the periods centred around 1985, 2000 and 2013, respectively (Figure 1). As background points, we created 10,000 random locations within the minimum convex polygon around all occurrences plus a 200-km buffer within the Chaco, to represent a conservative area of a priori expected jaguar range (Merow et al., 2013). To sample the predictor conditions throughout the study period, we randomly assigned a year between 1985 and 2013 to each background point, with half of the points assigned to a year in 1985–2000 and half of the points assigned to a year in 2001–2013). We then matched each occurrence record and background point with the predictor variable values from the closest year with available data (see Table 1; Sieber et al., 2015).

Our habitat modelling consisted of two steps (Figure 2). We generated one time-calibrated habitat model based on resource predictors only and a second time-calibrated habitat model based on hunting threat-related predictors only. We then projected each model to the predictor conditions of 1985, 2000 and 2013 in order to generate two habitat suitability maps (one per model) for each time period. Using time-calibrated models guarantees consistency as differences in the resulting maps between years can only be due to changes in predictor conditions over time, because model parametrization and the sample of occurrence and background points remain unchanged.

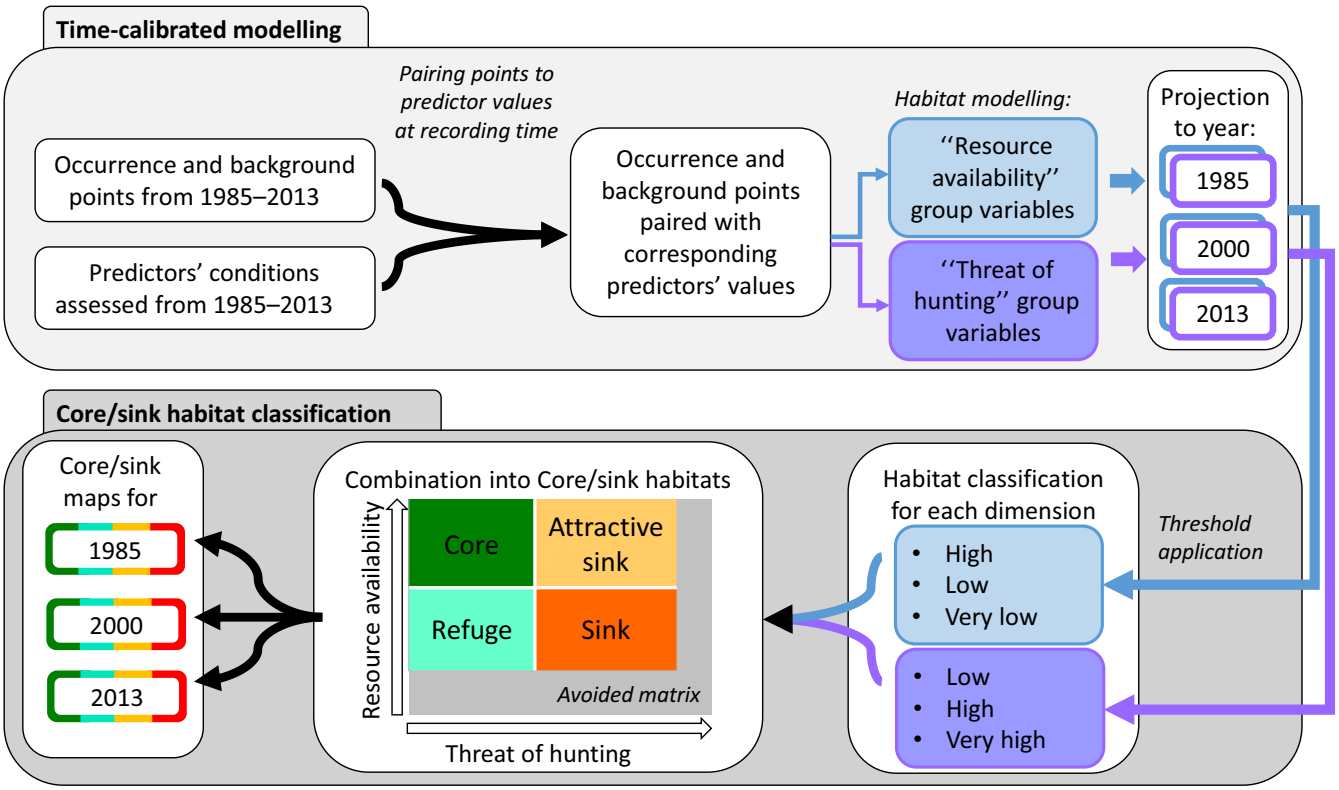

FIGURE 2 Flowchart of the habitat modelling approach. We first matched occurrence points with the predictor conditions from when occurrences were recorded. We then ran two time-calibrated habitat models, one characterizing resource availability and one characterizing hunting threat. Projecting these models into space and overlaying them yielded a single core/sink habitat map for each time period

Second, to identify core/sink habitat, we first classified each of the two resulting maps per time period (suitability in relation to resource availability and hunting threats) into the three habitat quality levels, indicating high, low and very low resource availability, and very high, high and low hunting threats (Figure 2). We did so using the lower 5% quantile of predicted habitat values at occurrence locations and the maximum sensitivity plus specificity value as thresholds (Bleyhl et al., 2015; Liu, White, & Newell, 2013). We then overlaid the resulting categorical maps for both models to produce core/sink habitat maps for each year (Figure 2). The resulting maps contained an *avoided matrix* (very low resource availability or very high mortality risk) and four habitat categories: *core areas* (high resource availability and low hunting threat), *refuges* (low resources but safe), *attractive sinks* (high resources but risky; Figure 2) and *sinks* (low resources and risky; Bleyhl et al., 2015; De Angelo et al., 2013; Naves et al., 2003).

