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Understanding geographies of threat: impacts of habitat destruction and hunting on large mammals in the Chaco

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**Understanding geographies of threat:
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on large mammals in the Chaco**

Alfredo Romero-Muñoz

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Abstract

The main drivers of the current human-caused global biodiversity crisis are habitat destruction and overexploitation. Yet, detailed knowledge of the individual and combined spatial impact of these threats on different aspects of biodiversity, and how they change over time, is lacking. Because both threats are common, especially in the tropics, these knowledge gaps prevent us from developing more effective conservation strategies. The overarching goal of this thesis was to understand the impacts of habitat destruction and overexploitation on biodiversity, and how these impacts change in space and over time. I assessed these *geographies of threat* at high spatial resolutions and over three decades for different biodiversity hierarchies (species and communities), and biodiversity facets (taxonomic, phylogenetic, and functional diversity). I focused on the 1.1 million km² Gran Chaco region, the largest tropical dry forest globally, and a global deforestation hotspot due to agricultural expansion. Results reveal that over 30 years, the spatial impacts of each threat expanded over larger areas than the area deforested. The expanding threats produced widespread losses of high-quality and safe areas for the jaguar, the entire larger mammal community and for all facets of the mammalian diversity. Such declines suggest a generalised defaunation and biotic impoverishment that includes the loss of species, evolutionary history, and ecological functions across much of the Chaco. Both threats contributed considerably to biodiversity declines, and the relative importance of the threats varied among species and biodiversity facets. Moreover, the areas where both threats synergize increased over time, likely exacerbating biodiversity losses. I identified, for each biodiversity aspect assessed, priority areas for proactive protection of high-quality habitats, and hotspots where threats have large effects on biodiversity. This information could guide complementary proactive and reactive management actions that lead to more effective conservation strategies. This thesis highlights the importance of simultaneously assessing the impact of multiple major threats over time to better understand the impact of humans on biodiversity and to identify effective ways to mitigate those impacts.

Zusammenfassung

Die Hauptursachen der gegenwärtigen, vom Menschen verursachten globalen Biodiversitätskrise sind die Zerstörung und Übernutzung von Lebensräumen. Es fehlt jedoch an detaillierten Kenntnissen über die individuellen und kombinierten räumlichen Auswirkungen dieser Bedrohungen auf verschiedene Aspekte von Biodiversität und darüber, wie sie sich im Laufe der Zeit verändern. Da beide Bedrohungen, insbesondere in den Tropen, sehr häufig auftreten, hindern uns diese Wissenslücken daran, wirksamere Erhaltungsstrategien zu entwickeln. Das übergeordnete Ziel dieser Arbeit war es, die Auswirkungen von Habitatzerstörung und Raubbau auf Biodiversität zu verstehen und zu verstehen, wie sich diese Auswirkungen räumlich und zeitlich verändern. Ich bewertete diese *Bedrohungsgeographien* in hoher räumlicher Auflösung und über drei Jahrzehnte hinweg für verschiedene Biodiversitätsebenen (Arten und Gemeinschaften) und Biodiversitätsfacetten (taxonomische, phylogenetische und funktionale Vielfalt). Ich konzentrierte mich auf die 1,1 Millionen km² große Gran Chaco Region, den weltweit größten tropischen Trockenwald, der gleichzeitig durch starke Expansion an Landwirtschaft zu einem globalen Abholzungs-Hotspots zählt. Meine Ergebnisse zeigen, dass sich im Laufe von 30 Jahren die räumlichen Auswirkungen der einzelnen Bedrohungen auf größere Gebiete ausdehnten als die Gebiete, die abgeholzt wurden. Die sich ausbreitenden Bedrohungen führten zu weitreichenden Verlusten an hochwertigem und sicherem Habitat für Jaguare, die gesamte Großsäuger-Gemeinschaft und für alle Facetten der Säugetiervielfalt. Solche Rückgänge deuten auf eine allgemeine Defaunierung und biotische Verarmung hin, einschließlich eines Verlusts an Arten, evolutionärer Geschichte und ökologischer Funktionen in weiten Teilen des Chaco. Beide Bedrohungen trugen erheblich zum Rückgang der biologischen Vielfalt bei, und die relative Bedeutung der Bedrohungen variierte je nach Art und Facette der biologischen Vielfalt. Darüber hinaus nahmen die Gebiete, in denen beide Bedrohungen zusammenwirken, im Laufe der

Zeit zu, was den Verlust der biologischen Vielfalt wahrscheinlich noch verschlimmert hat. Ich identifizierte für jeden bewerteten Aspekt der Biodiversität Prioritäts-Gebiete für den proaktiven Schutz hochwertiger Lebensräume und Hotspots, in denen die Bedrohungen hohe Auswirkungen auf die Biodiversität haben. Diese Informationen können eine wichtige Steuerungshilfe für proaktive und reaktive Managementmaßnahmen sein, die zu wirksameren Erhaltungsstrategien führen. Diese Arbeit unterstreicht die Bedeutung der gleichzeitigen Bewertung der Auswirkungen mehrerer Bedrohungen über einen größeren Zeitraum, um die Auswirkungen des Menschen auf die biologische Vielfalt besser zu verstehen und wirksame Wege zur Minderung dieser Auswirkungen zu finden.

Contents

| | |
|--|--------------|
| Acknowledgements | i |
| Abstract | iii |
| Zusammenfassung | v |
| Contents | vii |
| List of Core Chapter Figures | xi |
| List of Core Chapter Tables | xvi |
| List of Appendix Figures | xviii |
| Chapter I: Introduction | 1 |
| 1 The human-caused global biodiversity crisis | 2 |
| 2 The impact of habitat destruction and overexploitation on biodiversity | 3 |
| 3 The biodiversity crisis in tropical forests | 7 |
| 4 Defaunation and the decline of animal species, their evolutionary history, and ecological functions | 10 |
| 5 The Importance of assessing the geographies of threat for conservation planning | 12 |
| 6 Importance of studying the geographies of threats on larger mammals | 13 |
| 7 The Gran Chaco | 15 |
| 8 Research questions and objectives | 20 |
| 9 Thesis structure | 24 |
| Chapter II: Habitat loss and overhunting synergistically drive the extirpation of jaguars from the Gran Chaco | 27 |
| Abstract | 28 |
| 1 Introduction | 29 |

| | | |
|-----|---|----|
| 2 | Methods | 31 |
| 2.1 | Study Region | 31 |
| 2.2 | Habitat modelling | 32 |
| 2.3 | Predictor variables | 35 |
| 2.4 | Assessing jaguar habitat patterns in the Chaco | 36 |
| 3 | Results | 39 |
| 3.1 | Changes in habitat extent from 1985 to 2013 | 39 |
| 3.2 | Relative importance of threats in driving jaguar habitat change | 40 |
| 3.3 | Changes in core habitat areas in countries and in protected areas | 41 |
| 3.4 | Validating sink habitats | 44 |
| 4 | Discussion | 45 |
| | Acknowledgements | 50 |
| | Biosketch | 50 |
| | Supplementary Information | 51 |

| | |
|---|-----------|
| Chapter III: Increasing synergistic effects of habitat destruction and hunting on mammals over three decades in the Gran Chaco | 55 |
|---|-----------|

| | | |
|-----|--|----|
| | Abstract | 56 |
| 1 | Introduction | 57 |
| 2 | Methods | 59 |
| 2.1 | Study region | 59 |
| 2.2 | Data preparation | 60 |
| 2.3 | Mapping the footprints of habitat destruction and hunting pressure | 63 |
| 3 | Results | 64 |
| 4 | Discussion | 69 |
| | Acknowledgements | 74 |
| | Supplementary information | 75 |
| | Extended Methods | 75 |

| | |
|--|-----------|
| Chapter IV: Habitat destruction and overexploitation drive widespread declines in all facets of mammalian diversity in the Gran Chaco | 89 |
|--|-----------|

| | | |
|---|--------------|----|
| | Abstract | 90 |
| 1 | Introduction | 91 |
| 2 | Methods | 94 |

| | | |
|-------|---|------------|
| 2.1 | Study region | 94 |
| 3 | Datasets used | 95 |
| 4 | Depicting biodiversity facets | 96 |
| 4.1 | Threat effects on biodiversity facets | 99 |
| 5 | Results | 100 |
| 6 | Discussion | 105 |
| | Acknowledgements | 110 |
| | Supplementary information | 111 |
| <hr/> | | |
| | Chapter V: <i>Synthesis</i> | 121 |
| <hr/> | | |
| 1 | Summary and conclusions | 122 |
| 2 | Crosscutting insights | 126 |
| 3 | Implications for conservation practice | 129 |
| 4 | Future research | 131 |
| <hr/> | | |
| | References | 133 |
| | | |
| | Appendix A: Beyond fangs: beef and soybean trade drive jaguar extinction | 155 |
| | | |
| | Eidesstattliche Erklärung | 161 |
| <hr/> | | |

