





## RESEARCH ARTICLE

## OPEN ACCESS

# Hunting and Habitat Destruction Drive Widespread Functional Declines of Top Predators in a Global Deforestation Hotspot

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## ABSTRACT

**Aim:** We investigated the effects of habitat destruction and hunting on the functional decline of top predators, specifically jaguar and puma, in the Gran Chaco.

**Location:** The 1.1 million km<sup>2</sup> South American Gran Chaco.

**Methods:** We used spatially explicit, individual-based models for jaguars and pumas, incorporating detailed information on habitat suitability and hunting pressure. We parameterized our models with literature data and calibrated them through a Delphi expert-elicitation process. We simulated population trajectories under a hypothetical, threat-free, baseline versus different threat scenarios.

**Results:** Under combined threats of hunting and habitat loss, jaguar and puma populations declined by 88% and 80%, respectively, compared to range contractions of 48% and 35%, respectively. Both species remained regionally viable, particularly due to large protected areas, which acted as population sources but were surrounded by strong sinks. We observed a widespread weakening of the top carnivore guild function, with at least one species extirpated across 67% of the Chaco and strong declines (> 80%;

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considered here as functional loss) for both species concurrently across 61% of their area of historical co-occurrence. Hunting was a much stronger driver of population declines (88% and 77% for jaguars and pumas, respectively) compared to habitat destruction (26% and 22%).

**Main Conclusions:** Large predators play key functional roles in ecosystems. Our findings reveal that these functions can be lost over vast areas due to the combined effects of habitat destruction and hunting, with functional loss extending far beyond the areas of species' extirpation. Very large protected areas, like Kaa-Iya in Bolivia, are crucial for maintaining viable populations of top predators, highlighting the pressing need for increased protection and connectivity in the Chaco to prevent further trophic downgrading. More generally, our research underscores the value of spatially detailed, mechanistic models for disentangling the complex dynamics of multiple threats on ecological functioning at broad scales.

## 1 | Introduction

The ongoing biodiversity crisis, driven by multiple anthropogenic threats, leads to both local and global extinctions (Díaz et al. 2019; Jaureguiberry et al. 2022). While much research focuses on these extinction events (e.g., Ceballos, Ehrlich, and Dirzo 2017; Wolf and Ripple 2017), it is crucial to recognise that populations decline gradually well before extinction occurs (Dirzo et al. 2014). These declines are ecologically significant, as dwindling populations play weakened functional roles within ecosystems (Terborgh et al. 2001; Ordiz, Bischof, and Swenson 2013; Valiente-Banuet et al. 2015). Early detection of population declines is therefore important to design and implement conservation actions to halt these declines before it is too late (Pires et al. 2023).

Large carnivores are particularly vulnerable to human pressures, as their natural rarity and slow life histories make them sensitive to disturbances (Treves and Karanth 2003; Cardillo et al. 2005; Ripple et al. 2014). Additionally, their extensive home ranges and areas of dispersal often bring them into human-dominated areas, where they are often persecuted in response to real or perceived threats to livestock or even humans. Consequently, large carnivores have been extirpated from many regions, especially in the tropics (Wolf and Ripple 2017). Such declines are important because large carnivores exert strong top-down functional effects within ecosystems. They influence prey abundance through direct predation and can indirectly alter prey behaviour and habitat use through 'landscapes of fear' (Estes et al. 2011; Ripple et al. 2014). This, in turn, can cascade through the ecosystem affecting disease dynamics, carbon cycles, nutrient cycling, and overall ecosystem function (Estes et al. 2011; Ripple et al. 2014; Malhi et al. 2016). While most research has focused on the consequences of carnivore extinctions, these regulatory roles can be severely weakened or lost before extinction, as carnivore populations dwindle (Johnson, Isaac, and Fisher 2006; Ordiz, Bischof, and Swenson 2013; Dorresteijn et al. 2015). Moreover, the decline of multiple large carnivore species can diminish the overall regulatory role of the entire top predator guild (Sih, Englund, and Wooster 1998). However, assessing such multi-species population trajectories, and identifying areas where declines may lead to functional loss, remains a challenge—especially in rapidly changing areas like global deforestation frontiers (Dalerum et al. 2009; Wolf and Ripple 2017).

Habitat destruction and hunting are the primary threats to large carnivores, particularly in the tropics, where these

threats often co-occur, but they affect populations differently (Ripple et al. 2014). Habitat destruction generally reduces resource availability (such as prey and shelter) indirectly affecting reproduction and survival, while hunting directly increases mortality, indirectly affecting reproduction (Chapron et al. 2008). These threats have a complex spatial distribution: landscapes impacted by deforestation are not always unsuitable for large carnivores, and they can persist in human-dominated areas if not actively persecuted (Morato, Connette, et al. 2018; Romero-Muñoz et al. 2019; Nanni et al. 2023). As a result, large carnivores might be safe in some parts of their range and face local extirpation in others (Jędrzejewski et al. 2018). This complexity leads to source-sink dynamics (i.e., locations with population surpluses vs. deficits) in large carnivore populations (Pulliam 1988). Identifying such population sources and sinks is crucial for developing targeted conservation interventions that aim to reduce mortality rates in population sinks and protect population sources. However, such identification is challenging over broad scales as the impact of different threats on demographic parameters, like fecundity, mortality, and movement, varies across space according to the threats present and their intensity. Large-scale telemetry can derive multiple population parameters (e.g., mortality rates over space, and dispersal distances) for such detailed identification of sources and sinks (Lamb et al. 2020; Nisi et al. 2023), but such assessments are often costly or unfeasible in tropical contexts (Gilroy and Edwards 2017). Other approaches have used habitat suitability models (De Angelo et al. 2013; Romero-Muñoz et al. 2019). Yet, these often neglect crucial biological processes like reproduction, survival, movement, and connectivity (Zurell et al. 2022). A more mechanistic approach is needed to assess the impacts of these threats on key functional groups across both space and time.

Spatially explicit, individual-based models (IBMs) offer a powerful tool for such source-sink assessments. IBMs explicitly simulate the movement, survival, reproduction, and interactions of individuals within a population (Schumaker et al. 2014). Recent IBM developments allow for a nuanced, spatially explicit representation of multiple threats acting individually or simultaneously (Lurgi et al. 2015; Schumaker and Brookes 2018). This permits more comprehensive insights into their combined impacts where they overlap compared to previous broad scale model-based assessments. Previous approaches used correlative methods (De Angelo et al. 2013; Romero-Muñoz et al. 2019; Lee-Yaw et al. 2022) and assumed specific interaction types where threat footprints overlapped (Darling and Côté 2008) or employed mechanistic models with

uniform threat levels across space (e.g., Chapron et al. 2008; Heurich et al. 2018; Bleyhl et al. 2021). While still dependent on input spatial layers and parameter data quality, the new generation of IBMs can assess spatially variable threats (Schumaker and Brookes 2018), opening up opportunities for a mechanistic understanding of threat geographies and their impact on ecological functioning.

Here, we apply a spatially explicit IBM framework to explore how habitat destruction and hunting affect population dynamics of the jaguar (*Panthera onca*) and puma (*Puma concolor*) across the 1.1 million km<sup>2</sup> Gran Chaco in South America. The Gran Chaco is recognised as a global deforestation hotspot, primarily driven by the expansion of soy agriculture and cattle ranching (Baumann et al. 2022; Buchadas et al. 2022). Against this backdrop, habitat destruction and hunting are key threats that contribute to widespread defaunation in the region (Periago, Chillo, and Ojeda 2014; Romero-Muñoz, Benítez-López, et al. 2020). Jaguar and puma, the top predators of the Gran Chaco and broader Neotropics, have suffered major range and population declines both within the Chaco and elsewhere (Quiroga et al. 2014; Wolf and Ripple 2017; Thompson et al. 2022; WWF 2022). Despite their ecological similarities, pumas tend to be smaller, to prey on smaller species, to be socially subordinate to jaguars, to use a wider diversity of habitats, and to be more resilient to anthropogenic changes (De Angelo, Paviolo, and Di Bitetti 2011; Quiroga et al. 2014; Elbroch and Kusler 2018). We parameterized IBMs for each species using a literature review and a Delphi process with regional experts. To assess the impacts of anthropogenic threats, we developed a baseline representing historical conditions without habitat destruction or hunting and compared it to scenarios representing the current distribution and intensity of these threats. We address three main research questions:

- What is the current population size of jaguars and pumas in the Chaco and where are the current population sources and sinks?
- Where have top predator declines potentially led to a decline of their functional role?
- What are the relative contributions of habitat destruction and hunting to these declines?