2.3 | Predictor variables

As explained above, we used two groups of predictor variables, one variable group related to resource availability and one variable group related to direct threat of hunting by humans (Table 1). We produced predictor variable as raster layers at 1-km² resolution for multiple times between 1985 and 2013 for the entire Chaco ecoregion plus a 30-km buffer to integrate potentially influencing conditions from neighbouring ecoregions. We produced land use/cover variables (forest, grasslands and croplands; Baumann et al., 2017) for 1985 and yearly from 2000 to 2013 by assigning the year of land use conversion from Hansen et al. (2013) to the land use category of 2013 from Baumann et al. (2017). We selected the final list of predictors after excluding other potential variables that were highly correlated ($r > 0.75$), dropping the variable with less explanatory power based on the initial jackknife analysis (Supporting Information Figure S1).

The final resource-related predictors were *%Forests*, *%Cropland*, *%Edge_Forest*, *Annual_Prec*, *Annual_Temp* and *Dist_Water* (Table 1). We generated *%Edge_Forest* through an MSPA analysis considering a 1-km forest edge (Soille & Vogt, 2009). We derived the average climate predictors (*Annual_Prec*, *Annual_Temp*) throughout the study period using the software ClimateSA v1.0 (Hamann, Wang, Spittlehouse, & Murdock, 2013). The final hunting threat-related predictors included *Cost_dist*, *Dist_2ryRoads*, *Dens_2ryRoads*, *Dist_ForestBorder* and *%Grassland* (Table 1). We considered *%Grasslands* here because virtually all grasslands are used for livestock ranching in the Chaco and are thus areas where predator persecution takes place (Altrichter et al., 2006; Baumann et al., 2017; Quiroga et al., 2014). We reconstructed primary and secondary road networks for 1985, 2000 and 2013 from OpenStreetMap.org, historical road atlases and historical imagery in Google Earth. Preliminary model runs revealed a peaked response between distance and habitat suitability. We limited distance to roads, cost distance to towns and *%Forest*

to maximum suitability values for distances beyond these peaks, as declining habitat suitability for remote areas is ecologically not meaningful (see Table 1).

Because habitat selection of wide-ranging species occurs at various spatial scales, we systematically compared models where our land cover variables were summarized at different scales to assess the scale sensitivity of our results (De Angelo et al., 2013). We sampled *%Forest*, *%Cropland* and *%Grassland* within the 1-km^2 target cell and then in the neighbouring cells at radii lengths of 3, 7 and 11 km (i.e., areas of 1, 28, 154 and 380 km^2, respectively.), which represent extents spanning from daily movement patterns to complete female home ranges (McBride & Thompson, 2018).

2.4 | Assessing jaguar habitat patterns in the Chaco

We evaluated changes in core areas and attractive sinks across time per country, as well as inside and outside protected areas (from The World Database on Protected Areas—https://www.protectedplanet.net/). We also assessed habitat patterns inside the proposed Jaguar Conservation Units and Jaguar Conservation Corridors (Rabinowitz & Zeller, 2010; Zeller, 2007). Additionally, we gathered 28 independent records of killed jaguars from the authors' work, not used as occurrence records in our model, and compared them with our core/sink habitat maps. We expected to find most kill sites in or close to attractive sinks and sinks. Finally, we evaluated the extent of overlap of jaguar habitat with smallholder ranches (plus a 5-km buffer, which is equivalent to their footprint of influence (Altrichter et al., 2006; Quiroga et al., 2014)).

3 | RESULTS

Our habitat modelling approach resulted in robust models and plausible habitat maps. Testing across a range of spatial scales showed that models using land cover variables summarized at an 11 km radius performed best, and we therefore used these in our final models. In the resource availability model, the variables with the highest contribution were *%Cropland*, negatively related to habitat suitability; *%Forest*, positively related; and *Annual_Temp*, peaking at low and high values (Supporting Information Table S2). In the hunting threat model, the most important variables were *Dist_2ryRoads*, positively related to suitability; *Cost_Dist*, positively related; and *%Grassland*, negatively related to habitat suitability (Supporting Information Figure S1). The area under the curve values, as a measure of model performance, was 0.71 for the resource availability model and 0.70 for the hunting threats model (Supporting Information Table S3).

3.1 | Changes in habitat extent from 1985 to 2013

Assessing the resulting habitat maps highlighted that core areas contracted by 33% from 1985 to 2013, losing about 82,400 km^2 (from