List of Core Chapter Figures

Main Text

| | |
|---|----|
| Figure I-1: The relative contributions of direct drivers, or threatening mechanisms, to declines in terrestrial, freshwater, and marine biodiversity. The relative importance of these threats is based on the frequency of mentions in assessments of species conservation statuses by experts. Modified from Díaz et al. (2019) and IPBES (2019)..... | 4 |
| Figure I-2: Tropical dry forests and the Gran Chaco. (A) Global distribution of the tropical dry forests and savannahs, highlighting the Gran Chaco (data source: Olson et al. 2001). (B) Current (2015) land cover in the Gran Chaco and its composing ecoregions: The Dry Chaco (West), and the Wet Chaco (East) (data source: Baumann et al. 2017). (C) A forest in the Dry Chaco (Photo: T. Kuemmerle). ... | 9 |
| Figure I-3: Some of the larger mammals inhabiting the Gran Chaco, representing different ecological roles (e.g. carnivores, insectivores, herbivores, and frugivores) and phylogenetic groups (Photos: A. Romero-Muñoz) (<i>Continues in next page.</i>) | 17 |
| Figure II-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..... | 33 |
| Figure II-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..... | 35 |
| Figure II-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. | 40 |
| Figure II-4: Area change of the four habitat categories for jaguar for 1985, 2000 and 2013 across the entire Chaco. | 41 |

| | |
|--|----|
| Figure II-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. | 43 |
| Figure II-6: Transition between jaguar habitat categories between 1985 and 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 (c) Jaguar Conservation Units and Corridors..... | 44 |
| Figure II-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. | 45 |
| Figure III-1: Framework for reconstructing ‘ <i>geographies of threat</i> ’ due to habitat destruction and hunting pressure for 48 larger mammals in the Chaco from 1985 to 2015. We first modelled the spatial footprint of each threat per species, then stacked these footprints across the community, and then used this information to assess how spatial footprints of threats changed over time (including threat overlaps). | 62 |
| Figure III-2: Spatial footprints of habitat destruction and hunting pressure in the Chaco for 48 larger mammals. Number of species affected by habitat destruction (A) and hunting pressure (C) in 2015. Change in species numbers affected by habitat destruction (B) and hunting pressure (D) between 1985 and 2015..... | 65 |
| Figure III-3: Expansion in the footprints of habitat destruction and hunting pressure for 48 Chacoan mammals between 1985 and 2015 (as a percentage of their range in 1985). (A) Change in the footprints of habitat destruction vs. that of hunting pressure (see Figure SI III-5 for all species’ names). Positive values indicate an expansion and negative values a contraction of threat footprints. Dashed lines indicate averages across all mammals. (B) Relative change from 1985 to 2015 for each threat footprint across the three Chaco countries..... | 66 |
| Figure III-4: Numbers of species (in 10% quantiles) affected by poor habitat (blue gradient), high hunting pressure (yellow gradient), or both (grey-to-purple gradient) in 1985 and 2015, for a total of 48 larger mammals. Thick lines | |

| | |
|---|-----|
| represent country limits whereas thin lines denote protected areas in the Chaco | 67 |
| Figure III-5: Relative changes in the footprints of poor habitat and hunting pressure, and areas where both threats acted simultaneously, between 1985 to 2015 in the Chaco | 68 |
| Figure III-6: Priority areas (i.e., the most important areas with high-quality habitat and low threat levels) and hotspots of threats (i.e., areas where threats have disproportionally high impacts) for larger mammals in the Chaco, based on the rarity-weighted richness (i.e., sum of inverse range sizes). (A) Hotspots of core areas in 2015, which represent priority areas for conservation. (B) Bivariate map of hotspots of habitat destruction (1985-2015) and high hunting pressure (2015), which represent priority areas for threat-specific conservation action. | 69 |
| Figure IV-1: Framework to quantify and map changes in the three facets of mammalian diversity (taxonomic, phylogenetic and functional diversity) across our study region. | 99 |
| Figure IV-2: Change in the three facets of mammalian diversity of the Chaco between 1985 and 2015. (a) Standardized facet values (percentage of maximum values) per country for the baseline year of 1985. (b) Changes in standardized facet values between 2015 and 1985 across 21,462 communities (5x5 km ² gridcells). ... | 101 |
| Figure IV-3: Changes in the taxonomic, phylogenetic, and functional facets of mammalian diversity in the Chaco from 1985 to 2015, assessed for communities with ≥ 5 species in both 1985 and 2015. Red areas represent communities with higher losses, blue with higher increases, and grey no change. In white we represent all communities that were not assessed because they had ≤ 4 species in either 1985 or 2015. All facets are standardized so that 100% represents the diversity of this facet for the full Chacoan community of 48 larger mammals. | 102 |
| Figure IV-4: Relative importance of threats for losses in biodiversity facets between 1985 and 2015. Relative importance is measured by attributing a threat category to each species lost from a community, and weighting species by their distinctiveness in the community. (a) Relative importance of threats across all cells that experienced facet decline. (b) Relative importance of threats in the top 25% of cells with highest declines per facet. | 103 |

| | |
|---|-----|
| Figure IV-5: Top 25%, 17%, 10% and 5% of gridcells for each facet of mammalian diversity in the Chaco in 2015. | 104 |
| Figure IV-6: Overlap among the 17% of gridcells with the highest values for each of the three facets of mammalian diversity in the Chaco in 2015. Colours indicate facet overlap. The legend also indicates the percent of the total Chaco area inside each combination of facets. | 105 |

Supplementary Information

| | |
|--|----|
| Figure SI II-1: Correlation matrix to test for collinearity among predictor variables. Values for Pearson correlation coefficients shown. When correlation was high (>0.75) we selected the variables with higher contribution according to the Jackknife analysis in preliminary modelling in Maxent (selected variables denoted with an 'x' at the end). 'H' and 'R' at the end of variable names indicate predictor group, as hunting threats, and resource availability groups, respectively. 'pct' = percentage. | 53 |
| Figure SI II-2: Distance of core area cells for jaguar to the closest international borders in (a) a map of core areas in 2013, and (b) histogram of number of 1-km ² core area cells by distance. Median distance to border is 80 km. | 54 |
| Figure SI II-3: Coverage of habitat categories in areas of 5-km and 10-km buffers around 28 independently collected sites of jaguars killed by humans in the Chaco. ... | 54 |
| Figure SI III-1: Correlation matrix of the predictor variables of resource availability. | 83 |
| Figure SI III-2: Average Training Area Under the Curve scores for the habitat suitability models for the resource-related models for the mammals of the Chaco. | 84 |
| Figure SI III-3: Number of core areas – where both threats are low – of the 48 larger mammals of the Chaco in 2015 (left) and their change between 1985 and 2015 (right). On the right, red = loss of core areas, grey = stable, blue = gain of core areas). Thick lines represent country limits whereas thin lines denote protected areas in the Chaco. | 85 |
| Figure SI III-4: Habitat destruction and hunting pressure change over time inside and outside protected areas from 1985 to 2015 (A). (B) Area change (in km ²) of threats inside and outside protected areas. (C) Change in % core area change among Chaco countries and (D) between protected and unprotected areas across Chaco countries. | 86 |

| | |
|--|-----|
| Figure SI III-5: Expansion in the footprints of habitat destruction and hunting pressure for 48 Chacoan mammals between 1985 and 2015 (as a percentage of their range in 1985) with the species names for all evaluated mammals. Change in the footprints of habitat destruction vs. that of hunting pressure, where positive values indicate an expansion of that threat. The grey dashed line indicates the average change per threat for all mammals. | 87 |
| Figure SI III-6: Hotspots of core areas and of habitat destruction and hunting pressure for the Chaco larger mammals in a global context, based on the rarity-weighted richness considering the global extent of species ranges from IUCN. (A) Hotspots of core area in 2015, where high values indicate more species that have small core areas. (B) Bivariate map of hotspots of habitat destruction (1985-2015) and high hunting pressure (2015), where higher scores mean more species that have small overall area of their core area + the area under each threat. | 88 |
| Figure SI IV-1: Correlation matrix among traits and trait levels (see Table SI IV-1) used to calculate Functional diversity..... | 113 |
| Figure SI IV-2: Quality of the functional space and the trade-off between number of dimensions included and the area excluded from the functional diversity (FD) calculation. (A) Quality of the functional space assessed with the mean squared deviation (mSD) resulting from the use of two to seven PCoA dimensions (2D to 7D; the lower the mSD value, the more accurately the functional space represents the initial trait values). (B) Area of the Gran Chaco (total area = 1,100,000 km ²) that would be excluded from the FD calculation for each number of dimensions, and the associated minimum species number required per community to calculate FD (e.g. when using four dimensions, FD can be calculated only for communities with five or more species). (C) Area of the Chaco for which FD can be included (blue) and area excluded (grey) when using four dimensions. | 114 |
| Figure SI IV-3: Change in the metrics for biodiversity facets within and outside protected areas across communities with ≥ 5 larger mammal species in the Chaco region. | 115 |
| Figure SI IV-4: Decomposition of the temporal community dissimilarity between 1985 and 2015 in the Gran Chaco into its species richness change and turnover components based on the Sorensen dissimilarity index. (A-C) maps of each | |

| | |
|---|-----|
| component and of total dissimilarity in the Gran Chaco. (D) boxplots of the values of each component. | 116 |
| Figure SI IV-5: Values of the taxonomic, phylogenetic, and functional distinctiveness of the species that became affected by single or co-occurring threats between 1985 and 2015 across the Gran Chaco region..... | 117 |
| Figure SI IV-6: Change in the taxonomic and phylogenetic facets of mammalian diversity across the entire Chaco from 1985 to 2015 (43,941 communities). (A) Maps of change of taxonomic and phylogenetic diversity across the Chaco. Red areas represent communities with higher losses. Facets are standardized so that 100% represents the diversity of this facet for the full Chacoan community of 48 larger mammals. (B) Boxplot of the change in the two facets across Chaco countries. | 118 |
| Figure SI IV-7: Relative contribution of threats to losses in taxonomic, phylogenetic and functional distinctiveness between 1985 and 2015 focused on the areas with ≥ 5 species (where FD could be calculated). These results are shown for comparison to those for the entire Chaco shown in Figure IV-4. | 119 |

List of Core Chapter Tables

Main text

| | |
|---|----|
| Table II-1: Predictor variables for the two-dimensional habitat modelling for jaguar in the Chaco. | 37 |
| Table II-2: Area covered by (1) high hunting threats, (2) low resource availability, and (3) 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. | 42 |