## 2 | Methods

### 2.1 | Study Area

The Gran Chaco region (hereafter: Chaco) is an extensive tropical and subtropical dry forest and savanna region spanning Argentina, Bolivia, and Paraguay. The Chaco consists of the Dry Chaco and Humid Chaco ecoregions (Olson et al. 2001). Climatically, the region transitions from tropical in the north to subtropical in the south. Precipitation is seasonal, ranging from over 1200mm/year in the east to less than 400mm per year in the drier west, north, and south (Prado 1993). The Chaco's natural vegetation is dominated by xerophilous forests, interspersed with gallery forests and savannas (Navarro and Maldonado 2002). The Chaco hosts diverse ecological

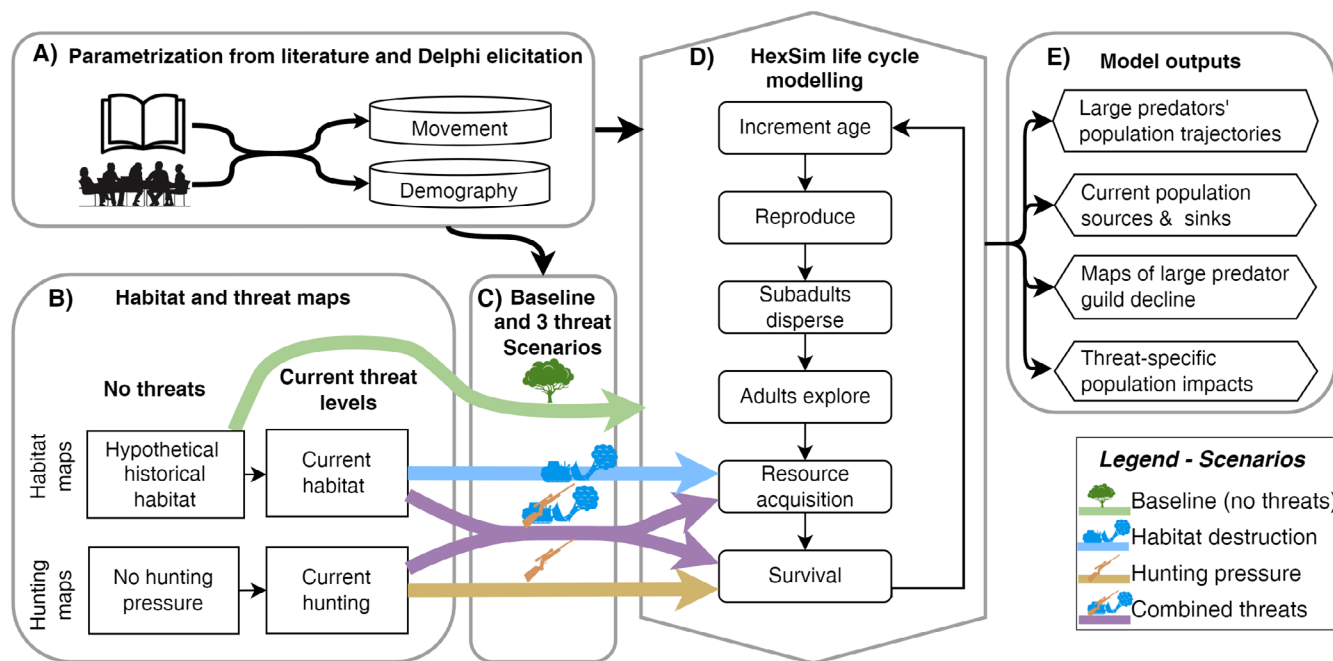
communities, including 150 mammals, 500 birds, 100 amphibians and reptiles, and 3000 plant species (TNC et al. 2005).

The Chaco has undergone extensive land-use change, driven first by indigenous use practices for millennia followed by more recent criollo people who initiated subsistence ranching about 200 years ago. Recent decades have seen rapid commodity-driven agricultural expansion, primarily for beef and soybean production (Baumann et al. 2022). This has resulted in a conversion of about 25% of the Chaco to agriculture (Baumann et al. 2017). Moreover, hunting is widespread across the Gran Chaco, practiced by a range of actors, including indigenous peoples, smallholder subsistence ranchers, large-scale ranchers, and soybean producers, who hunt wildlife for subsistence, leisure, or retaliatory reasons (Altrichter 2005; Camino et al. 2018; Saldivar-Bellassai et al. 2021). Unsustainable hunting practices likely contribute to declines of multiple species (Periago, Chillo, and Ojeda 2014; Romero-Muñoz, Benítez-López, et al. 2020). Of particular concern are retaliatory killings of large carnivores in response to livestock depredation, constituting a main cause of large carnivore mortality (Quiroga et al. 2014, 2016; McBride and Thompson 2018). However, despite the prevalence of these threats, less than 10% of the Chaco is currently protected.

### 2.2 | Model Structure

We used the spatially explicit individual-based modelling (IBM) platform HexSim to simulate the life history, movement, and interactions of jaguars and pumas with their environment (Figure 1). HexSim is a generic, flexible IBM platform that permits the incorporation of multiple spatial layers describing environmental conditions, such as habitat or threats (Lurgi et al. 2015; Schumaker and Brookes 2018). HexSim simulates individuals of a population through a set of user-defined sequences of life cycle events, which are defined by multiple demographic and movement parameters and can change according to varying environmental conditions (Figure 1).

The model's basic spatial structure is defined by a habitat suitability map for each species, which influences resource use, movement, and reproduction of the simulated individuals. We used Maxent (v3.4.1) to model habitat suitability, incorporating species' presence points, land cover, and climate variables from 1985 to 2015 (Phillips et al. 2017; Elith et al. 2010). We used a time-calibrated model that enables utilising long-term presence data to reconstruct habitat suitability consistently over time, permitting assessing changes in habitat due to environmental changes (Nogués-Bravo 2009). To parameterize these models, we matched each presence point with its corresponding predictor values for the specific year it was recorded. Additionally, we created 10,000 background points with a similar spatial distribution to the presence points, assigned them random years, and extracted their corresponding predictor values. We assessed model robustness and the predictive performance using 10-fold cross-validation with area under the curve values. In the absence of historical, pre-anthropogenic threat land-cover maps, we developed for each species a habitat suitability model using exclusively climate variables to establish a baseline habitat map comparable to the current one. To maintain temporal consistency, we assigned to the baseline map the highest suitability



**FIGURE 1** | Modelling framework to assess the changes in large predator populations in the Gran Chaco. (A) Demographic and movement parameters based on the literature search and expert elicitation. (B) Habitat suitability and hunting pressure maps for a hypothetical historical baseline without threats and for the current level of threats. (C) The threat-free baseline and the threat scenarios (i) only habitat destruction, (ii) only hunting pressure, and (iii) both threats together, which directly affected parameters related to specific life cycle events (as shown with coloured arrows) but which also have indirect effects on other parameters in other life cycle events. (D) Simulation of scenarios through IBM implemented in HexSim through a life cycle sequence. (E) Four main model outputs to answer each research question.

value for each pixel by comparing the current and baseline habitat suitability maps. This approach is appropriate for the Chaco, a relatively flat region where most natural habitats within the region are potentially suitable for jaguar and puma, rendering climate the primary historical constraint to their distribution.