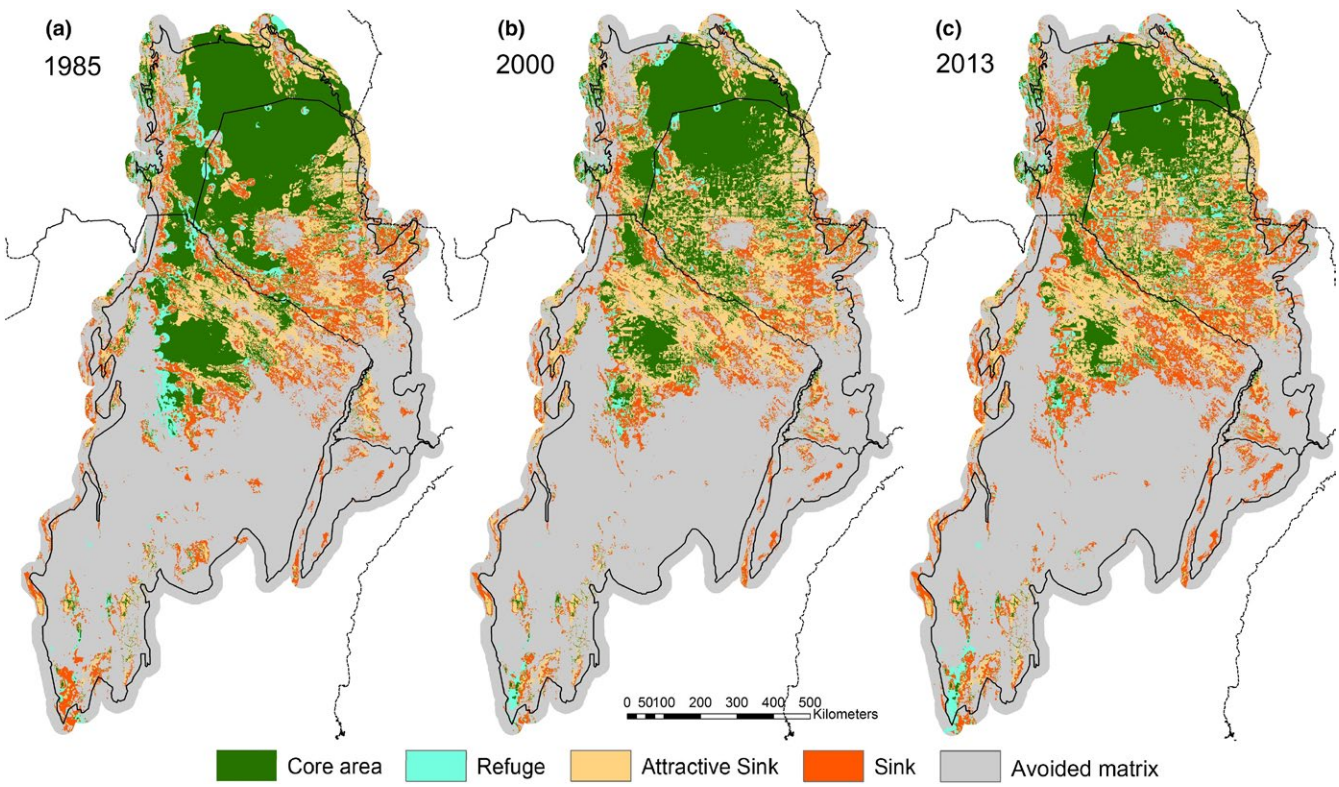

FIGURE 3 Source/sink habitat change for jaguars for (a) 1985, (b) 2000 and (c) 2013 in the Gran Chaco ecoregion. Legend of habitat categories and scale apply to all three maps

TABLE 2 Area covered by (a) high hunting threats, (b) low resource availability and (c) both in the Chaco and within each country. The percentage of sinks in areas covered by either threat indicates the overlap with the other threat

		Area (km^2)				% of sinks in areas of:	
Region	Year	Core	High hunting threat	Low resource availability	Spatial overlap of both threats	High hunting threat	Low resource availability
Entire Chaco	1985	247,423	237,453	167,534	117,658	50%	70%
	2000	208,633	265,892	134,026	100,105	38%	75%
	2013	165,052	302,420	200,586	150,496	50%	75%
Argentina	1985	62,967	111,909	81,464	57,341	51%	70%
	2000	42,755	123,157	65,414	50,482	41%	77%
	2013	28,857	136,143	92,158	72,571	53%	79%
Bolivia	1985	70,791	25,021	21,240	11,826	47%	56%
	2000	60,970	30,208	17,912	11,776	39%	66%
	2013	58,261	33,926	23,915	16,859	50%	70%
Paraguay	1985	113,665	100,523	64,830	48,491	48%	75%
	2000	104,908	112,527	50,700	37,847	34%	75%
	2013	77,934	132,351	84,513	61,066	46%	72%

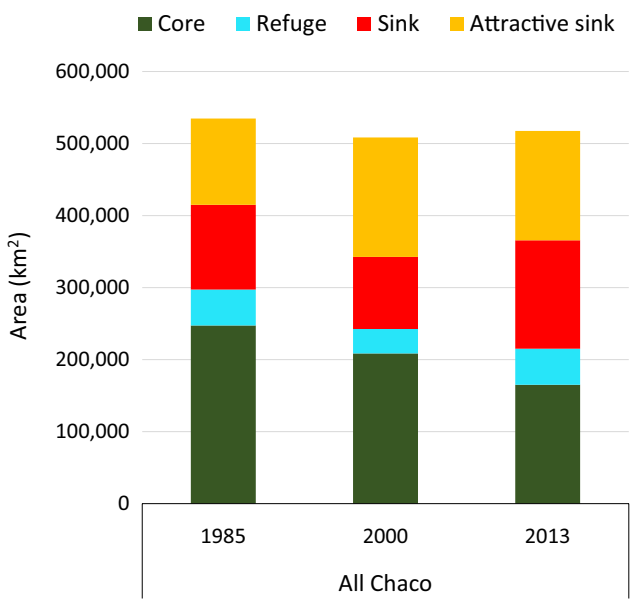

FIGURE 4 Area change of the four habitat types categories for jaguar for 1985, 2000 and 2013 across the entire Chaco

about 247,400–165,100 km^2; Figure 3). Core areas covered 46% of all habitat in 1985 (i.e., all four habitat categories excluding avoided matrix) and 31% in 2013. The estimated average yearly rate of core area loss across all the Chaco was higher between 2000 and 2013 (3,350 km^{2}per year) than between 1985 and 2000 (2,590 km^2 per year). Sinks and attractive sinks, which were mostly limited to the central and eastern Chaco in 1985, expanded by around 27% each, at the expense of core areas, and by 2013 both covered most of the jaguar range in the Chaco (Figure 4). Finally, refuges were not as widespread and their extent remained fairly stable, but their distributions changed markedly since 1985.