Supplementary Information

| | |
|---|----|
| Table SI II-1: Sources of occurrence records of jaguars across the Gran Chaco ecoregion. | 51 |
| Table SI II-2: Variable contribution to the resource availability and hunting threats models in Maxent performed for jaguar in the Chaco..... | 51 |

| | |
|--|-----|
| Table SI II-3: Performance of the models incorporating land cover variables' coverage (%Forest, %Cropland, %Forest_Border and %Grassland) sampled at three different radii from the target cell. Performance is based on the AUC (Area Under the Curve) value and is shown for each group of variables | 52 |
| Table SI II-4: Frequency and total area of core area patches of different size classes in 1985, 2000, and 2013 for jaguar across the Chaco. The total number and cumulative areas are shown for all fragments and for those larger than 5,000 km ² . The columns "2013-puestos" show values after subtracting the overlapped area between 2013 core areas and the locations of smallholder ranches ("puestos") plus a 5-km buffer to account for potential time-delayed effects in jaguar decline by 2013. | 52 |
| Table SI III-1: Sources of presence locations for the 48 mammal species from across the Chaco ecoregion. | 78 |
| Table SI III-2: Description of predictor variables used in the habitat suitability and hunting pressure models. All variables covered the entire study region and were generated at a resolution of 1 km ² (see Supporting Information for details). . | 79 |
| Table SI III-3: Characteristics of the 48 larger mammals analysed. | 81 |
| Table SI IV-1: Species, traits and trait values for each species in the Chaco. Abbreviations: Ar = Arboreal, G = Ground dwelling, S = Scansorial; invert = invertebrates, vert = vertebrates. | 111 |

List of Appendix Figures

Main text

Figure A 1: Trade volume of soybeans and beef from Latin America to the main importing regions and the associated contraction of the jaguar range. Arrow thickness represents the yearly average volumes exported from Latin American countries between 2013 and 2017, expressed in thousand tons of soy and beef (data: <http://resourcetrade.earth>). Arrow thickness reflect the values as scaled in the Exports legend, where thickness range from the lowest to highest export volumes. The historical and recent jaguar ranges are shown in yellow and orange, respectively (data: Sanderson *et al.* 2002). The lower left inset shows the forest loss within the recent jaguar range in 2001 and 2015 due to commodity production (mainly beef and soybeans) (data: Curtis *et al.* 2018).

156

Chapter I:
Introduction

1 The human-caused global biodiversity crisis

Current biodiversity declines caused by human activities signal that the Earth has entered the sixth mass extinction in its 4.5-billion-year history (Barnosky et al. 2011; Ceballos et al. 2015). Current human activities are driving about 1 million species towards extinction (IPBES 2019). This widespread biodiversity decline is currently the main component of the global environmental crisis, affecting the integrity of ecosystems globally, and the provision of nature's contributions that underpin human societies (Cardinale et al. 2012; Hooper et al. 2012a; Díaz et al. 2019). Over recent decades, the biodiversity crisis has been accentuating particularly fast in the tropics, which harbour most of the biodiversity of the world (Hansen et al. 2013; Ceballos et al. 2017; Barlow et al. 2018). Given this global environmental crisis, saving biodiversity and consequently human societies constitutes an enormous, but vital, challenge for humanity (Díaz et al. 2019).

The current global biodiversity crisis is a consequence of the widespread and increasing human footprint in ecosystems across the world. Currently, human activities are substantial over more than 75% of the global land area (Ellis & Ramankutty 2008; Venter et al. 2016). Human pressure around the world is so pervasive that humans are likely taking the planetary conditions – which have remained relatively stable and benign to human societies for about 11,700 years – to a different, less hospitable, state (Steffen et al. 2015). So far, anthropogenic perturbations may have already taken four out of nine Earth System processes outside proposed planetary boundaries beyond which the functioning of the Earth system may be substantially altered: climate change, biosphere integrity (biodiversity), biogeochemical flows, and land system change (Steffen et al. 2015). Two of those boundaries, climate change and biosphere integrity, are considered core planetary boundaries, as each of them could on its own push the Earth System into a different state (Steffen et al. 2015).

Land system change and biosphere integrity are highly integrated Earth System processes, and are connected to all other planetary boundaries (Steffen et al. 2015). Indeed, land-use change – a major global driver of biodiversity loss through habitat destruction (Kehoe et al. 2017; Díaz et al. 2019) – and related impacts have already pushed the state of biodiversity beyond the planetary boundary across 58% of the global land area, including in biodiversity-rich biomes such as tropical rainforests, dry forests, and savannas (Newbold et al. 2016). Although such figures are already high, they do not directly account for other

major threats that are often associated with land-use change. For instance land use change, and the policies to incentivize it, often also encourage road development and human settlements, which promote overexploitation of natural resources, such as hunting, fishing, and logging (Brook et al. 2008; Laurance et al. 2014). This highlights the need to consider multiple major drivers of biodiversity loss in order to better understand humans' impact on biodiversity, particularly in regions already moving outside the planetary boundary for biosphere integrity.

The impact of humans on nature follows a causal chain of elements at different scales that ultimately lead to biodiversity decline. Following the classification by Balmford et al. (2009), this chain starts with *underlying drivers* of biodiversity loss, such as increasing per capita consumption of land-intensive food types. An underlying driver promotes one or more *sources of the threat*, such as agriculture or road development. This in turn triggers one or more *threatening mechanisms*, such as habitat destruction and overexploitation, which directly produces an *unfavourable state of a biodiversity feature*, such as contraction of suitable habitat for a species (Balmford et al. 2009). The impact of the threatening mechanisms – hereafter *threats* – of habitat destruction and overexploitation on biodiversity on is the subject of this thesis.

Often, the underlying drivers and sources of threat cause multiple threats that simultaneously affect biodiversity within a region (Brook et al. 2008; Côté et al. 2016). For instance, agricultural expansion directly produces habitat destruction, but also promotes overexploitation by increasing accessibility for hunters into previously remote forests (Peres 2001). Consequently, biodiversity declines may occur across larger areas, or at higher rates, when threats act together than when a single threat is present (Brook et al. 2008). Indeed, where threats act simultaneously in an area, they may synergise, producing impacts even larger than their simple sum (Brook et al. 2008; Côté et al. 2016). Despite this, most studies over broad areas consider threats in isolation (Brook et al. 2008; Dirzo et al. 2014), and likely underestimate the anthropogenic impact on biodiversity.

2 The impact of habitat destruction and overexploitation on biodiversity

Habitat destruction and overexploitation have been and continue to be the main anthropogenic threats directly driving biodiversity loss (Maxwell et al. 2016; Tilman et al. 2017; WWF 2018; Díaz et al. 2019). Both threats account for 50% of the impact of humans

on species' status assessed by experts globally (IUCN 2018; Díaz et al. 2019)(see Figure I-1). Both threats also account for 80% of the decline in 3,789 animal populations monitored over time (WWF 2018). The other major threats to biodiversity account for the remaining impacts and include, in decreasing importance, invasive species, disease, pollution, and climate change (Figure I-1) (WWF 2018; Díaz et al. 2019; IPBES 2019).

Although these global assessments of threats provide an idea of the global relative importance of threats, they quantify threats' relative importance as the frequency of mentions by experts in species assessments (Díaz et al. 2019), or the frequency of mentions in publications of animal populations trends (WWF 2018). Therefore, they cannot be used to guide on-the-ground conservation actions beyond the individual populations assessed, which highlights the need for more ecologically meaningful measures of threat magnitude and relative importance.

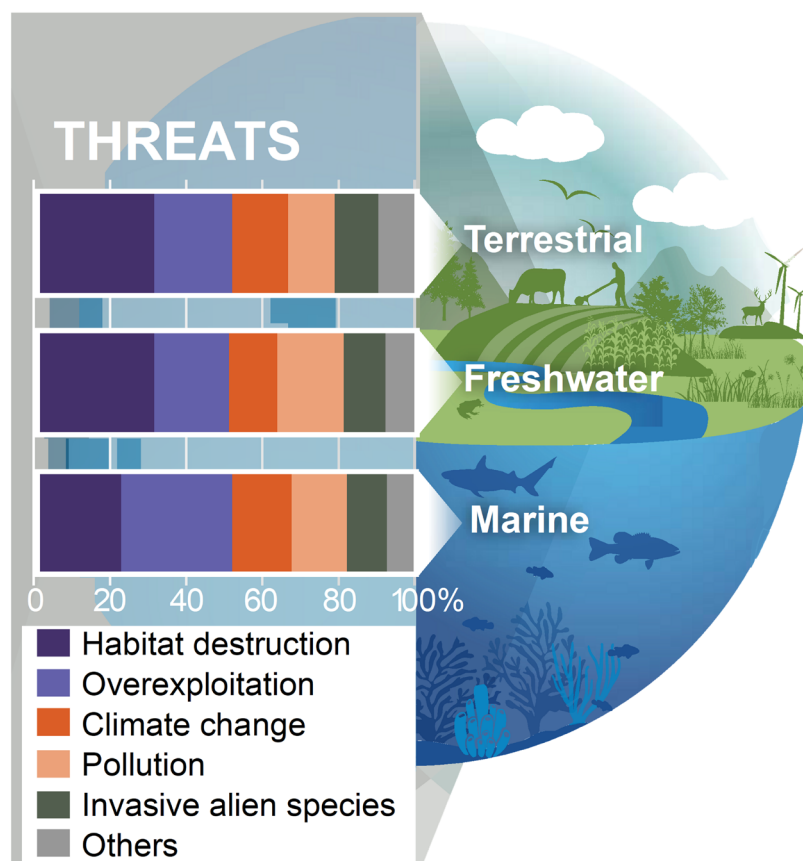


Figure I-1: The relative contributions of direct drivers, or threatening mechanisms, to declines in terrestrial, freshwater, and marine biodiversity. The relative importance of these threats is based on the frequency of mentions in assessments of species conservation statuses by experts. Modified from Díaz et al. (2019) and IPBES (2019).