To depict current threat levels, we projected the habitat suitability model incorporating climate and land cover variables to the land cover conditions of 2015. To model species-specific hunting pressure across space, we employed the hunting pressure model from Benítez-López et al. (2019), trained on 1945 ratios of mammal abundance change due to hunting across the Neotropics. Predictors were human population density, species body mass, and distance to hunter access points (identified by regional experts to be towns, roads, forest homesteads, and cattle pastures). The two-stage mixed model uses a binomial model to distinguish between extant and locally extinct species and a Gaussian model for abundance changes due to hunting. This resulted in a hunting pressure index, which we inverted to represent survival probability due to hunting pressure (1 = survival unaffected by hunting and 0 = total survival declines due to hunting). We min-max transformed this range by applying a minimum survival under high hunting levels identified for each predator (see Table 1). As our baseline assumed no hunting, we excluded the layer and interaction event of survival and hunting in the IBM model. For compatibility with HexSim, we converted all spatial layers to hexagons of 25 km<sup>2</sup> each, resulting in 43,390 hexagons covering the region. This resolution is appropriate for modelling jaguar and puma, given their large home ranges (70–800 km<sup>2</sup>) (McBride and Thompson 2018; Thompson, Martí, and Quigley 2020), while it allows for flexible home

range adjustments in response to changing threats in portions of ranges and provides enough detail to inform conservation planning.

### 2.3 | IBM Model Parameterization

We obtained demographic and movement population parameters at various threat levels from across species' ranges from the literature for jaguar (Desbiez et al. 2012; De Carvalho-Jr and Desbiez 2013; Watkins et al. 2015; Zanin, Palomares, and Brito 2015; McBride and Thompson 2018; Morato, Thompson, et al. 2018; Finnegan et al. 2021; Thompson et al. 2021) and puma (compiled in LaRue and Nielsen 2016; Azevedo et al. 2021). However, information on how parameters vary for different threat levels and potential regional parameter variations for the Chaco was limited. We addressed these data limitations and refined parameterization through a structured Delphi expert elicitation process with 15 regional jaguar and puma experts (Mukherjee et al. 2015). The Delphi technique is an iterative, participatory, anonymous expert process for addressing complex, multi-faceted problems with limited information, while reducing social pressures among respondents (Mukherjee et al. 2015). Each round involved individual experts' comprehensive evaluations, followed by reevaluation based on anonymous peer arguments, ultimately converging to a stable range after three iterations. The process involved three iterative steps: (a) an online survey presenting literature-derived parameter values, soliciting experts' assessment of their applicability to the Chaco context and potential modifications under different threat scenarios and (b) online workshops to discuss parameter values.



**TABLE 1** | Individual population parameters for jaguar and puma used in individual-based models across different threat scenarios. Parameters were derived from the literature and then calibrated for the Chaco and different threats through a Delphi-based expert elicitation. As the model only considers females, reproduction parameters are halved (assuming a 50% male/female ratio) (starting literature values come from: Jaguar: Desbiez et al. 2012; De Carvalho-Jr and Desbiez 2013; Watkins et al. 2015; Zanin, Palomares, and Brito 2015; McBride and Thompson 2018; Morato, Thompson, et al. 2018; Finnegan et al. 2021; Thompson et al. 2021; Puma: compiled in LaRue and Nielsen 2016; Azevedo et al. 2021).

Parameter (units)	Jaguar-values			Puma-values		
	Literature	Baseline	High habitat destruction	Literature	Baseline	High habitat destruction
<b>Demographic</b>						
Litter size max ( <i>Individuals</i> )	1.5–2	1.5	1.5	1.5–1.6	1.5	1.5
Litter size mean ( <i>Individuals</i> )	1	0.75	0.65	1.25	0.75	0.65
Litter size SD ( <i>Individuals</i> )	0.5	0.5	0.5	0.5	0.5	0.5
Senescence age ( <i>Years</i> )	13–14	12	12	12–14	13	13
Max survival Juveniles (%)	0.75	0.7	0.7	0.57–0.7	0.7	0.7
Max survival subadults (%)	0.8	0.8	0.8	0.6–0.8	0.8	0.8
Max survival adults (%)	0.93–0.95	0.95	0.95	0.75–0.95	0.95	0.95
<b>Environmental stochasticity (affects fecundity and survival rates)</b>						
Environmental stochasticity (%)		0.1	0.1		0.1	0.1
<b>Individual range (depends on cumulative suitability across hexagons)</b>						
Maximum range area ( $km^2$ )	25–600	600	600	40–200	200	200
Maximum range span length (km)	115	115	115	50	50	50
Resource targets ( <i>cumulative suitability</i> )		3.56	3.56		2.66	2.66
Minimum suitability per hexagon ( <i>suitability</i> )		0.25	0.25		0.25	0.25
<b>Dispersal and new territory exploration (affects subadults and adults)</b>						
Beginning with dispersal step ( <i>Year</i> )	3	3	3	3	3	3
Maximum number of explorations to stablish territory (#)		2	2		2	2
Maximum path length bounds (km)	200	215	215	70	70	70
Minimum path length bounds (km)	15	16	16	11	11	11
Maximum explored area ( $km^2$ )	750	750	750	250	250	250
Minimum movement autocorrelation (%)		60	60		60	60

(Continues)

TABLE 1 | (Continued)

Parameter (units)	Jaguar-values			Puma-values				
	Literature	Baseline	High habitat destruction	High hunting	Literature	Baseline	High habitat destruction	High hunting
Maximum movement autocorrelation (%)		100	100	100		100	100	100
Multiplier autocorrelation (%)		10	10	10		10	10	10
Trend period (steps)		5	5	5		5	5	5
Mean resource suitability to stop dispersal		0.44	0.44	0.44		0.44	0.44	0.44
Maximum number of explorations ( <i>Adults only</i> )		1	1	1		1	1	1

We ensured anonymity of responses and justifications, encouraging participants to re-evaluate their answers. This iterative process led to consensus on parameter values, which were then used to inform our IBM.

Hexsim simulates individuals within a population through a user-defined sequence of life cycle events (Figure 1D), with parameters informed by the Delphi elicitation process (Table 1). Our simulation modelled females only across three life stages with stage-specific vital rates and density-dependent reproduction and survival rates. Demographic stochasticity was introduced through normally distributed reproduction rates (Table 1). Subadults disperse from natal territories with 60% average movement autocorrelation (straight-line movement = 100%), constrained by maximum dispersal distances and exhibiting preference for higher resource levels, informed by the habitat suitability layers. Adults seek unoccupied territories with sufficient cumulative resources across hexagons (informed by habitat suitability), which results in varying territory sizes and density-dependence. Resource availability within territories influences both litter size and survival probability. Survival is further dependent on age and, in scenarios with hunting pressure, is additionally impacted by a spatial hunting-induced mortality layer. We included both demographic stochasticity and environmental stochasticity, the latter modelled by randomly assigning a ‘year quality’ value (range: 0.9–1.1) that modifies reproduction rates and survival annually by  $\pm 10\%$ . The sensitivity of the population model to parameter variations was tested by altering parameter values by  $\pm 5\%$  and  $\pm 10\%$ .

## 2.4 | Threat Scenarios

To assess the impacts of different threats on jaguar and puma population dynamics, we developed species-specific hypothetical threat-free baselines and three scenarios reflecting current threat levels (Figure 1C). The baseline population characteristics and distribution were used to initialize all threat scenarios. These scenarios incorporated spatial layers representing the distribution and magnitude of each threat, influencing life history parameters of individuals located within each hexagon (Figure 1). Our baseline was modelled using a hypothetical historical habitat suitability map without habitat destruction and assuming zero hunting-induced mortality. We randomly allocated 1000 individuals across the Chaco and allowed the population to stabilise for 100 years. We used the resulting final population (i.e., the spatial allocation and life history stages all individuals) as the initial population for all threat scenarios. The habitat destruction scenario used the current habitat suitability map, reflecting reduced resource availability in many areas compared to the baseline. The hunting scenario retained the baseline habitat suitability but incorporated a current hunting pressure map that spatially modifies survival probability. The combined threats scenario (Figure 1C) uses the layers for current habitat suitability and hunting pressure, and the final parameter value (e.g., survival) for an individual within a hexagon is sequentially affected by the level of each threat there during the same time-step, following Table S1. We ran each scenario for 100 years with 10 replicates, deriving population trajectories, final sizes (by country and protected/unprotected areas), and maps of current occupancy, which indicates the number of

individuals that used a hexagon during a year. Occupancy maps were produced by averaging the last 10 stable years of each simulation and compared to the baseline to map occupancy under different threats. Note that protected status did not directly influence demographic parameters in our models.