Core areas fragmented substantially since 1985 (Figure 3 and Supporting Information Table S4). The large, continuous patch occupying most of the northern Chaco (169,000 km^2) in 1985 split into three main patches by 2013 (with areas of 96,000; 9,300; 5,600 km^2, Figure 3c), with interspersed attractive sinks and sinks. The key patch in the Central Chaco shrank from 27,500 to 9,800 km^2 from 1985 to 2013 (Figure 3). Considering only core area fragments larger than 5,000 km^2—an area that may sustain 50 jaguars based on a density of ~1 individual/100 km^2 estimated in the Bolivian Chaco—suggests an even larger decrease in core area (42% since 1985; Supporting Information Table S4).

3.2 | Relative importance of threats in driving jaguar habitat change

Assessing the relative importance of predictors capturing resource availability versus direct hunting threats in reducing habitat quality showed that although both threats affected an increasing area over time, hunting threats expanded more. In 1985, hunting threats affected 44% (i.e., attractive sinks and sinks) of all remaining habitat area and this share increased to 58% by 2013. Low resource availability (i.e., refuges + sinks) affected 31% of the jaguar habitat in 1985 and 39% in 2013. The total area with hunting threats increased by 27% between 1985 and 2013, while the area with low resource availability increased by 20% (Table 2). The areas where both threats acted in synergy (i.e., sinks) covered 22% of all habitats in 1985 and 29% in 2013 (Figure 4). Half of the areas under hunting threats also overlapped with low resource availability (i.e., in sinks) in 1985 and again in 2013, although the overlap areas had declined to 38% in 2000 (Table 2). Most area (>70%) under low resource availability also overlapped with hunting threats across time (Table 2). The proportion of overlapping threats varied with years and among countries (see Table 2).

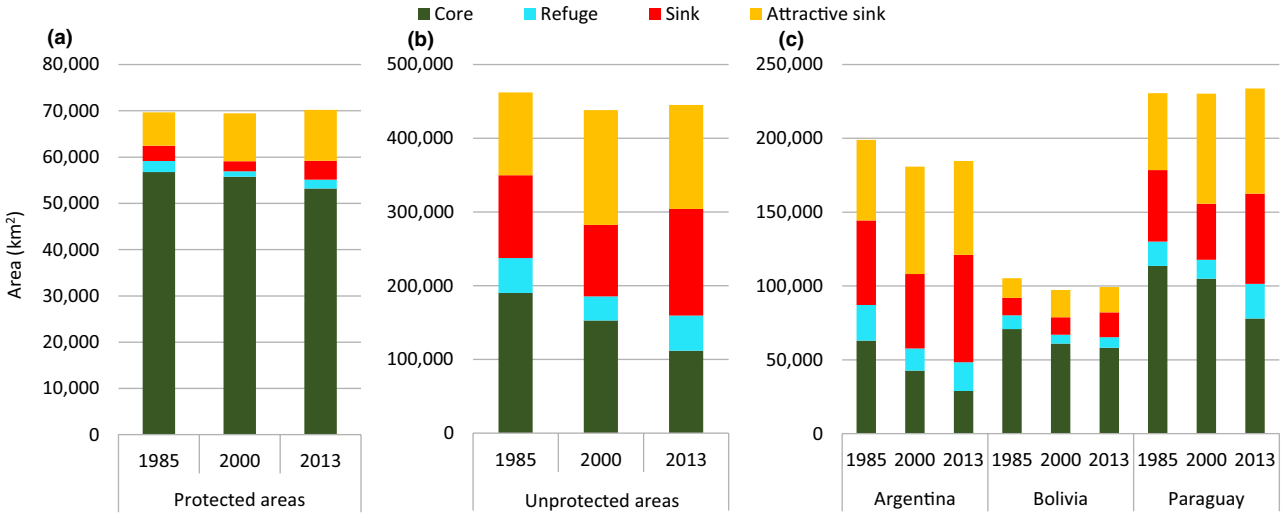

FIGURE 5 Area change of the four habitat categories for jaguar in the Chaco for 1985, 2000 and 2013 in (a) protected areas, (b) unprotected areas and (c) the three Chaco countries

3.3 | Changes in core habitat areas in countries and in protected areas

Country-wise, Paraguay contained the largest extent of core areas (47% in 2013), while Bolivia contained 35% and Argentina 18% (Figure 5c). However, Paraguay also lost most core area (35,700 km^2) from 1985 to 2013 (31% loss since 1985), while Argentina lost 34,100 km^2 (54% loss) and Bolivia 12,500 km^2 (18% loss; Figure 5c). Most remaining core area cells were close to an international border, with a median distance of core area cells to borders of 80 km and 90% of cells within 213 km of a border (Supporting Information Figure S2).

Protected areas in the Chaco overlapping with jaguar habitat were dominated by core areas (75% in 1985 and 70% of protected areas in 2013; Figure 6a,b). Overall, protected areas lost 3,600 km^2 of core area in three decades, 72% of which occurred after 2000. Most of the core area loss inside protected areas occurred due to expanding attractive sinks (50% expansion inside protected areas since 1985; Figure 6a). Protected area size correlated negatively with the proportion of core area loss since 1985 (Spearman's $\rho = -0.53$, $p < 0.005$). By 2013, protected areas maintained 32% (53,200 km^2) of all core jaguar habitat in the Chaco, whilst 68% (111,700 km^2) remained unprotected (Figure 5b). Comparing among countries, core areas halved from 1985 to 2013 in Argentinean protected areas, but decreased only by 1.5% and 10% in Bolivia and Paraguay, respectively (Figure 5c). However, attractive sinks doubled between 1985 and 2013 in protected areas of Paraguay and increased by 16% and 76% in Argentina and Bolivia, respectively. Sinks increased by 76% in Argentina's protected areas and changed little in Bolivia and Paraguay (Figure 6b).