Therefore, assessing how the spatial impact of threats to biodiversity change over time could help better understand the individual and combined impact of major threats to biodiversity. I refer to this an assessment of the '*geographies of threat*'. Understanding the geographies of threat can also guide conservation planning by identifying key areas where mitigating specific threats could return large conservation benefits. However, a lack of data and approaches have limited the development of such spatially-explicit understanding of threats at fine enough spatial detail to inform conservation strategies (Joppa et al. 2016).

Habitat destruction is the transformation of the environment where a species' population lives. This threat is mainly driven in terrestrial ecosystems by agricultural expansion and intensification, but also by road development and urbanization (Balmford et al. 2009). Across terrestrial and freshwater ecosystems, habitat destruction is the dominant threat, accounting for over 30% of the human impact on species, measured as the frequency of mentions of threats in the IUCN Red List of Threatened Species assessments (Díaz et al. 2019; IPBES 2019) (Figure I-1). Moreover, across monitored vertebrate populations, habitat destruction is mentioned as the cause of decline for almost 50% of birds, reptiles and amphibians, 45% of mammals, and 27% of fishes in the Living Planet Index (the Living Planet Index – WWF 2018).

Overexploitation is the unsustainable direct extraction of individual organisms from their environment through hunting (including poaching), collection, and harvesting. Overexploitation is itself driven by the subsistence protein consumption of local people, bushmeat trade, the pet trade, trade in body parts, recreational hunting, and persecution of animals thought to cause economic losses, such as attacks on crops and livestock. Overexploitation is the second most important threat to biodiversity globally, mentioned as a threat for about 20% of the species in terrestrial and freshwater ecosystems, and about 30% in the sea (Díaz et al. 2019) (Figure I-1). For monitored vertebrate populations, overexploitation is mentioned as a cause of decline for about 20% of birds, reptiles and amphibians, 37% of mammals, and 55% of fishes (WWF 2018).

Beyond their individual impacts, habitat destruction and overexploitation often affect biodiversity simultaneously within a region, and even in the same site, potentially exacerbating biodiversity losses (Peres 2001; Brook et al. 2008). Indeed, some sources of threats such as agricultural and road expansion are often associated, and both can promote both threats (Brook et al. 2008). For instance, deforestation for agricultural expansion directly produces habitat destruction, but also allows more people to access and hunt in

previously remote habitats (Laurance et al. 2014), and to persecute species believed to attack on livestock (Woodroffe et al. 2005). Likewise, road construction directly increases accessibility of hunters to remote areas, but also encourages new human settlements and further deforestation for agricultural expansion (Laurance et al. 2009; Benítez-López et al. 2019). Indeed, habitat destruction and overexploitation are the two threats most mentioned as affecting species simultaneously (Maxwell et al. 2016). The fact that both threats often act simultaneously on populations within a region means that the overall area under anthropogenic threats may be larger than the area under a single threat, as each threat may act in different areas. Moreover, where both threats act simultaneously in the same site, they may synergise, producing impacts that are larger than the sum of their parts (Brook et al. 2008; Dirzo et al. 2014). Therefore, biodiversity in regions where both threats are present is likely declining faster and more extensively than if only one threat was prevalent. This highlights the importance of assessing the impact of both threats on biodiversity simultaneously.

Even though habitat destruction and hunting pressure often threaten biodiversity in the same region, most previous broad-scale, spatially-explicit studies have either focused on habitat destruction (Ocampo-Peñuela et al. 2016; Semper-Pascual et al. 2018) or hunting (Ripple et al. 2016; Benítez-López et al. 2017). The few studies that have assessed the species-specific footprint of both threats simultaneously over broad scales, have all applied a 'core/sink' approach to simultaneously model the individual and combined impact of each threat, but they all focused on single species at single snapshot in time (Naves et al. 2003; Kanagaraj et al. 2011; De Angelo et al. 2013; Bleyhl et al. 2015).

More recently, a few studies have assessed the spatial impacts of habitat destruction and hunting pressure simultaneously on multiple species (Symes et al. 2018; Allan et al. 2019; Gallego-Zamorano et al. 2020). However, these studies assumed a uniform response for multiple species to at least one threat, by using author-defined rules to depict the extent of a threats' footprint (e.g., equating area deforested to the footprint of habitat destruction or fixed distances from roads to the footprint of hunting), rather than assessing the species-specific response to each threat. Furthermore, these multiple-species studies have relied on expert-derived range maps (IUCN 2016), which have a strong taxonomic and geographic biases in knowledge and contain false presences and absences and can therefore only be used at very coarse resolutions and with high spatial uncertainties (Hurlbert & Jetz 2007; Ficetola et al. 2014). Therefore, such results have little relevance for conservation planning at local and regional scales. On the other hand, no study has yet assessed the impact of

multiple major threats on all facets of biodiversity (taxonomic, phylogenetic, and functional diversity). These knowledge gaps prevent better understanding the geographies of threat (Brook et al. 2008; Dirzo et al. 2014), and informing where we should focus efforts to mitigate those threats (Tulloch et al. 2015).

Therefore, an important challenge to understanding the geographies of threat is to build ecologically meaningful maps of habitat and threats at fine-enough resolutions to be valuable for conservation planning. The ‘core/sink’ modelling approach previously applied to single species at a single snapshot in time to map the high quality and unthreatened habitat (core areas), and the areas under one or two threats (Naves et al. 2003; De Angelo et al. 2013; Bleyhl et al. 2015), could serve as a basis for developing such understanding. This approach, based on habitat suitability models for each threat, could be expanded to multiple species. However, because biodiversity sampling and hunting pressure often have similar spatial sampling bias (e.g., both are more intensive along roads), modelling hunting pressure with habitat suitability models will likely return inaccurate maps of hunting pressure for most species, except very few species with relatively large datasets with low spatial bias. An opportunity to consistently mapping hunting pressure for multiple species is brought by a newly developed model that allows for mapping the species-specific footprint for hunting pressure based on intrinsic species characteristics and the distribution of known spatial sources of hunting (Benítez-López et al. 2019). Combining habitat suitability models and hunting pressure models to depict the footprints of habitat destruction and of hunting pressure, respectively, could provide the opportunities to assess the geographies of threat of habitat destruction and hunting pressure over broad scales for multiple species.

3 The biodiversity crisis in tropical forests

The tropics maintain the overwhelming majority of biodiversity on Earth, harbouring about 90% of terrestrial bird, 77% of terrestrial mammal, and 83% of amphibian species (Barlow et al. 2018). However, the tropics also have become the regions with highest rates of biodiversity loss (Bradshaw et al. 2009; Ceballos et al. 2017; Tilman et al. 2017; Barlow et al. 2018). Indeed, most species classified as threatened by the IUCN Red List of Threatened Species depend on the tropics for their survival, and 85% of vertebrate extinctions have occurred in the tropics (Ceballos et al. 2017; Barlow et al. 2018).

Such high rates of biodiversity loss in the world's most biodiverse areas occur due to the pursue of economic growth through agricultural production and extractive industries, the increasing distal pressures from other regions, an increasing population, and the increasing per-capita consumption (Bradshaw et al. 2009; Dirzo et al. 2014; Barlow et al. 2018). Particularly, the growing local, domestic, and international demand for agricultural commodities such as beef, livestock feed, and biofuels have been the main driver of agricultural expansion and deforestation in the tropics (Laurance et al. 2014; Barlow et al. 2016; Benítez-López et al. 2019). The increasing national and international commodity trade is allowing an increasing global consumption of agricultural commodities that are produced predominantly in some tropical regions that have become global deforestation hotspots (Curtis et al. 2018; Pendrill et al. 2019). Such socio-economic processes at regional, national and international levels are the underlying factors behind extensive habitat destruction, degradation, and fragmentation, and, more indirectly, of encouraging overexploitation across large areas, which are producing widespread biodiversity declines in the tropics (Laurance et al. 2014; Barlow et al. 2016; Benítez-López et al. 2019). Despite their richness, and the extensive and increasing pressures they experience, the biodiversity in the tropics, as well as their threats, are under-researched compared with temperate regions (Barlow et al. 2018).

Within the tropics, tropical dry forests – characterized by rainfall concentrated in a few months and drought extending for several months – have been and continue to be subject to even more pressures than tropical rainforests (Miles et al. 2006). Tropical dry forests and savannahs are widely distributed across the world's tropics (Figure I-2A), but most are associated with large human populations, who have preferentially settled there due to the relative fertile soils (Steininger et al. 2001). Consequently, deforestation in dry forests has preceded and surpassed that of rainforests (Steininger et al. 2001). These pervasive pressures have made tropical dry forest the most threatened biome across the world, with about 50% of tropical dry forest area already converted by 2004 (Hoekstra et al. 2005). Over the last 35 years, tropical dry forests have continued to be the biome with the largest proportional forest loss (15% of the 1982 forest cover lost) (Song et al. 2018b). Moreover, about 97% of the remaining area of tropical dry forests is at risk from anthropogenic threats (Miles et al. 2006).