## 2.5 | Sources and Sinks and Estimation of Functional Decline

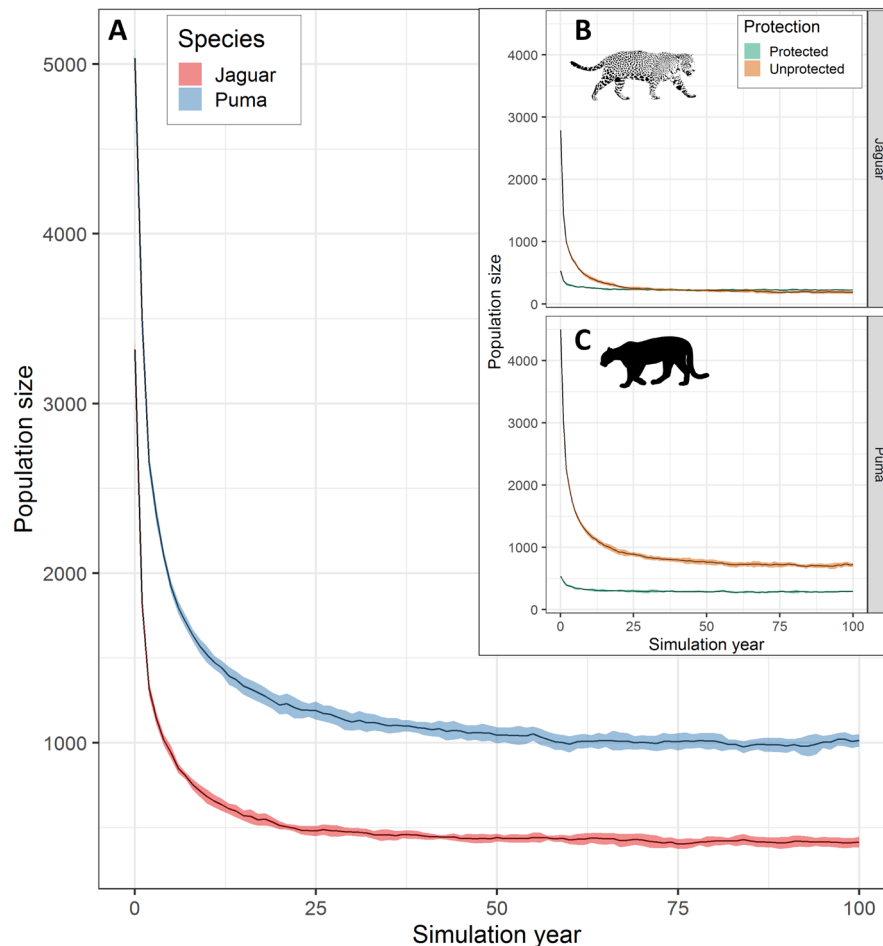
To identify population sources and sinks, we calculated births minus deaths of resident individuals within each hexagon over the final 30 simulation years, when population numbers were stable. Positive values indicated sources; negative values indicated sinks. We estimated extinction probability over 100 years for each species/scenario combination using the *Pext* function in HexSimR (Pacioni et al. 2018), run in R version 4.2.1 Patched (R Core Team 2024).

Given the lack of established thresholds indicating functional loss due to population rarity, we assessed the functional decline of the large carnivore guild by calculating proportional population declines per hexagon, thus providing a context-specific representation of functional declines. We used the IUCN Red List decline thresholds to categorise species' threat levels (30%, Vulnerable;

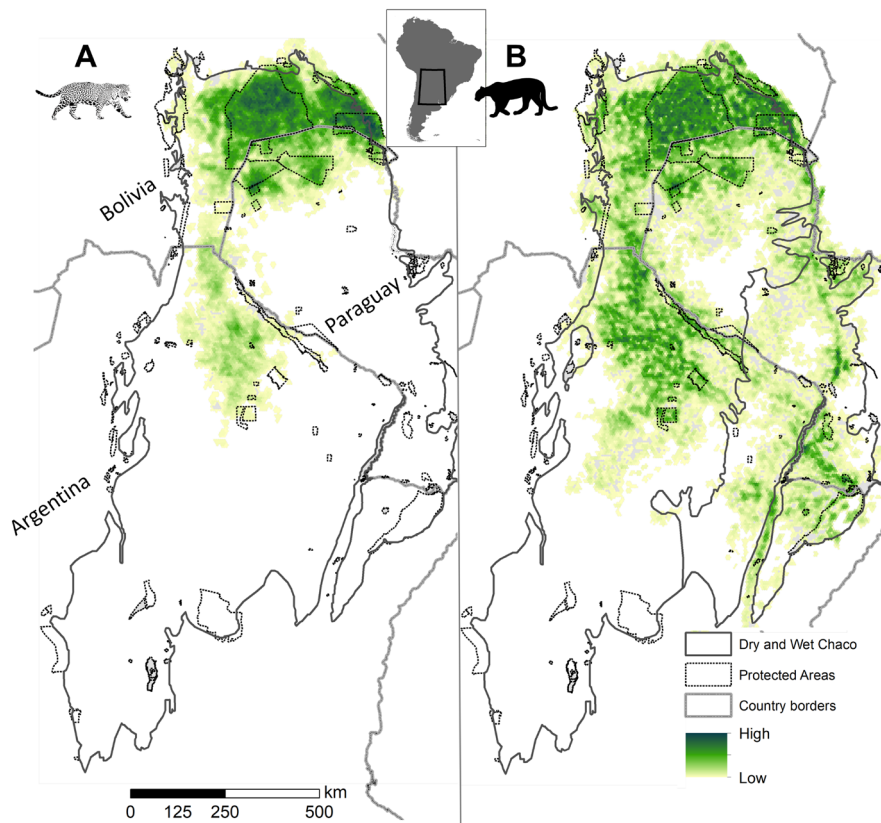
50%, Endangered; 80%, Critically Endangered; and 100%, Extinct) (IUCN 2012). We conservatively considered population declines exceeding 80% to represent functional loss for individual species and the guild as a whole. These thresholds are suitable for broad-scale assessments, as previous research demonstrates that substantial rarity in large carnivores can severely weaken their ecological roles (Johnson, Isaac, and Fisher 2006; Ordiz, Bischof, and Swenson 2013; Kuijper et al. 2016). To provide a nuanced representation of functional loss of the top carnivore guild, we mapped the spatial overlap of the four decline thresholds for both species and calculated the extent of this overlap. While these proportional declines might hide details of the numerical change in occupancy, we also provide spatially explicit maps of the numerical occupancy change under both threats.

## 3 | Results

For the threat-free baseline, our models predicted an adult population size of 3318 ( $\pm 37$  SD) jaguars and 5034 ( $\pm 656$ ) pumas across the Chaco. Simulations incorporating current levels of habitat destruction and hunting pressure revealed severe declines in both species over 100 years (jaguar: 88% decline to  $414 \pm 31$  individuals; puma: 80% decline to  $1014 \pm 37$  individuals; Figure 2A; Figure S1). Despite these severe declines, both



**FIGURE 2** | Population trajectories for jaguar and puma under current levels of habitat destruction and hunting pressure in combination (A) for the entire Chaco and (B) and (C) in currently protected and unprotected areas for jaguar and puma, respectively. In this model, current levels of threats were introduced to the historical baseline population with no threats in year zero.



**FIGURE 3** | Predicted population distribution and occupancy per 25 km<sup>2</sup> hexagon of jaguar and puma across the Gran Chaco under current levels of habitat destruction and hunting pressure (after 100 years of simulation, average from the last 10 years).

species were predicted to persist in the Chaco with a 0% extinction probability largely due to within protected areas buffering declines. However, populations declined drastically outside protected areas (jaguars by 93%, pumas by 83%), resulting in most jaguar and puma individuals surviving within protected areas by the end of the simulation (Figure 2B). Nonetheless, our simulations also indicate significant, albeit much lower, declines within protected areas, by 57% for jaguars and 45% for pumas.