Core areas inside Jaguar Conservation Units contracted by 10% between 1985 and 2013 (from 82,100 to 74,500 km^2; Figure 6c), with attractive sinks almost tripling. Core area contraction was faster in the central Chaco unit, where sinks increased fivefold and attractive sinks doubled, than in the larger northern Gran Chaco unit, where sinks increased by 50% and attractive sinks tripled (Figure 6c,d). Within jaguar conservation corridors, core areas declined by 40% between 1985 and 2013, while attractive sinks increased by 34% and sinks by 45%. By 2013, the corridor connecting the two Jaguar Conservation Units was composed mainly of core and attractive sink habitat, whereas corridors connecting them to units outside the Chaco consisted mainly of sinks and avoided matrix (Figure 6c,d).

3.4 | Validating sink habitats

Our 28 independent locations of jaguars killed by humans were generally inside or very close to predicted areas of threats of hunting (sinks and attractive sinks), with a median distance of 400 m (average distance of 1,400 m; range: 0–17 km, Figure 7). Only one hunting location was farther away from hunting threats areas than 4 km and inside a protected area. Areas with predicted high hunting threats covered 62% of 5-km buffer areas around each hunting point and 65% in 10-km buffer areas (Figure 7, Supporting Information Figure S3). Finally, regarding the overlap of smallholder ranchers and jaguar habitat, all remaining larger core area patches in Argentina overlapped heavily with areas dominated and used by smallholder ranchers (Figure 7, Supporting Information Table S4).

4 | DISCUSSION

Understanding how habitat loss and overhunting interact in space and time to threaten wide-ranging species such as large predators is fundamental to identify appropriate conservation responses at broad scales and across international borders. By for the first time

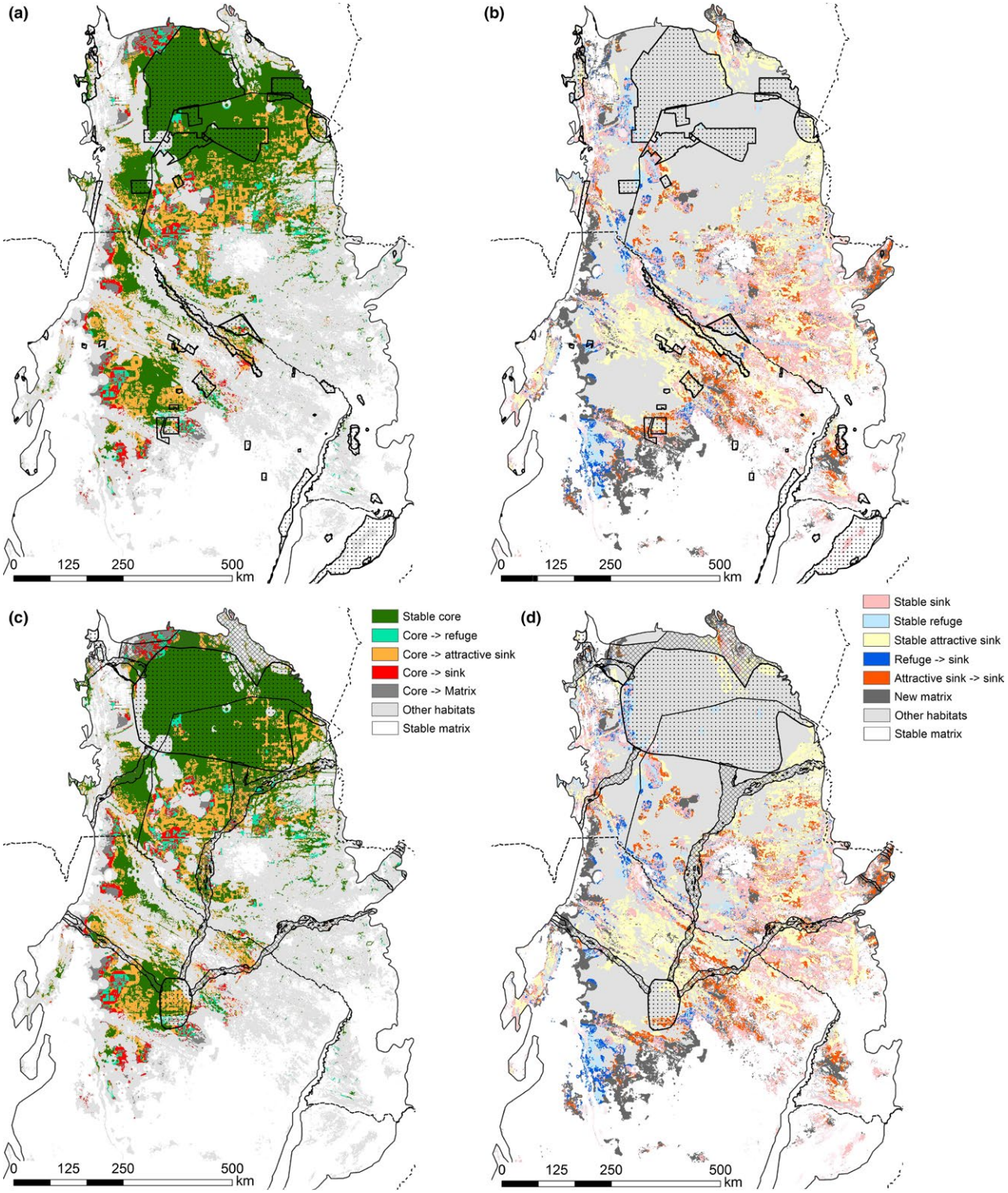

FIGURE 6 Transition between jaguar habitat categories between 1985–2013 in the Chaco. Left: transitions *from* core areas to other habitat categories overlapped with the (a) protected areas and (c) with Jaguar Conservation Units and Corridors. Right: transitions among the other habitat categories (refuge, attractive sink and sink) overlapped with (b) protected areas and (d) Jaguar Conservation Units and Corridors