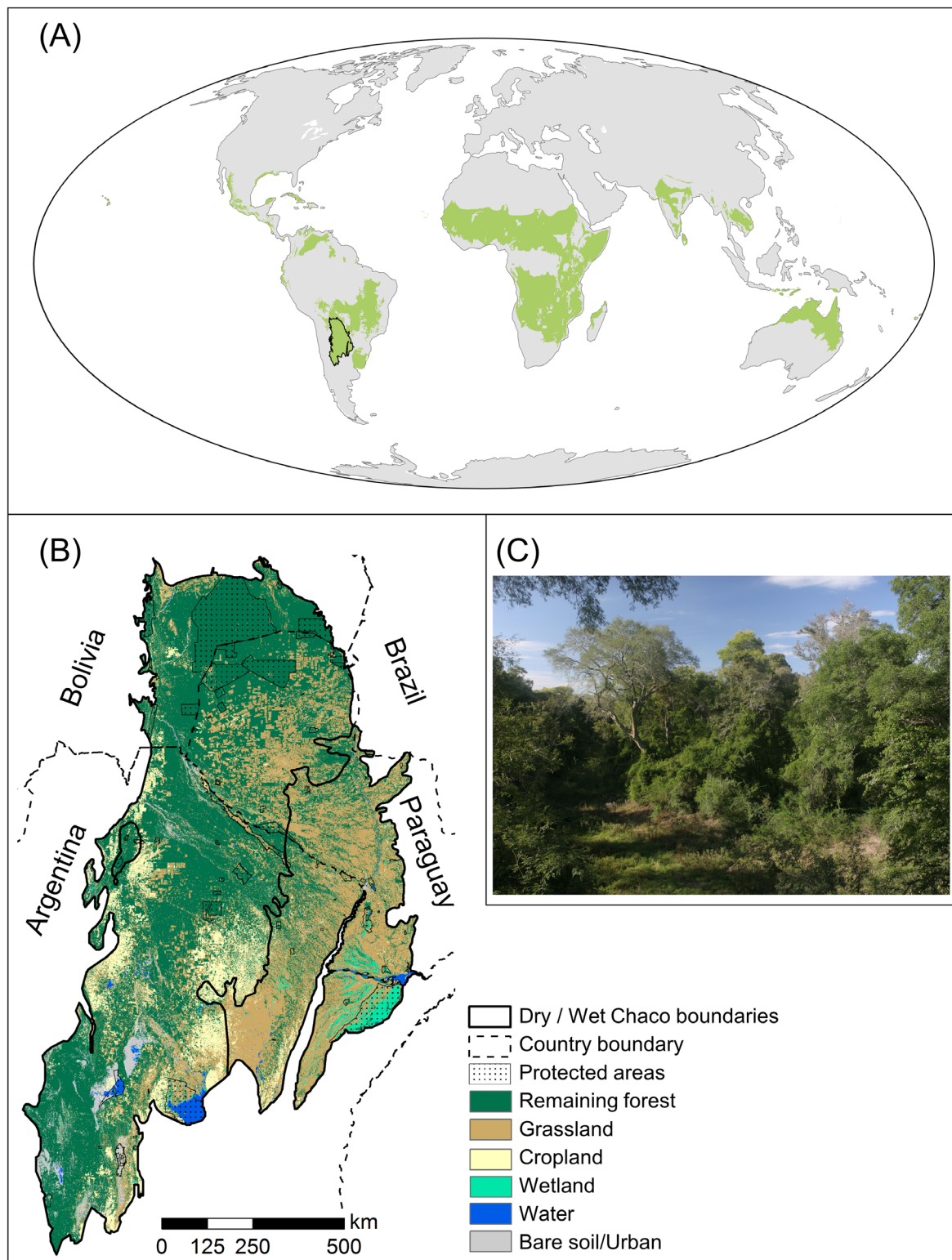


Figure I-2: Tropical dry forests and the Gran Chaco. (A) Global distribution of the tropical dry forests and savannas, highlighting the Gran Chaco (data source: Olson et al. 2001). (B) Current (2015) land cover in the Gran Chaco and its composing ecoregions: The Dry Chaco (West), and the Wet Chaco (East) (data source: Baumann et al. 2017). (C) A forest in the Dry Chaco (Photo: T. Kuemmerle).

Currently, over half of the dry forest of the world remains in South America, including the largest continuous dry forests globally – the Gran Chaco, the Chiquitano, and the Caatinga (Miles et al. 2006) (Figure I-2A), which are under increasing threat from agriculture. The main driver of the extensive deforestation across dry forests over the last few decades has been the expansion of pastures and croplands for the production of commodities such as beef, soy and maize (Gibbs et al. 2010; Curtis et al. 2018). Despite the huge pressures on tropical dry forests, they have received little conservation attention, and only about 7.6% of their area is protected (Hoekstra et al. 2005). Furthermore, tropical dry forests have received little research attention even compared to other tropical biomes (Blackie et al. 2014; Barlow et al. 2018). Therefore, understanding the impacts of agricultural expansion and related anthropogenic pressures in these rapidly vanishing forests is critical to identify where to implement specific conservation actions.

4 Defaunation and the decline of animal species, their evolutionary history, and ecological functions

Although human impacts on biodiversity across broad tropical regions are often assessed by monitoring deforestation (Gibbs et al. 2010; Hansen et al. 2013; Baumann et al. 2017), the loss of animal species and populations, or *defaunation*, is more cryptic, and therefore more challenging to monitor at broad scales (Dirzo et al. 2014). However, defaunation is a widespread and pervasive component of the current biodiversity crisis (Dirzo et al. 2014). Globally, the abundance of 16,704 monitored animal populations across the world have declined by on average 60% since the 1970s (WWF 2018). Moreover, about 32% of 27,600 vertebrate species assessed by experts in the IUCN Red List are deemed to be decreasing (Ceballos et al. 2017). Such trends illustrate that defaunation is a major driver of the environmental crisis on its own right and comparatively as important as deforestation (Dirzo et al. 2014). This is due to the crucial ecological roles that animals play in ecosystems, such as seed dispersal, pollination, and top-down regulation of plant and animal populations. The loss of such roles through defaunation affects key components of ecosystem functioning such as forest regeneration, nutrient cycling and fire regimes (Estes et al. 2011; Dirzo et al. 2014; Gardner et al. 2019).

Although studies of global patterns of animal populations illustrate their widespread declines, the available data on population trends over time is concentrated in temperate, developed countries (Young et al. 2016; WWF 2018). As biodiversity declines are increasing

in the biologically diverse tropical regions, it is crucial to understand how animal diversity is changing in those regions (Young et al. 2016). Since ecological processes occur over time, understanding patterns of defaunation requires assessing trends over time (Dornelas et al. 2014; Damgaard 2019). Such assessments cannot be easily replaced by space-for-time substitutions, as several other processes may play out over space that lead to similar spatial patterns, particularly across broad scales, therefore leading to erroneous conclusions (Damgaard 2019). This represents a major challenge to understand trends in animal diversity in tropical regions, as most such regions lack long-term monitoring schemes. Fortunately, opportunities are increasing to reconstruct changes of past environments through analyses of historical satellite imagery of land-cover (Hansen et al. 2013; Baumann et al. 2017; Song et al. 2018b). Such reconstructions of the environment can be linked with time-calibrated habitat models that use historical biodiversity data to consistently reconstruct species' habitats over time (Nogués-Bravo 2009; Kuemmerle et al. 2012). Moreover, such time-calibrated habitat models could be used in the context of core/sink habitat models that spatially depict unthreatened good quality habitat (core areas) as well as areas threatened by a single or multiple threat (Naves et al. 2003). Reconstructing animals' habitats over time could help better understand patterns of defaunation even in regions lacking long-term monitoring schemes, such as the rapidly changing regions of the tropics. Moreover, reconstructing the footprints of threats alongside available good quality habitat over time would allow us to attribute patterns of decline to a specific threat, thereby further advancing our understanding of defaunation over broad scales.

The patterns of defaunation can vary widely among groups of species in different evolutionary lineages and with different functional traits (Purvis et al. 2000; Dirzo et al. 2014). Therefore, it is important to understand how such facets of biodiversity – taxonomic, phylogenetic, and functional diversity – change (Monnet et al. 2014; Jarzyna & Jetz 2017). Regarding evolutionary lineages, some are more vulnerable to the specific human threats than others. For instance, amphibians have a larger proportion of species threatened than birds (Dirzo et al. 2014). Maintaining the unique evolutionary histories of species within different branches of the tree of life is important for their own sake and because phylogenetic diversity determines the ability of species to adapt to future environmental changes (Winter et al. 2013; Davis et al. 2018). Regarding functional traits, species with traits such as large body size, large home ranges, and slow reproduction rates are more threatened on average (Cardillo et al. 2005). The diverse intrinsic traits of animals determine their ecological roles, which contribute to ecosystem functioning and nature's

contributions to people (Cadotte et al. 2011; Winter et al. 2013; Pimm et al. 2014; Díaz et al. 2018). Thus, defaunation can have important consequences for ecosystem functioning, as well as on nature's contribution to human well-being, now and into the future (Cadotte et al. 2011; Winter et al. 2013; Díaz et al. 2018).

To better understand the consequences of anthropogenic defaunation, it is important to assess how the different facets of animal diversity change over time (Cadotte et al. 2011; Winter et al. 2013; Díaz et al. 2018). However, most research on biodiversity trends over time has focused on taxonomic diversity only (e.g. Tingley & Beissinger 2013; Dornelas et al. 2014; Blowes et al. 2019), and, to my knowledge, no study has linked changes across biodiversity facets to specific threats in a spatially-explicit manner. Very few studies have focused on assessing the change over time of all three facets of biodiversity, and all focused on birds in temperate regions (Monnet et al. 2014; Jarzyna & Jetz 2017). A lack of long-term monitoring has prevented such analysis in tropical regions, where biodiversity is concentrated. Reconstructing habitat and threats over time could open the opportunity to gain crucial insights into how multiple biodiversity facets have been changing in recent decades across tropical regions. Furthermore, the reconstructions of threat footprints could open the possibility to link the decline in specific facets to specific threats in a spatially-explicit way, further advancing our understanding of how anthropogenic threats are affecting the different facets of biodiversity.