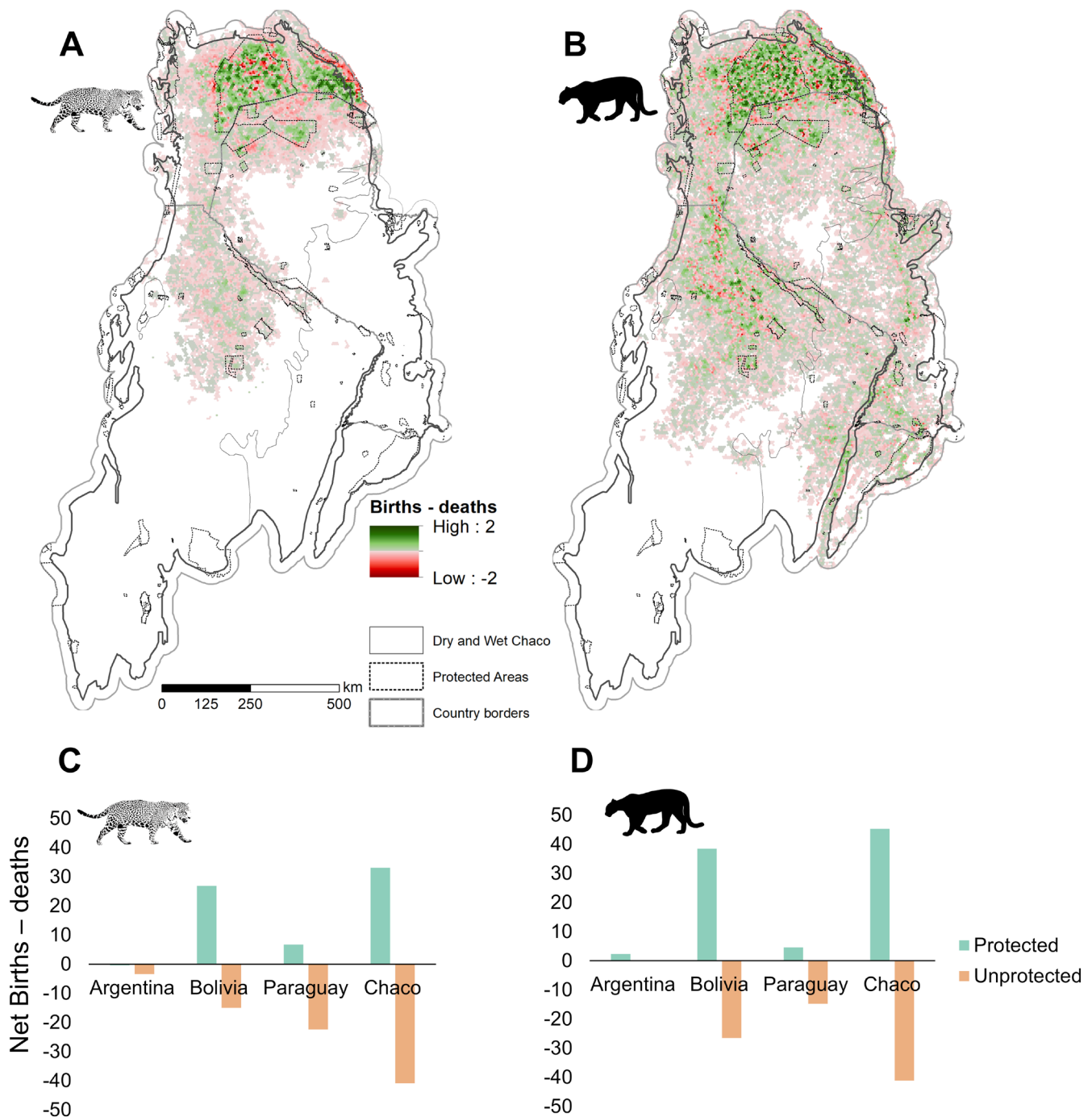
Under current threat levels, our simulations predict contracted ranges for both species. Jaguar range contracted to 36% of its baseline, covering approximately 250,000 km<sup>2</sup> primarily in the northern Chaco in Bolivia and Paraguay, with a southern limit in the central Argentine Chaco (Figure 3A). Puma range contracted by 65% but spread wider, across 593,200 km<sup>2</sup> in the central and northern Chaco, broadly overlapping with jaguars (Figure 3A). Additionally, the puma was predicted to inhabit the eastern Wet Chaco (Figure 3B), while our model did not predict puma populations in the southern Chaco, despite known populations there.

Spatial analysis of population sources and sinks revealed that jaguar sources under both threats occupied 48% of the current range, with sinks covering 49% and stable areas 3%. Sources were concentrated within large protected areas in the northern Chaco of Bolivia and Paraguay, with smaller, weaker sources scattered across central Chaco in northern Argentina (Figure 4A). Sinks surrounded all sources, with the strongest population sinks (i.e., highest net deaths) concentrated just outside large protected areas in the northern Chaco, along the

Chaco-Pantanal interface and between large protected areas in Bolivia and northern Paraguay (Figure 4). Pumas exhibited a similar pattern, with sources covering 55% of their current range, sinks 42%, and stable areas 3%. Key sources were located within large protected areas in Bolivia, northern Paraguay, and northern Argentina (Figure 4D). As with jaguars, the strongest puma sinks occurred outside large protected areas in the northern and northwestern Chaco but were less widespread than jaguars, and sources were more continuous. Overall, protected areas were a net source for jaguars, particularly in Bolivia, but acted as net sinks within Argentina (Figure 4C). Unprotected areas were net sinks for jaguars across all countries. For pumas, protected areas consistently served as net sources particularly in Bolivia, while unprotected areas were net sinks in Bolivia and Paraguay but not Argentina (Figure 4C).

The severe declines we observed highlight the risk of functional loss of the top predator guild across vast areas of the Chaco (Figure 5B). Our simulations indicated complete extirpation of at least one top predator in 67% of the Chaco (737,000 km<sup>2</sup>), with 15% predicted to lose both. Individually jaguars experienced extirpation across 48% of their historical range, and pumas across 35% (Figure 5B). However, occupancy declines were even more widespread, with roughly 906,000 km<sup>2</sup> experiencing declines in both species (jaguar: 93% of historical range, puma: 71%), while only a small fraction (4%) experienced no declines (Figure 5). If functional extinction is assumed at  $\geq 80\%$  local occupancy decline, across the area of species co-occurrence in the threat-free baseline (683,350 km<sup>2</sup>; 62% of Chaco), our results suggest a functional loss for jaguars across