combining time-calibrated and core/sink habitat modelling, we consistently reconstructed jaguar habitat dynamics over the three-decade time span that saw most of the expansion of intensified agriculture in the Chaco ecoregion. We found that jaguars lost a third of their core areas—an area the size of Austria—from 1985 to 2013, as threats expanded. Hunting threats affected an area 20%

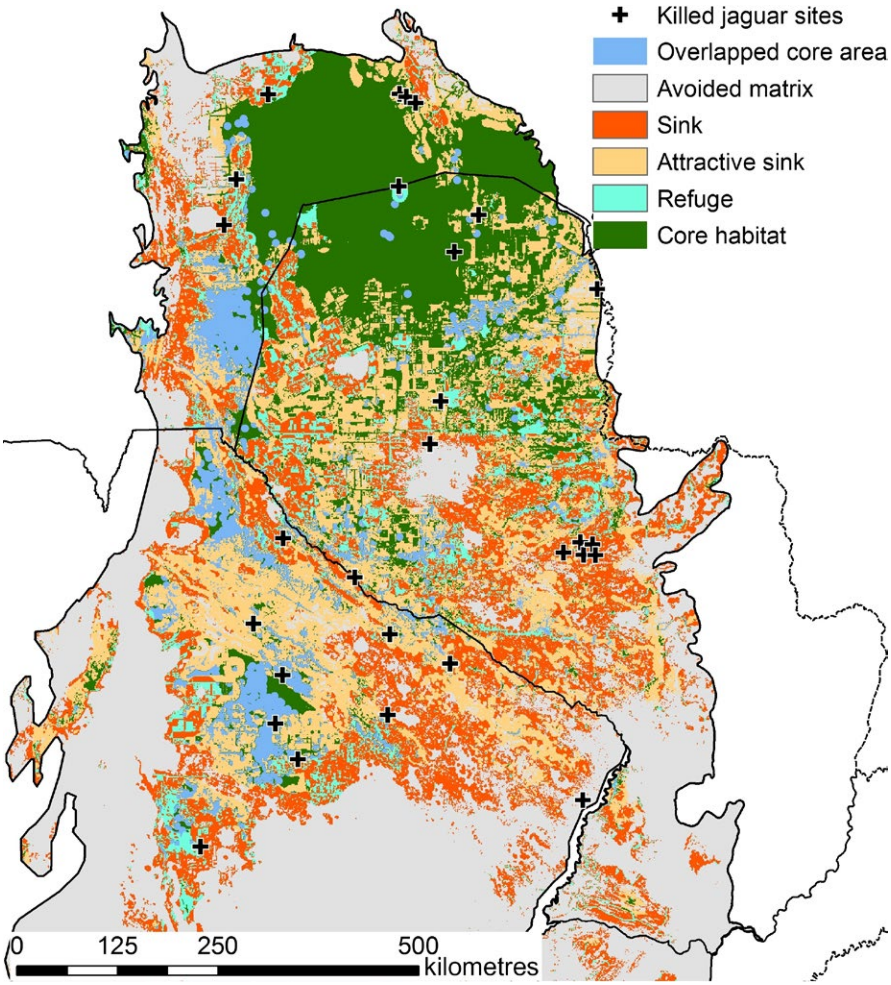

FIGURE 7 Smallholder ranches locations plus a 5-km buffer overlapped with core areas for jaguar in the Chaco in 2013 (shown in blue). Such overlap areas may indicate time-delayed effects on jaguars and potential decline by 2013, and they may thus act as attractive sinks. Locations of jaguars killed by humans (crosses) are also shown

larger than areas affected by deteriorating resource availability, while both threats acted in concert across 29% of the jaguar habitat in 2013. The sinks we identified are likely losing, or may have already lost, jaguar populations, a conclusion that is supported by the fact that most confirmed kill sites of jaguars are located in these sinks. Protected areas lost core areas that turned into attractive sinks as the surrounding areas transformed to agriculture, and larger protected areas lost proportionally less core areas than smaller ones. However, 95% of the total core area loss occurred outside protected areas, two-thirds of all core area in 2013 remained unprotected, and most remaining core areas occurred along borderlands. Beyond documenting the rampant pace at which the top predator of the Gran Chaco is losing its habitat, our study also highlights two major conservation opportunities. First, large expanses of high-quality habitat could be protected in international borderlands through transboundary conservation efforts. Second, jaguar decline can be averted in the extensive attractive sinks by controlling hunting, particularly along corridors connecting core area patches. As agriculture keeps expanding, swift multilateral coordination of conservation action is necessary to avert jaguar's extinction.