5 The Importance of assessing the geographies of threat for conservation planning

Assessments of anthropogenic impact on biodiversity have been most often conducted at either global or local scales (Isbell et al. 2017). However, policy and land-use decisions are made at the intermediate scales of large landscapes and regions (Isbell et al. 2017). Moreover, anthropogenic threats impact ecosystem services at such intermediate scales (Isbell et al. 2017). At regional scales, anthropogenic threats drive population declines and local extinctions at rates that are orders of magnitude higher than global species extinctions (Hughes et al. 1997; Ceballos et al. 2017). As populations decline regionally, they can become functionally extinct, affecting ecosystem functioning and the provision of nature's contributions to people, even before they are completely extirpated (Isbell et al. 2017). Therefore, assessing how different aspects of biodiversity change due to anthropogenic threats at regional scales can directly inform conservation planning.

Understanding the geographies of threat for multiple aspects of biodiversity at regional scales can inform more effective conservation planning. Conservation planning – the process of locating, implementing, and managing areas to promote the persistence of biodiversity – has traditionally focused on relatively unthreatened areas containing conservation targets (Margules & Pressey 2000). More recently, conservation planning has moved to incorporate areas where key aspects of biodiversity are under one or more threats (Wilson et al. 2005; Pressey et al. 2007; Tulloch et al. 2016). Such foci can allow biodiversity to persist even in areas where it is both exposed and vulnerable to threats, by identifying and implementing the specific actions to mitigate threats within and outside conservation areas. However, research identifying where different biodiversity aspects are both exposed and vulnerable to threats in order to inform multiple threat-specific actions has been rare (Wilson et al. 2005; Pressey et al. 2007). Moreover, when considering multiple threats, assessments have often used independent maps of biodiversity and of threats, but not maps of the *impacts* of those threats on biodiversity (Halpern et al. 2015; Tulloch et al. 2015; Venter et al. 2016; Albouy et al. 2017). This information is necessary to plan for complementary strategies of proactive actions such as habitat protection, and reactive actions such as threat-specific management actions. Such complementary actions likely bring larger conservation benefits than separate actions in isolation (Pressey et al. 2007; Wilson et al. 2007; Tulloch et al. 2015). This highlights the need to understand the geographies of threat at fine spatial resolutions that are relevant for conservation planning at local, landscape, and regional levels, and to prioritise key areas for specific conservation actions, particularly in regions where multiple threats are substantially altering biodiversity, such as in tropical deforestation frontiers.

6 Importance of studying the geographies of threats on larger mammals

Larger mammals (about 1 kg or larger) have four characteristics that make them a suitable group to study the geographies of threat. First, different species of larger mammals vary in their vulnerability to habitat destruction and hunting pressure, from species that are relatively resilient to both, such as the pampas fox (*Lycalopex gymnocercus*), to species whose populations are vulnerable to both, such as jaguar (*Panthera onca*). Nevertheless, many larger mammals are among the most vulnerable species to extinction. Indeed, about 300 mammal species have already vanished globally since the Late Pleistocene (Davis et al. 2018), and the overall biomass of wild mammals has decreased approximately seven-fold

since prehistoric times (Bar-On et al. 2018). The varying vulnerability to threats among species results from external factors, such as hunters preferentially targeting certain species, and intrinsic characteristics that determine how vulnerable a species is to a threat, such as different reproductive rates, species body size, baseline population densities, and area requirements (Cardillo et al. 2005; Ripple et al. 2017).

Second, given their wide variation in intrinsic traits such as size, diet, and home range size, larger mammals play a wide range of ecological roles that contribute to several aspects of ecosystem functioning, with some unique to large mammals. For instance, only larger mammalian herbivores disperse the seeds of some of the largest trees, and often only large mammalian carnivores can regulate the populations of other large animals through predation (Terborgh et al. 2001; Lacher et al. 2019). Such ecological roles have significant effects on ecosystem functions such as nutrient cycling, energy flow, fire regimes, and forest structure (Terborgh et al. 2001; Estes et al. 2011; Lacher et al. 2019). Many ecosystem functions by larger mammals indirectly translate into nature's contributions to people, such as in promoting forest regeneration and carbon storage, pest control, water quality, and human health (Dirzo et al. 2014; Bello et al. 2015; Gardner et al. 2019). More directly, larger mammals often contribute to people's health and wellbeing as sources of protein for local communities (Noss et al. 2005). Therefore, anthropogenic threats to larger mammals can disrupt the functioning of ecosystems, as well as the provision of nature's contributions to people (Dirzo et al. 2014; Lacher et al. 2019).

Third, the high diversity of mammalian species, forms, and functions is the result of millions of years of evolutionary history (Davis et al. 2018). The vulnerability of evolutionary lineages to threats, however, is not homogeneous. In fact, some of the most ancient lineages of mammals have fewer species, and are more threatened, than more recent lineages (Purvis et al. 2000). This means that anthropogenic threats could cut entire branches off the tree of life that evolved over millions of years. Furthermore, some of such unique evolutionary branches are geographically restricted to regions experiencing increasing threats, such as the unique lineage represented only by the Chacoan peccary (*Catagonus wagneri*) who only exists in the Gran Chaco (Nori et al. 2016), making such branches at even greater risk of being irreversibly lost. Therefore, identifying the areas that harbour higher evolutionary history, and more unique evolutionary heritage for the mammalian tree of life, could help protect those branches (Winter et al. 2013).

Finally, some larger mammal species are among the most emblematic species for people at regional and global levels (Caro 2010). Some such species additionally possess traits, such as large area requirements that make them effective surrogates for overall biodiversity conservation. That means that by applying conservation actions to effectively conserve such species, much of the biodiversity associated with that species could also be conserved (Caro 2010). For instance, across Latin America, the predominant example of such a species is the jaguar (*Panthera onca*) (Caro 2010). The jaguar is South America's top predator, and the continent's most emblematic species, appearing on the bank notes and coins of several countries, including Argentina, Brazil, and Mexico. Recent research demonstrated that by conserving the key areas and corridors for jaguar across Latin America, many more species across taxonomic groups would be conserved (Thornton et al. 2015). Actions to protect this and other wide-ranging, emblematic species from anthropogenic threats would likely benefit many other species and the wider ecosystem.

7 The Gran Chaco

This thesis focusses on South America's entire Gran Chaco as the study region (Figure I-2B). Extending over 1,100,000 km², the Gran Chaco is the most extensive tropical dry forest in the world, and the second largest forest in South America after the Amazon. The Chaco maintains high biodiversity levels but has become a global hotspot of deforestation in recent decades, putting its rich biodiversity at risk (Periago et al. 2014; Torres et al. 2014). However, little is known about how the unprecedented agricultural expansion and accompanying threats to biodiversity, such as habitat destruction and hunting pressure, is affecting biodiversity across the region.

The Gran Chaco covers north-eastern Argentina (60%), the northern half of Paraguay (28%), south-eastern Bolivia (11%), and a small area in central-western Brazil (<1%) (Figure I-2). The Gran Chaco region comprises two ecoregions, the Wet Chaco in the east and the Dry Chaco in the west (Olson et al. 2001). The Gran Chaco is situated on a largely flat plain at about 300 m above sea level and covers a large latitudinal gradient from 18° to 31° South. Temperature decreases with latitude, with a tropical climate in the north, and subtropical in the south. Average annual temperature is 22°C (min: >0 degrees Celsius, max: >50°C). Annual rainfall ranges from > 1200 mm per year in the eastern Wet Chaco, to <400 mm per year in the western Dry Chaco. The entire Gran Chaco is highly seasonal, and >70% rainfall is concentrated in the summer months of November through March (Prado 1993).

The Gran Chaco has high species richness and endemism, particularly for a semi-arid region (Nori et al. 2016; Arnold & Brown 2018). Over 3,400 plant species have been identified, as well as over 500 birds, 150 mammals, 120 reptiles, and about 100 amphibian species. Furthermore, about 63 vertebrate species are considered mostly endemic to the Gran Chaco (at least 70% of the distribution within the region): 21 amphibians, 22 birds, and 20 mammal species (Nori et al. 2016). Despite its high diversity, biodiversity in the Gran Chaco has received little research attention (Nori et al. 2016; Kuemmerle et al. 2017), but available knowledge on Chacoan animal diversity indicates a worrying decline from local to regional scales (Torres et al. 2014; Nori et al. 2016; Kuemmerle et al. 2017; Semper-Pascual et al. 2018).

Larger mammals of the Gran Chaco (Figure I-3) play several ecological roles. Large herbivores, who disperse seeds, and control vegetation through seed predation and herbivory, include the tapir (*Tapirus terrestris*), the grey and red Brocket deers (*Mazama americana*, and *M. gouazoubira*), and three species of peccaries, including the endemic Chacoan peccary (*Catagonus wagneri*), the white lipped peccary (*Tayassu pecari*), and the collared peccary (*Pecari tajacu*). Other herbivores and frugivores include primates, such as the black howler monkey (*Alouatta caraya*), the cappuccino monkey (*Sapajus cay*), and the much smaller black-tailed marmoset (*Mico melanurus*). The Chaco harbours a diverse assemblage of carnivores as well, including the two largest felids of the Americas, the jaguar and the Puma (*Puma concolor*), and smaller felids, such as the ocelot (*Leopardus pardalis*), margay (*L. wiedii*), Geoffroy's cat (*L. geoffroyi*), and the jaguarundi (*Puma jagouarundi*). Canids include the crab eating fox (*Cerdocyon thous*), pampas fox (*Lycalopex gymnocercus*), and the much larger maned wolf (*Chrysocyon brachiurus*), which in addition to its role as a carnivore, it is also a well-known seed disperser. The Chaco is also rich in insectivore fauna, including several armadillo species, the great anteater (*Myrmecophaga trydactyla*) and the Tamandua (*Tamandua tetradactyla*), which form a very primitive group largely endemic to South America. Furthermore, several armadillos, such as *Cabassus chacoensis*, and *Tolypeutes matacus* (the 'ball armadillo'), are endemic to the Gran Chaco (Cuéllar & Noss 2003; Periago et al. 2014). These examples illustrate the diversity across ecological roles and phylogenetic groups of mammals in the Gran Chaco.