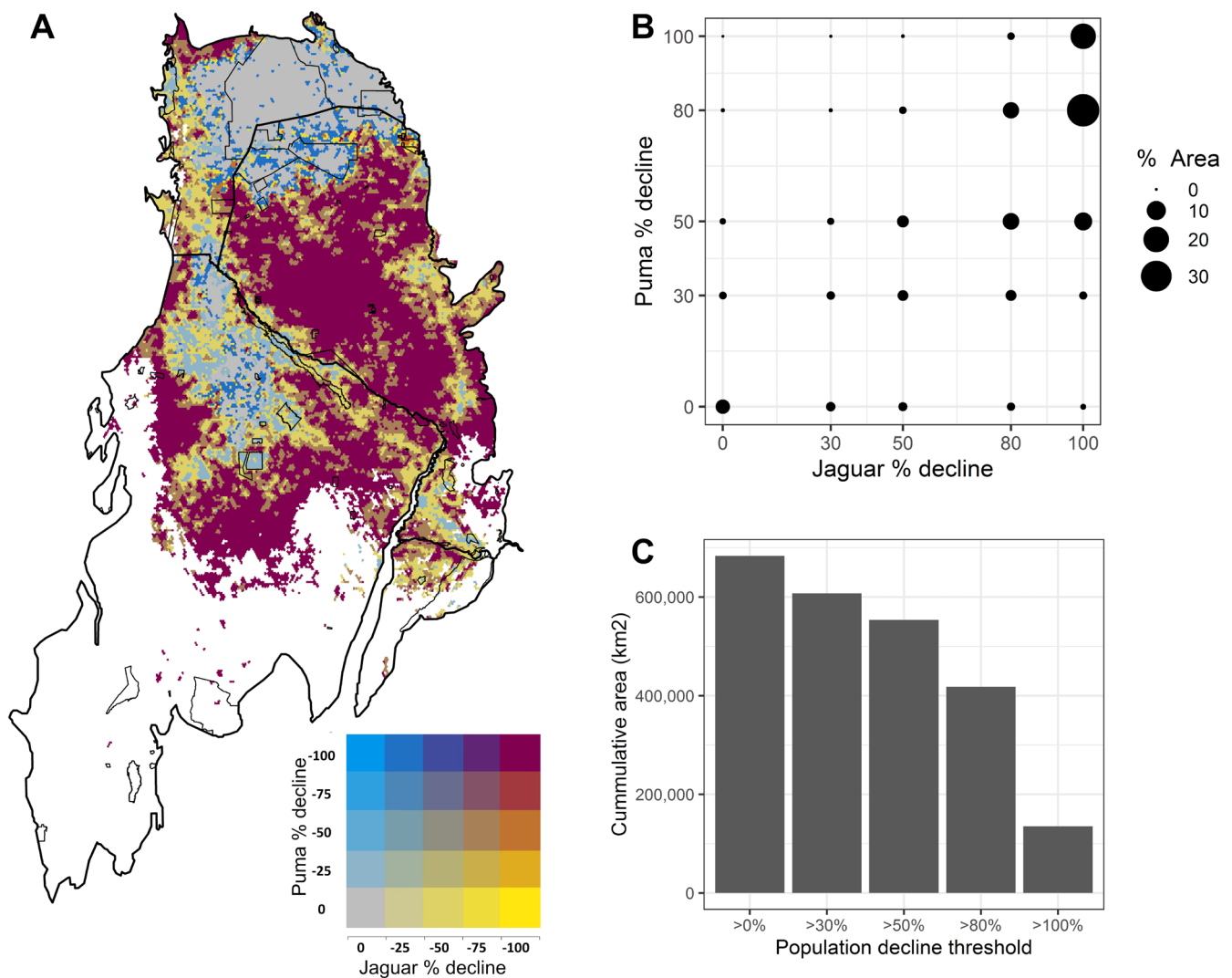


**FIGURE 4** | Current population sources and sinks for jaguar (A) and puma (B) across Chaco under current threat levels (average numbers over the last 30 years of simulation). Positive values indicate sources (in green) and negative values (in red) indicate population sinks. Panels (C, D) show simulated average annual births minus deaths in protected areas (PA) and unprotected areas (NoPa), where positive and negative values represent net sources and sinks, respectively.

81% of the area, pumas across 62%, and the entire top carnivore guild across 61% (Figure 5B). These mapped proportional declines can be numerically contextualised by comparing them to the mapped numerical occupancy declines in Figure 6D,H for jaguar and puma.

We found greater declines under hunting pressure (jaguar: 88% decline, to  $406 \pm 27$  individuals; puma: 77% decline, to  $1148 \pm 42$  individuals) compared to habitat destruction (jaguar: 26% decline, to  $2453 \pm 39$  individuals; puma: 22% decline, to  $3942 \pm 60$

individuals). The combined threats scenario (habitat destruction and hunting) produced much greater declines than habitat destruction alone for both jaguars and pumas. Notably, population declines under the hunting-only scenario were nearly as severe as under the combined threats scenario (88% for jaguar and 80% for puma) (Figure 6). However, the combined threats scenario induced a faster population decline than hunting alone, which was particularly evident in the first 25 years of simulation, with population decreases 13% and 18% faster per year on average for jaguars and pumas, respectively (Figure 6).



**FIGURE 5** | Population declines of jaguar and puma across the Chaco under current levels of threats. (A) Bivariate representation of jaguar and puma population decline where they co-occurred in the threat baseline. (B) Proportion of the co-occurrence area experiencing different levels of population decline for both species. (C) Cumulative area of declines for both jaguar and puma across different decline thresholds corresponding to the IUCN guidelines to categorise species by threatened status.

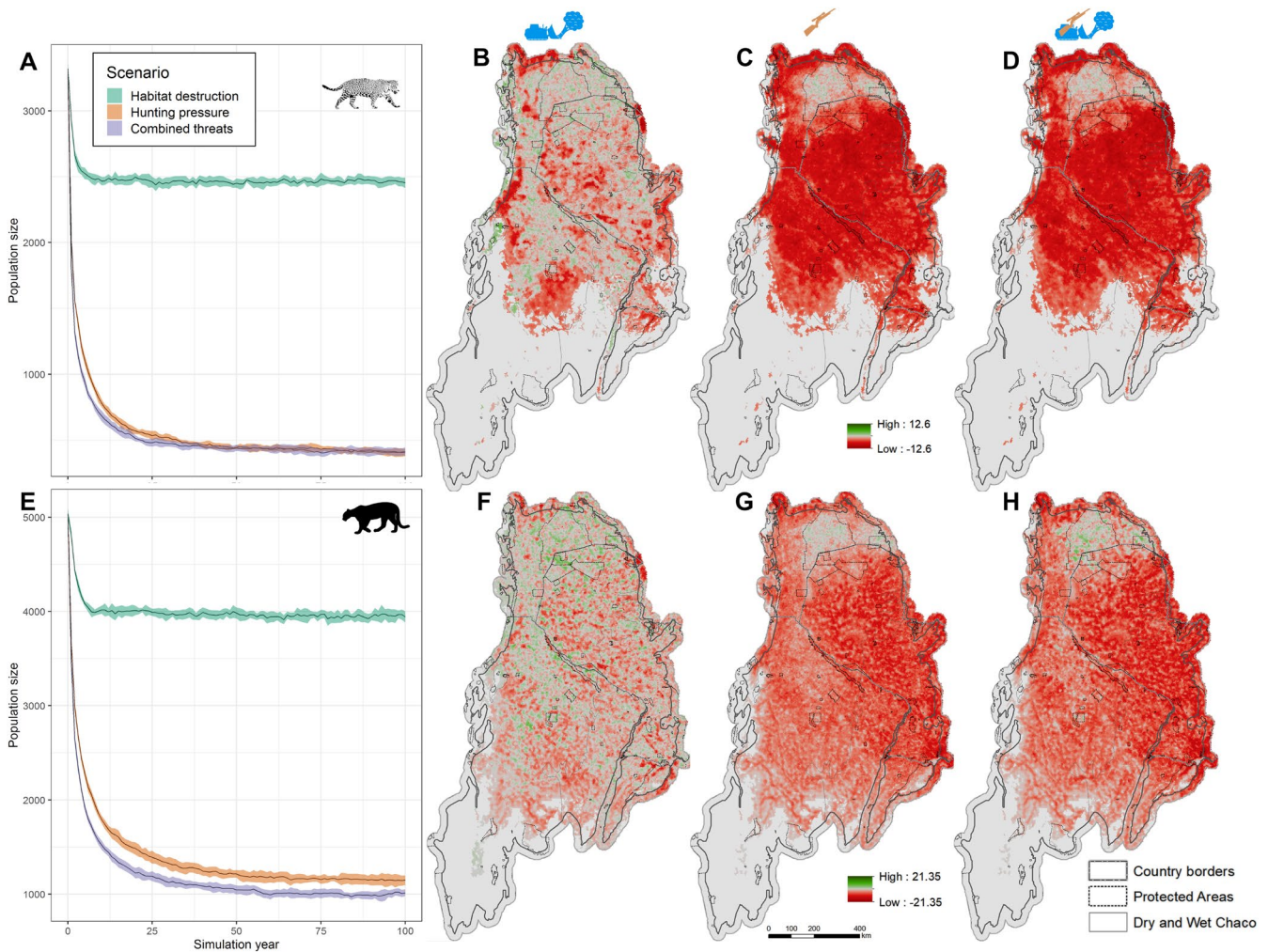
Spatially, both threats caused widespread declines, but with distinct spatial patterns per species (Figure 6B–D,F–H). The area impacted by hunting encompassed and extended beyond the areas affected by habitat destruction alone. The extent of decline under hunting pressure closely resembled that of the combined threats scenario for both species (Figure 6C,F). Compared to pumas, jaguar declines were more concentrated. Pumas exhibited larger areas of stability, particularly outside protected areas (Figure 6D,H).