Jaguar core area contracted 82,400 km^2 from 1985 to 2013 as habitat loss and hunting threats expanded over the Chaco. Considering that the entire Chaco was suitable habitat until the 18th century (Cuyckens et al., 2017), jaguars had lost 77% of core areas by 1985 and 85% by 2013 (about 920,000 km^2). This is higher than the 48% or 82% range contraction estimated for the entire Americas and for jaguar range outside Amazonia, respectively (de la Torre, González-Maya, Zarza, Ceballos, & Medellín, 2018), and comparable to the highest total range loss for a carnivore species (Ripple et al., 2014). The extirpation from the southern and central Chaco before 1985 likely occurred due to a longer land use history (Altrichter et al., 2006; Baumann et al., 2017; Cuyckens et al., 2017). The increasing core area fragmentation since 1985 may pose a further threat, as jaguar population persistence and genetic diversity are markedly affected by fragmentation (Haag et al., 2010; Zanin, Palomares, & Brito, 2015). Furthermore, jaguars in the Chaco exhibit some of the lowest densities and largest home ranges in the Americas (Giordano, 2015; McBride & Thompson, 2018; Noss et al., 2012; Quiroga et al., 2014). Our results therefore highlight the urgency of managing jaguars in the Chaco as a single population, by protecting the remaining core area patches and ensuring their connectivity along corridors which are currently dominated by hunting threats, particularly between the central and northern Chaco patches (Quiroga et al., 2014; Thompson & Velilla, 2017).

Habitat loss and hunting threats acted together in 29% of all habitats in 2013. As both threats likely synergize in these extensive

and rapidly expanding sinks, jaguars may face higher extirpation risk, if not already extinct (Brook et al., 2008; Naves et al., 2003). This widespread threat overlap may occur because these processes are often associated. For instance, much forest is converted into grazing lands, where jaguars are often killed due to fears of depredation on cattle (Arispe et al., 2009; Baumann et al., 2017; Giordano, 2015; McBride & Thompson, 2018). Similarly, deforestation often accompanies road expansion, which increases hunter accessibility (Benitez-Lopez et al., 2017; Piquer-Rodríguez et al., 2015). Hunting threats expanded faster than deteriorating resource availability and occupied two-thirds of all habitats in 2013. These hunting threats occurred in otherwise resource-rich areas (i.e., attractive sinks), in 29% of the jaguar's Chaco range. This likely occurs because jaguars range widely are often persecuted by ranchers, and their populations are highly susceptible to hunting, even in otherwise suitable forests (Arispe et al., 2009; Jędrzejewski et al., 2017; McBride & Thompson, 2018; Paviolo et al., 2016). Yet, jaguars are also vulnerable to habitat loss (De Angelo et al., 2013; Paviolo et al., 2016), most of which co-occurred with hunting threats in sink areas. Hunting threats also covered a larger area than habitat loss in studies on jaguar in the Atlantic Forest (De Angelo et al., 2013), tiger (*Panthera tigris*) in the India-Nepal border (Kanagaraj et al., 2011) and European bison (*Bison bonaus*) in the Caucasus (Bleyhl et al., 2015), although the opposite occurred for brown bears (*Ursus arctos*) in Spain (Naves et al., 2003).

Protected areas lost less core area than unprotected areas, where 95% of all core area loss occurred. However, hunting threats expanded inside protected areas by 50% as the surrounding landscape changed. Smaller protected areas seemed more susceptible to these changes, losing proportionally more core areas, and becoming increasingly dominated by attractive sinks. Indeed, the largest six protected areas in northern Chaco alone contained >90% of all core area under protection by 2013 and Kaa-Iya National Park in Bolivia alone contained 59%. Furthermore, only two protected areas maintained >5,000 km^2 of core area, an area likely to maintain >50 individual jaguars over 100 years (Paviolo et al., 2016; Zanin et al., 2015). Additionally, two-thirds of core areas remained unprotected in 2013, emphasizing the urgency to expand the protected area network. Protected areas are scattered and cover only 9.1% of the Chaco, with only 6.5% of Argentina's, only 5% of Paraguay's and 32% of Bolivia's Chaco being protected. Several other studies have found that protected area size contributes to conservation effectiveness—particularly for large carnivores—because they are susceptible to threats occurring outside them (Balme, Slotow, & Hunter, 2010; Geldmann et al., 2013; Laurance et al., 2012; Terborgh et al., 2001; Woodroffe & Ginsberg, 1998).

Countries varied in core area lost, with Paraguay and Argentina losing more than Bolivia from 1985 to 2013. These differences may relate to the high pressures of agricultural expansion to produce beef and soybeans in Argentina and Paraguay, while in Bolivia most of the agricultural expansion has occurred in the Chiquitano forest north of the Chaco (Baumann et al., 2017; Gasparri & le Polain de Waroux, 2015). Second, protected area coverage is higher in Bolivia than in Paraguay and Argentina. Our finding that most of the remaining core area occurs along international boundaries suggests important opportunities for protecting large expanses of high-quality jaguar habitat through multilateral coordination. Moreover, these areas provide opportunities for the Chaco countries to achieve 17% effective protection under the Aichi Target 11 to which they are committed (Nori et al., 2016). The Cabrera-Timane National Park in Paraguay, which protects core jaguar habitat while linking larger protected areas in Bolivia and Paraguay, is an excellent example of such cross-border conservation efforts.