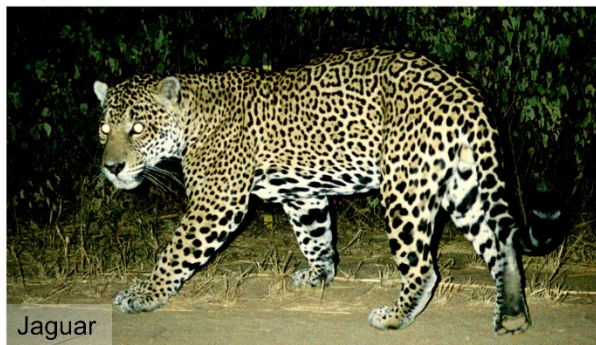


Figure I-3: Some of the larger mammals inhabiting the Gran Chaco, representing different ecological roles (e.g., carnivores, insectivores, herbivores, and frugivores) and phylogenetic groups (Photos: A. Romero-Muñoz) (Continues in next page.)

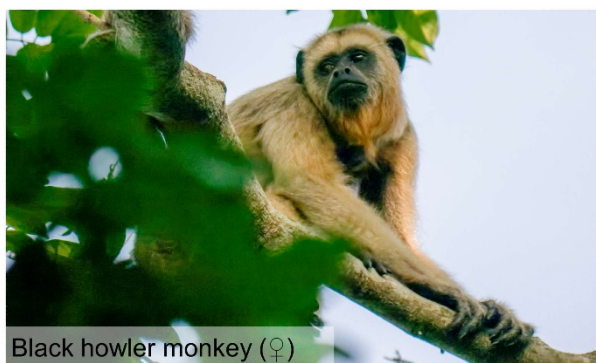


Figure I-3: (Cont.)

About 9 million people live in the Gran Chaco, including 27 Indigenous Peoples; 'criollo people' of mixed European and Native South American descent who settled in the forest starting about 200 years ago; and more recent foreigner settlers, including Mennonites, Europeans, and Asians (Arnold & Brown 2018). Most people in the Chaco live below the

average poverty levels for their respective countries (Arnold & Brown 2018). The main economic activities for export are cattle ranching to produce beef, dairy, and leather; industrial soy production, particularly in Argentina; oil and gas extraction; and timber and charcoal production (Arnold & Brown 2018).

High levels of biodiversity declines have been linked to the rapid expansion of large-scale agriculture into forests (Torres et al. 2014; Semper-Pascual et al. 2018; Macchi et al. 2019). In recent decades, the Gran Chaco has become a global centre of agricultural commodity production, mainly beef and soybeans, both for domestic and, increasingly, for international markets (Gasparri et al. 2013; Gasparri & le Polain de Waroux 2015). This production is driving the clearing of forests across at least 12 deforestation frontiers spread across all Chaco countries, but mainly in Argentina and Paraguay (Le Polain de Waroux et al. 2018). Overall, agricultural expansion has driven the loss of about 20% of the Gran Chaco forests (140,000 km²) since 1985, making the Gran Chaco a global deforestation hotspot (Hansen et al. 2013; Baumann et al. 2017; Curtis et al. 2018), and one of the most threatened regions globally (Hoekstra et al. 2005; WWF 2015). Furthermore, other activities, such as extensive livestock grazing, selective logging, and charcoal production have further degraded large areas where forest remains (Grau et al. 2008; Rueda et al. 2015).

Although much less is understood at broad scales, several local actors across the Gran Chaco frequently hunt animals, particularly mammals, for different purposes (Altrichter 2005; Noss et al. 2005). Indigenous Peoples and criollo people living inside the forest often hunt several mammal species, particularly large herbivores, for subsistence (Altrichter 2005; Noss et al. 2005; Camino et al. 2016). Furthermore, criollo people, and larger farmers often persecute animals perceived to cause damage to their livestock or crops, particularly larger carnivores such as jaguars and pumas. Additionally, some hunting is carried out in the Chaco for the pet trade, as well as for recreation (Altrichter 2006).

The closed and thorny vegetation in the Chaco makes it very difficult for people to get into the forest, therefore, deforestation for roads or for agriculture facilitates hunters' accessibility to forests. In many cases, people involved in road building, land clearing, charcoal production, and logging hunt out the animals in the increasingly smaller and accessible patches that remain (Altrichter 2006; Torres et al. 2014; Semper-Pascual et al. 2018; Macchi et al. 2019). This indicates that hunting may be strongly associated with deforestation in the Gran Chaco. Furthermore, such observations suggest that both threats

may often synergise in the Gran Chaco, producing rapid defaunation. Despite the potentially large impacts of hunting on biodiversity, this issue has received even less attention than the impacts of deforestation in the Gran Chaco (Núñez-Regueiro et al. 2015; Semper-Pascual et al. 2019). Furthermore, no study has yet assessed the impacts of hunting pressure on biodiversity across the Gran Chaco.

The worrying trends in forest cover and biodiversity in the Gran Chaco has encouraged the development of conservation planning exercises. In 2005, several regional and international conservation organisations produced the "Gran Chaco Americano ecoregional assessment", which assessed the conservation status of biodiversity and human pressures in the region (TNC et al. 2005). This assessment identified priority areas for biodiversity conservation, as well as corridors to link them. However, this assessment was largely based on expert knowledge on biodiversity, which has been limited in such an under-researched region, together with forest cover information. In 2018, that assessment and prioritization was updated by regional conservation organisations across the three countries (Arnold & Brown 2018). However, the changes were mainly based on the updated forest cover in the region, but not on updated knowledge on the spatial patterns of biodiversity nor on their responses to threats. Another recent assessment identified priority areas for conserving the endemic vertebrates of the Gran Chaco, finding that protected areas only represent 9.1% of the distribution of those species (Nori et al. 2016). These efforts are important, but they focus on either scarce biodiversity data, or on a limited number of species. In addition, they focus on the protection of forests patches, without consideration of the distribution of the main threats to biodiversity inside or surrounding these areas. Information on human pressures is necessary to design more informed conservation strategies that focus on protecting remaining patches, as well as identifying the key areas where to focus efforts to mitigate threats.

8 Research questions and objectives

Biodiversity is increasingly threatened by human activities that affect species directly and indirectly. Among the direct threats, habitat destruction and overexploitation are the main ones in driving biodiversity declines worldwide, particularly in tropical regions where both threats are often present simultaneously. It is therefore important to learn where these threats act individually or in combination on different aspects of biodiversity, such as species, communities, and the taxonomic, phylogenetic, and functional facets of

biodiversity, and how these threat footprints change over time. However, assessing the geographies of threat at broad scales and fine resolutions has been challenging due to a lack of biodiversity data at high spatial resolutions, long-term monitoring biodiversity trends, and of approaches to link changes in biodiversity to specific threats. Against this background, the overarching goal of this thesis is to *understand the impact of habitat destruction and overexploitation on biodiversity, and how these impacts change in space and over time*. To achieve this goal, I answered three main research questions. Each of the three research chapters contributes to answering each main research questions by focusing on a specific research question (hereafter “specific questions”).

Research Question 1: *Where do habitat destruction and hunting pressure affect mammalian diversity, and how do the spatial footprints of these threats change over time?*

Despite their dominance in driving global biodiversity declines, the spatial effects of habitat destruction and hunting pressure (the main form of overexploitation for larger mammals) are not well understood. Previous efforts have limited such assessments to single species, but only at a single snapshot in time. Alternatively, in the context of multiple species, they have relied on expert-based range maps, which due to gaps in knowledge for many regions and taxa can only be used at coarse resolutions; and on rule-based definitions on the extent of the footprint of threats, therefore not accounting for the species-specific responses to each threat.

The specific questions related to *Research Question 1* were:

- Chapter II.1) How did the extent and distribution of core areas and areas under threat for jaguar change between 1985 and 2013 across the Chaco?
- Chapter III.1) How did the footprints of habitat destruction and hunting pressure on larger mammals change between 1985 and 2013 across the Chaco?
- Chapter IV.1) How did the taxonomic, phylogenetic, and functional diversity of larger mammals change between 1985 and 2013 across the Chaco?

In Chapter II, I combined for the first time time-calibrated habitat suitability models and core/sink models to map good quality habitat, as well as the areas affected by habitat destruction, hunting pressure or both threats together for the jaguar, and then assessed their changes over three decades.

In Chapter III, I extended the approach that I developed in Chapter II to the entire assemblage of larger mammals of the Gran Chaco. However, because accurately depicting hunting pressure through habitat suitability models requires large and spatially unbiased species datasets, habitat suitability models are unsuitable for many species in an under-researched region. Therefore, I used a newly developed model that permits consistent mapping of the species-specific impact of hunting pressure (Benítez-López et al. 2019). By combining time-calibrated habitat suitability models for depicting habitat destruction with hunting pressure models applied in a multitemporal context, I was able to systematically assess the footprints of each threat and their change over time.

In Chapter IV, based on the multi-temporal reconstructions of high-quality habitat and threats from Chapter III, I measured the change over time in the taxonomic, phylogenetic, and functional facets of the mammalian diversity of the Gran Chaco.