Our sensitivity analysis showed that final population sizes in the combined threat scenario were relatively robust to  $\pm 5\%$  and  $\pm 10\%$  changes in environmental stochasticity and fecundity for both species (Figure 7). Altering survival rates had a stronger impact. For jaguars, changes in survival across all age classes had similar effects, with decreased adult survival causing the greatest population reduction ( $-7\%$ , under 5% parameter change) and increased juvenile survival leading to the largest increase ( $+4\%$ ). For pumas, decreased juvenile survival had the most significant impact ( $-18\%$  population

change), while increased juvenile survival resulted in a  $+16\%$  change (Figure 7).

#### 4 | Discussion

Large predators are crucial to ecosystems and understanding how multiple threats change their populations is essential, particularly in areas with expanding threats. However, broad-scale population assessments that consider multiple threats, their spatial variation, and entire trophic guilds remain scarce. We addressed these research gaps by combining spatially explicit individual-based models (IBMs) for jaguar and puma, with spatially detailed threat maps under current and threat-free scenarios across the entire South American Chaco, a global hotspot of deforestation and defauna. Our simulations reveal three key insights for understanding how hunting and habitat destruction affect top predators' populations. First, habitat destruction and hunting have significantly reduced both predators' populations and ranges. Many Chaco regions are predicted to now

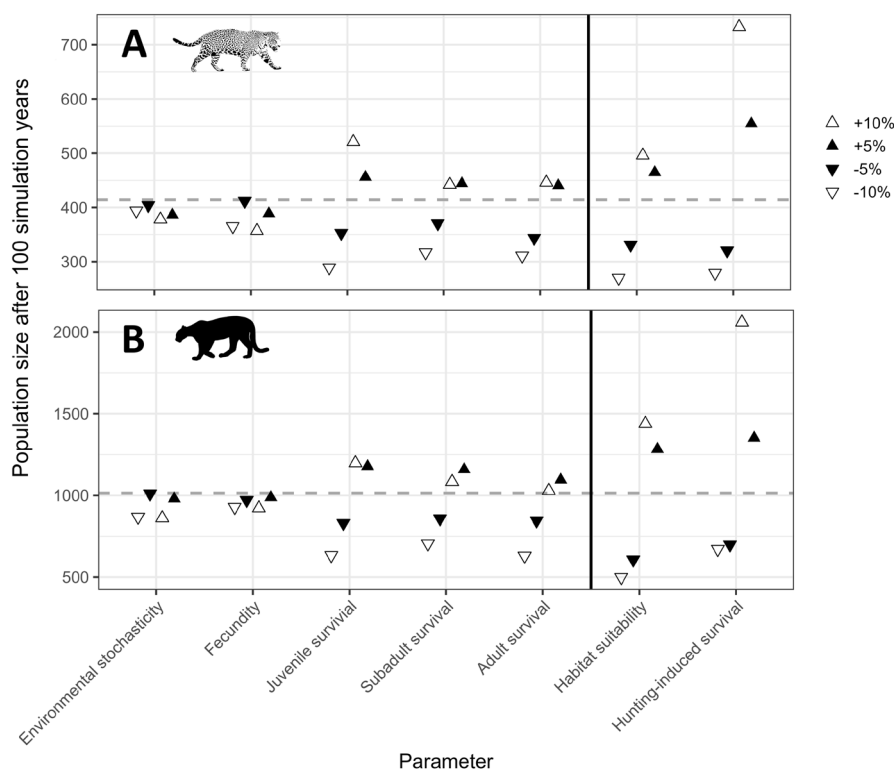


**FIGURE 6** | Population trajectories and spatial occupancy change for jaguar (upper row) and puma (lower row) under habitat destruction, hunting pressure, and combined threat scenarios resulting from individual based models with 10 replicates. (A, E) Chaco population trajectories under each scenario for jaguar and puma. (B–D, F–H) Spatial population occupancy changes between the threat-free baseline and the scenarios of habitat destruction, hunting pressure, and combined threats across the Chaco. These maps were created by subtracting the final populations (i.e., the averages of the last 10 simulation years) of the threat scenario from the baseline scenario. Red indicates decreased occupancy relative to the baseline, grey indicates stability, and green indicates increases.

be population sinks, with source populations largely confined to protected areas. The more vulnerable jaguar experienced a steeper decline (88% against our baseline) than puma (80%) and lost more range. Second, population declines extended far beyond areas of local extinction, suggesting substantial functional degradation. We estimate widespread functional loss of the top carnivore guild across the Chaco, according to conservative thresholds of functional loss (>80% decline). Finally, hunting caused much stronger range contractions and population declines than habitat destruction for both predators, emerging as the main driver of functional decline. However, both threats overlapped extensively, highlighting their intertwinement with the expansion of cattle ranching, agriculture, and associated human infrastructure. Our study underscores the value of spatially explicit IBMs in disentangling how multiple threats can impact wildlife populations and in mapping potential trophic downgrading. In the Chaco, trophic downgrading extends far beyond deforestation or species' range loss, a pattern likely mirrored in many tropical deforestation hotspots.

Our simulations revealed drastic declines in both jaguar and puma populations, compared to a hypothetical historical, threat-free baseline. Notably, population declines outside protected areas were so severe that now most jaguars occur within protected areas, despite protected areas covering only 9% of the Chaco. While local declines of this magnitude have been documented for some large carnivore populations (WWF 2022), few studies have reported such strong declines at regional scales. Assessments at broader scales tend to rely on contractions of ranges (Ceballos, Ehrlich, and Dirzo 2017; Wolf and Ripple 2017; Romero-Muñoz et al. 2019), likely underestimating total population loss in major ways. Indeed, in our study, contractions of the jaguar and puma ranges (48% and 35% respectively) were much smaller than the decline in their population sizes (88% and 80%). Furthermore, our simulations predicted current ranges to be more restricted than current IUCN ranges for these species in the Chaco. This finding underscores the value of spatially explicit IBMs in providing detailed assessments of population and range contractions.





**FIGURE 7** | Sensitivity of jaguar (A) and puma (B) population size in the combined threats scenario (after 100 years) to  $\pm 5\%$  and  $\pm 10\%$  changes in environmental stochasticity and demographic parameters and to changes in threat levels (shown to the right of the vertical line). The horizontal dashed line shows the mean population size in the combined threats scenario.

We validated our jaguar results against independent density estimates, which are rare for pumas due to uncertain individual identification in camera trapping studies. Our current total population estimate of 414 female jaguars was lower than Jędrzejewski et al. (2018) camera trap-based modelled prediction of 1394 females (50% of 2789 total individuals) for the Chaco. While comparable, this three-fold difference likely stems from their study containing surveys spanning two decades and predicting into areas potentially transformed since; not explicitly accounting for different threats' effects; and assuming a much wider distribution range, constrained only by expert maps, reaching areas our model predicts would not support jaguar populations long-term under current threats. Our spatial occupancy estimates correlated moderately with Jędrzejewski et al. (2018) spatial jaguar density estimates ( $r = 0.5$ ,  $p < 0.0005$ ), suggesting that our population estimate is realistic while highlighting that mechanistically accounting for different threats may reveal lower population sizes for large predators than previous predictions.

Current population sources for both species were predicted to be clustered within large protected areas of the northern Chaco, with puma having additional, albeit smaller, sources in the central Chaco. Sinks were widespread outside protected areas and the strongest were adjacent to the largest ones. These results align with empirical studies demonstrating that most sources cluster in large, low-threat areas, while the strongest sinks surround them, as individuals move into areas of high mortality risk (Woodroffe and Ginsberg 1998; Havmøller et al. 2019; Nisi et al. 2023). This is further supported by field surveys in the Chaco, finding lower jaguar density and occupancy outside

protected areas, even where suitable habitat remains (Quiroga et al. 2014; Thompson, Martí, and Quigley 2020; Thompson et al. 2022). Our findings that current populations remain viable under current threat levels likely hinge upon these large protected areas and remaining connecting forests, emphasising the need to preserve large tracts of remaining habitat and bolster effective connectivity between them. This is particularly urgent in southern Bolivia and northern Paraguay, where rampant deforestation is ongoing (Baumann et al. 2022). For the more range-restricted jaguar, ensuring conservation and connectivity within and toward the northern Chaco is likely critically important for its long-term viability in Gran Chaco.