Our study represents, to our knowledge, the first application of time-calibrated and core/sink habitat modelling in tandem, which can identify habitat transitions over time and can inform pertinent conservation responses according to the prevalent threat. For instance, we detected that most core area in the Chaco transformed into attractive sinks, which is a major conservation issue necessitating specific conservation responses. Neither these transitions, nor the primary threat turning core areas into sinks and attractive sinks, would have been detected with more traditional modelling approaches. This ability to discern between threats at broad scales is critical for large carnivores given their high, but differential vulnerability to habitat loss and hunting (Benitez-Lopez et al., 2017; Paviolo et al., 2016; Ripple et al., 2014). Our jaguar habitat models are also the first for the Chaco and are consistent with local research and expert-based assessments (Altrichter et al., 2006; Giordano, 2015; McBride & Thompson, 2018; Noss et al., 2012; Quiroga et al., 2014; Rumiz et al., 2011). The congruence between our predicted areas of high hunting threat and the locations of records of killed jaguars furthermore suggest that our core/sink maps are reasonable and can be used for broad-scale conservation planning. Similar approaches helped validate jaguar core/sink maps in the Atlantic Forest (De Angelo et al., 2013).

Our study, however, still contains limitations. First, our presence-only models do not necessarily reflect underlying demographic dynamics, and population studies are needed to confirm population sources and sinks (Naves et al., 2003). Second, our models likely miss time-delayed responses to threats, particularly for predicted core areas in Argentina, which have had a longer land use history than the time span of our study. Local research found that jaguars tend to disappear about 25 years after smallholders settle in, a process which started up to 90 years ago in some areas (Altrichter et al., 2006). Although we had the location of smallholder farms, including this variable in our models did not improve model performance, likely because their overall distribution remained relatively stable over the time period we studied. Information on the age of smallholder ranches would be a very valuable variable, but this information does unfortunately not exist. Assuming that by 2013 core areas cannot overlap with smallholder ranches reduces the extent of core area patches in Argentina and southernmost Bolivia substantially, and some of these areas likely are in fact attractive sinks (Figure 7). Third, additional potential synergies may have escaped our analysis, like the decline of natural prey—a resource—along with the expansion of hunting threats (Benitez-Lopez et al., 2017). Finally,

when increasing the temporal resolution of our land use predictors between 2001 and 2012, we may have missed potential grassland-to-cropland transitions, although such transitions are uncommon in the northern Chaco (Baumann et al., 2017).

Regarding jaguar conservation planning, our reconstruction of core/sink habitat dynamics for the Chaco ecoregion across three decades provides three key insights. First, despite a dramatic contraction, extensive core areas remain, particularly along international boundaries, and they would likely suffice to maintain a viable Chaco jaguar population in the long run if these areas were protected. Second, most core areas that were lost were replaced by attractive sinks and sinks, indicating that direct hunting threats can spread more rapidly for large carnivores in changing landscapes than the actual expansion of the frontier. In the extensive attractive sinks, opportunities remain for reversing jaguar decline through enhanced control of hunting and improving ranchers' tolerance towards jaguars, particularly along corridors connecting core areas and inside or near protected areas, particularly smaller ones. Such coexistence strategies should focus on understanding the relationships between diverse local actors and jaguars to implement context-specific, culturally pertinent response strategies (Pooley et al., 2017). Third, larger protected areas seem more effective than smaller ones and unprotected areas at maintaining jaguar core areas. Considering that the extent of protected areas is low, and substantially below the Aichi target 11 of 17%, the large expanses of remaining core areas along international boundaries provide opportunities to expand protected area networks through multilateral coordination (Montesino Pouzols et al., 2014). Policymakers from the three Chaco countries should take action and jointly define coordinated priorities, informed by broad-scale analysis such as this study. As one of the most charismatic species of the Neotropics, conservation planning and implementation for the jaguar could help conserve several other components of biodiversity in the Chaco, a global hotspot of biodiversity loss (Hansen et al., 2013; Nori et al., 2016; TNC, FVS, FDSC & WCS, 2005; Torres et al., 2014). Such multilateral efforts should also include ensuring effective connectivity between core areas patches, particularly between those in Argentina and Paraguay. Additionally, these efforts require a re-assessment of jaguar conservation corridors as remaining core areas outside them could be incorporated. Given the extraordinary pace with which jaguar core habitat has been shrinking, and the continued pressures from expanding cattle ranching and soybean cultivation, coordinated efforts should be swiftly put into place while opportunities remain. Our work shows that considering the interactions between land use change and hunting threats on the habitat of a top predator over time can help to discern the resulting geographical patterns of threat and thus to define broad-scale, multilateral conservation planning.

ACKNOWLEDGEMENTS

We are grateful to H. Robinson, H. Castillo, the Panthera Foundation, S.P.E.CI.E.S. and Guyra Paraguay for sharing jaguar occurrence records. We thank M. Piquer-Rodriguez, B. Bleyhl and C. Levers for insightful discussions and help with preparing predictor variables. We gratefully acknowledge funding by the German Ministry of Education and Research (BMBF, project PASANOA, 031B0034A) and the German Research Foundation (DFG, project KU 2458/5-1). Two reviewers and associate editor George Stevens provided thoughtful and very constructive feedback, and we are grateful for their efforts.

DATA ACCESSIBILITY

The core/sink habitat maps are available via Humboldt University Berlin's cloud storage system (HU-Box): https://box.hu-berlin.de/d/650d96b0b5eb4f0fa6e8/.

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BIOSKETCH

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Author contributions: A.R.M. and T.K. conceived the ideas; A.R.M., R.T., A.J.N., A.J.G., V.Q., J.J.T., M.B., M.A., R.M., M.V. and R.A. collected the data; A.R.M. analysed the data; A.R.M. led the writing with substantial contribution from T.K.; all authors reviewed the manuscript critically and approved the final version.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Romero-Muñoz A, Torres R, Noss AJ, et al. Habitat loss and overhunting synergistically drive the extirpation of jaguars from the Gran Chaco. *Divers Distrib*. 2018;00:1–15. https://doi.org/10.1111/ddi.12843