Our simulations suggest that top predator populations declined to levels that indicate functional loss across a much larger portion of the region than the area over which they were fully extirpated (61%). Consequently, studies relying solely on range loss to identify suitable areas for trophic rewilding may underestimate the extent of carnivore functional loss (e.g., Wolf and Ripple 2017). A key challenge for identifying functional loss for large carnivore populations is that definitive thresholds signalling such a loss remain undetermined. We therefore approximate this by employing conservative criteria aligned with IUCN standards that indicate critical population status, by comparing a range of scenarios and by also presenting numerical occupancy declines. This approach is justified because it assesses functional decline at a localised level—per hexagon—by quantifying proportional population reductions due to current threats relative to a threat-free baseline. This proportional assessment offers the advantages of contextualising population changes and preventing the misinterpretation of a natural rarity as functional loss.



Consequently, our framework enables broad-scale detection of areas that might undergo population declines that significantly weaken the key ecological roles of large carnivores.

Considering that the extinction of top predators can trigger a range of effects, including mesopredator release, herbivore hyperabundance, and plant diversity decline (Terborgh et al. 2001), the widespread functional loss of the top carnivore guild that we found could have severe consequences for ecosystems across the Chaco. Specifically, in areas where both predators persist but have declined significantly, their crucial role in regulating mesopredator and prey numbers through direct predation is likely compromised or lost (Ordiz, Bischof, and Swenson 2013; Kuijper et al. 2016). While behavioural impacts via 'landscapes of fear' may linger at low predator abundances, these effects are less pronounced as they do not directly regulate mesopredator or prey populations (Kuijper et al. 2016). Furthermore, these behavioural effects likely diminish with declining predator numbers (Ordiz, Bischof, and Swenson 2013). Importantly, our results highlight how functional loss of top carnivores can extend into seemingly remote areas in tropical deforestation frontiers, largely due to the far-reaching effects of hunting.

Our findings also identify broad areas where only jaguar populations declined significantly, while puma populations persisted. This result reflects puma's greater resilience to anthropogenic threats compared to jaguar (De Angelo, Paviolo, and Di Bitetti 2011; Quiroga et al. 2016; Villalva 2022). Despite ecological similarities, jaguars are larger, are socially dominant, utilise larger home ranges, and tend to kill larger, more aggressive species like tapirs and peccaries (Taber 1997; Romero-Muñoz 2010; Elbroch and Kusler 2018; Thompson et al. 2021). While studies have linked jaguar extinction to the release of puma and mesopredators (Moreno, Kays, and Samudio 2006; Elbroch and Kusler 2018; Villalva 2022), reduced redundancy within ecological communities can diminish functioning and increase vulnerability to extinction cascades (Reich et al. 2012; Ripple et al. 2014; Sanders et al. 2018). Consequently, the functional loss of the jaguar alone could be very significant, though likely less severe than the loss of the entire top carnivore guild.

Our analysis reveals that while habitat destruction and hunting were both predicted to have significantly affected jaguar and puma populations, hunting exerted a far stronger and more widespread effect. This is likely due to these large carnivores' ability to persist in open habitats after deforestation if resources remain (Polisar et al. 2003; de Souza et al. 2018), at least temporarily (Tilman et al. 1994; Semper-Pascual et al. 2018). Conversely, hunting's greater impact reflects the slow reproductive rates and natural rarity of jaguars and pumas, hindering population recovery.

The comparable impact of hunting alone to the combined effect of both threats suggests that hunting potentially overshadows habitat destruction when both co-occur. This finding suggests that hunting is dominant, likely due to its more immediate impact on populations compared to the more gradual effects of habitat destruction (Cardillo et al. 2005; Chapron et al. 2008; Bleyhl et al. 2021). Nevertheless, our modelling approach did not explicitly account for more complex threat interactions (e.g., threat synergies) that would require different demographic

parameter values when threats co-occur. Instead, our approach allowed both threats to affect populations simultaneously but independently.

The generalised overlap between areas experiencing population declines due to both threats underscores their connection. Initiatives to increase agricultural commodity production often deforest land and build new roads, which facilitate hunting in remote areas (Laurance, Goosem, and Laurance 2009; Benítez-López et al. 2019; Buchadas et al. 2022). Additionally, habitat loss may force animals to range further, increasing their exposure to hunting (Woodroffe and Ginsberg 1998), as seen by the common predator killings associated with cattle ranching, the main deforestation driver (de Souza et al. 2018; Romero-Muñoz, Morato, et al. 2020). These findings underscore the need for land use and conservation planning targeting the underlying drivers of both threats.

Our process-based, spatially explicit population model allowed us to assess plausible large carnivore population dynamics under increasing threats across a vast, data-scarce, rapidly changing region, where spatial conservation planning is critical. Systematic expert elicitation helped address data scarcity and tailor population parameters to the region. Nevertheless, uncertainties remain, some stemming from model-based inputs, like habitat suitability and hunting pressure layers. First, accurately modelling hunting pressure across space is challenging (Benítez-López et al. 2019). Our hunting pressure model assumed uniform hunting behaviour across actors, potentially overestimating hunting impacts in areas where actors, like indigenous peoples and environmentally-minded ranchers, are less likely to kill predators (Figel et al. 2022; Camino et al. 2023). Our hunting models might also overestimate hunting pressure in regionally remote areas, where few people might use access features. Second, our 'no threats' baseline may not fully account for historical human impacts on jaguar and puma populations. Third, while prey depletion is a potential further threat that could exacerbate predator declines (Chapron et al. 2008; Bleyhl et al. 2021), we did not model it due to a lack of spatial data on the availability of multiple prey species under threat-free and hunting and habitat loss conditions. Fourth, habitat suitability outputs depend on the representativeness of input presence data, and some areas of the Chaco are under-sampled. Indeed, our habitat models underestimated puma suitability in the southern Chaco due to scarce occurrence records there, leading our population models to assume no puma populations there. However, this underestimation affects both the historical baseline and current threat scenarios, preserving the overall validity of puma population trajectories and the usefulness of the population maps for pumas for the central and northern Chaco.

The widespread functional loss of top predators in the Chaco demands urgent action to halt and reverse this regional-scale trophic downgrading. By mechanistically assessing the distribution and status of current jaguar and puma populations in more ecologically meaningful manner than previous correlative approaches (Romero-Muñoz et al. 2019), as well as identifying population sources, sinks, and where different threats affect populations, our study addresses critical knowledge gaps for conservation and informs robust conservation strategies. Our findings highlight that those large protected areas, primarily in

northern Chaco, in Bolivia and Paraguay, are crucial for halting top predator functional loss. However, gaps between these areas, particularly along country borders and transitions to neighbouring ecoregions (Chiquitano, Pantanal), are becoming population sinks, necessitating urgent corridor protection. In the central Chaco in Argentina, smaller protected areas and weaker population sources require enhanced connectivity within the region and with the northern Chaco to maintain jaguar viability. Crucially, our study reveals hunting as the primary threat to the large carnivore guild, requiring targeted, actor-specific interventions focused on stakeholder engagement, effective livestock management, and law enforcement (Pooley et al. 2017; König et al. 2020). Our population source/sink maps offer a blueprint for prioritising actions: protecting sources, reducing carnivore killing in sinks, and identifying key corridors. More proactively, land-use planning should prevent further agricultural and road expansion into remote areas to mitigate habitat destruction, hunting threats, and exacerbate trophic downgrading.

### Author Contributions

A.R.-M. and T.K. conceptualized the study. A.R.-M., B.B., M.C., J.D., A.S.N., A.N., A.J.G., V.A.Q., R.T., J.J.T., L.V., M.M.N.R. and C.D.A. participated in all iterations of the expert elicitation process. A.R.-M. analysed the data, with input from B.B., A.B.-L., and T.K. A.R.-M. led the writing of the manuscript with strong input from A.B.-L. and T.K. All authors contributed critically to the drafts and gave final approval for publication.

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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The data that support the findings of this study are openly available in Dryad at Dryad, at [https://datadryad.org/stash/share/53KHez9NLkNILVJWsxRgWarD\\_rGB4sCEi56RwvJnJk](https://datadryad.org/stash/share/53KHez9NLkNILVJWsxRgWarD_rGB4sCEi56RwvJnJk). doi: 10.5061/dryad.9cnp5hqss.

### Peer Review

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### Supporting Information

Additional supporting information can be found online in the Supporting Information section.