Research Question 2: *What is the relative importance of habitat destruction and hunting pressure in driving mammalian diversity change?*

A better understanding of human impacts on biodiversity, and better informed prioritisation of research and conservation actions requires knowledge on the relative importance of different anthropogenic threats. The relative importance of threats has often been measured by counting the frequency of mentions of each threat by experts in species assessments (Maxwell et al. 2016; Tilman et al. 2017; Díaz et al. 2019; IPBES 2019), or in publications for populations assessments (WWF 2018). A more ecologically sound manner to assess the relative importance of threats at broad scales would be to measure the extent to which each threat affects a species, a community, or the different facets of biodiversity. This has only been previously done for single, well studied species, whereas the coarse-resolution maps and high spatial uncertainty resulting from the use of expert-derived range maps and rule-based definitions of a threat's extent in previous multiple species assessments potentially limit the inferences we can make about threat importance (Symes et al. 2018; Gallego-Zamorano et al. 2020). Consequently, the specific questions related to Research Question 2 were:

- Chapter II.2). Which factors, habitat destruction or hunting pressure, were more important in driving jaguar habitat change in the Chaco, and how has this changed over time?

- Chapter III.2) What is the relative importance of these two threats acting alone versus together on the larger mammals, and how has this changed over time?
- Chapter IV.2) How have the individual and combined effects of habitat destruction and hunting contributed to changes in the taxonomic, phylogenetic, and functional facets of the mammalian diversity over time?

In Chapter II, I compared the footprints of habitat destruction and hunting pressure for each of the threats acting alone, as well as in concert, on the jaguar, and assessed the change in these areas over time.

In Chapter III, I focus on the change in the spatial footprint of habitat destruction and hunting pressure over three decades within the ranges of 48 larger mammal species to understand the relative importance of threats. This focus on temporal change can provide a better understanding of threats' relative importance than assessing threat footprints at a single time because, for many species, spatial variation in climatic conditions determine their habitat quality in the Gran Chaco. Therefore, multi-temporal assessments can disentangle the impacts of habitat destruction from that of spatial climate conditions in determining poor habitat quality.

In Chapter IV, I linked the change in each biodiversity facet's value to a specific threat by applying newly developed measures of a species' functional and phylogenetic distinctiveness. This allowed me to measure the relative impact of each threat on the change in each biodiversity facet.

Research Question 3: What are the priority areas for conservation actions to mitigate the impact of habitat destruction and hunting pressure on mammals in the Gran Chaco?

Conservation planning is increasingly focusing not only on preserving high quality and biologically diverse areas, but also on managing specific threats where they are already affecting biodiversity (Pressey et al. 2007; Tulloch et al. 2015). Multiple, complementary actions to abate prevalent threats to biodiversity can result in greater conservation benefits than single actions (Wilson et al. 2007). Therefore, identifying key areas for biodiversity where threats are low and can thus be protected (or 'priority areas'), as well as areas where biodiversity is affected either habitat destruction or hunting pressure or both threats together (or 'threat hotspots'), is crucial for developing more effective conservation strategies in rapidly changing regions such as the Gran Chaco. The ecologically sound and

high-resolution representation of the geographies of threat developed in the previous chapters are a suitable basis to identify priority areas and threat hotspots and to inform conservation planning. Consequently, the specific questions related to *Research Question 3* are:

- Chapter II.3. How are the remaining jaguar core areas – where threats are absent – distributed among the three Chaco countries and inside vs. outside protected areas?
- Chapter III.3) How did the distribution of core areas for the larger mammals of the Gran Chaco change between 1985 and 2015, and where are current hotspots of threats and priority areas for conservation?
- Chapter IV.3) Where are the priority areas for conserving each facet of mammalian diversity in the Chaco, and where do they overlap?

In Chapter II, apart from identifying the key areas without threats, as well as the areas under specific threats for jaguar, I assessed how such areas are distributed among protected and unprotected lands and across countries. I also assessed how core areas are distributed in relation to the international country boundaries.

In Chapter III, I applied the rarity-weighted richness measure as a prioritisation measure to identify the priority areas that contain more, and more geographically restricted, larger mammals in the Gran Chaco. I also applied this concept for the first time to identify hotspots where each threat has a disproportionate impact on increasingly geographically restricted mammals of the Gran Chaco.

In Chapter IV, I determined the highest value areas for the taxonomic, phylogenetic, and functional mammalian diversity, which can inform the key areas that deserve protection in order to preserve the different dimensions of the mammalian diversity in the Gran Chaco. Furthermore, I assessed where these highest-value areas overlap among the different biodiversity facets, which highlight opportunities to conserve two or more facets of biodiversity simultaneously.

9 Thesis structure

This thesis consists of the introduction (Chapter I), followed by three core research chapters (II-IV) that contribute to answering the three main research questions, and a synthesis

(Chapter V) that summarises the main results of the research chapters, synthesises the overarching findings, and provides potential applications and directions for future research. In addition, Appendix A consists of a short, peer-reviewed article that links the increasing threats from habitat destruction and hunting pressure on jaguars to the increasing trade in agricultural commodities from Latin America to serve international markets. The three research chapters and Appendix A were written as stand-alone publications, and all have either been published or are under review in international peer-reviewed journals. Because these chapters are articles on their own, there is a limited amount of recurrent material. The chapters were published in international scientific journals as follows:

- Chapter II: **Romero-Muñoz, A.**, Torres, R., Noss, A.J., Giordano, A., Quiroga, V., Thompson, J.J., Baumann, M., Altrichter, M., McBride, R., Jr., Velilla, M., Arispe, R. & Kuemmerle, T. (2019) Habitat loss and overhunting synergistically drive the extirpation of jaguars from the Gran Chaco. *Diversity and Distributions*, 25, 176-190.
- Chapter III: **Romero-Muñoz, A.**, Benítez-López, A., Zurell, D., Baumann, M., Camino, M., Decarre, J., Giordano, A.J., Gómez-Valencia, B., Levers, C., Noss, A.J., Quiroga, V., Thompson, J., Torres, R., Velilla, M., Weiler, A. & Kuemmerle, T. (2020) Increasing synergistic effects of habitat destruction and hunting on mammals over three decades in the Gran Chaco. *Ecography*, 43, 954-966.
- Chapter IV: **Romero-Muñoz, A.**, Fandos, G., Benítez-López, A., Kuemmerle, T. (2021) Habitat destruction and overexploitation drive widespread declines in all facets of mammalian diversity in the Gran Chaco. *Global Change Biology*, 27:755-767.
- Appendix A: **Romero-Muñoz, A.**, Morato, R. G., Tortato, F., & Kuemmerle, T. (2020). Beyond fangs: beef and soybean trade drive jaguar extinction. *Frontiers in Ecology and the Environment*, 18(2), 67-68.

Chapter II:

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

Diversity and Distributions, 2019, Volume 25, Pages 176-190

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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 and 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 to 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 km²) from 1985 to 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 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: large carnivores, land-use change, persecution, retaliation hunting, human-wildlife conflicts, species distribution models, resource deterioration, source/sink habitats, poaching.

1 Introduction

Global biodiversity is in decline, mainly due to habitat loss and overhunting (Maxwell et al. 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 et al. 2015), affecting wildlife populations through diminishing resources available as well as population fragmentation (Bradshaw et al. 2009). Overhunting is a second major threat (Woodroffe & Ginsberg 1998; Dirzo et al. 2014) and can quickly deplete populations even in otherwise intact habitats, turning such areas into population sinks (Redford 1992; Delibes et al. 2001; Dirzo et al. 2014; Benítez-López et al. 2017). Habitat loss and overhunting often co-occur, yet neither their relative importance nor their interactions are well understood (Brook et al. 2008).

Where habitat loss and overhunting co-occur, they can produce strong synergistic effects that are larger than their additive sum (Mora et al. 2007; Brook et al. 2008). For instance, habitat loss reduces and isolates populations, but also increases hunter accessibility in remaining habitat patches (Peres 2001; Brook et al. 2008). Habitat loss and hunting are rarely studied simultaneously though, which hampers our ability to understand their interactions, and thus to propose effective conservation strategies (Mora et al. 2007; Brook et al. 2008).

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 (Naves et al. 2003; De Angelo et al. 2013; Bleyhl et al. 2015). 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 (Naves et al. 2003; De Angelo et al. 2013; 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 (Nogués-Bravo 2009; Elith et al. 2010; 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 (Nogués-Bravo 2009; Kuemmerle et al. 2012; 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 et al. 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 (Naves et al. 2003; Kanagaraj et al. 2011; De Angelo et al. 2013). This is arguably most challenging in ecoregions that extend across national borders, requiring trans-national cooperation given the wide-ranging nature of large carnivores (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 (Hansen et al. 2013; Baumann et al. 2017; Kuemmerle et al. 2017), experiencing widespread defaunation (Altrichter 2005; Noss et al. 2005; Periago et al. 2014). The top predator in the Chaco, the jaguar (*Panthera onca*), occurs in low densities there (less than 1 individual/km²) and depends on very large home range areas (400-2,900 km²) (Romero-Muñoz et al. 2007; Noss et al. 2012; Giordano 2015; McBride & Thompson 2018). 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 et al. 2006; Rumiz et al. 2011; Quiroga et al. 2014; Giordano 2015; Cuyckens et al. 2017). 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 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 II-1) is the largest continuous tropical dry forest ecoregion in the world, at 1.1 million km² (Olson et al. 2001; Grau et al. 2008), 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, more than 150 mammal species, as well as 500 bird, 120 reptile, 100 amphibian, and 3,400 plant species (TNC et al. 2005; Nori et al. 2016). 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 km²) 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 et al. 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 et al. 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; Rumiz et al. 2011; Cuyckens et al. 2017). 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, (Zeller 2007; Rabinowitz & Zeller 2010). 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 et al. 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 et al. 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.

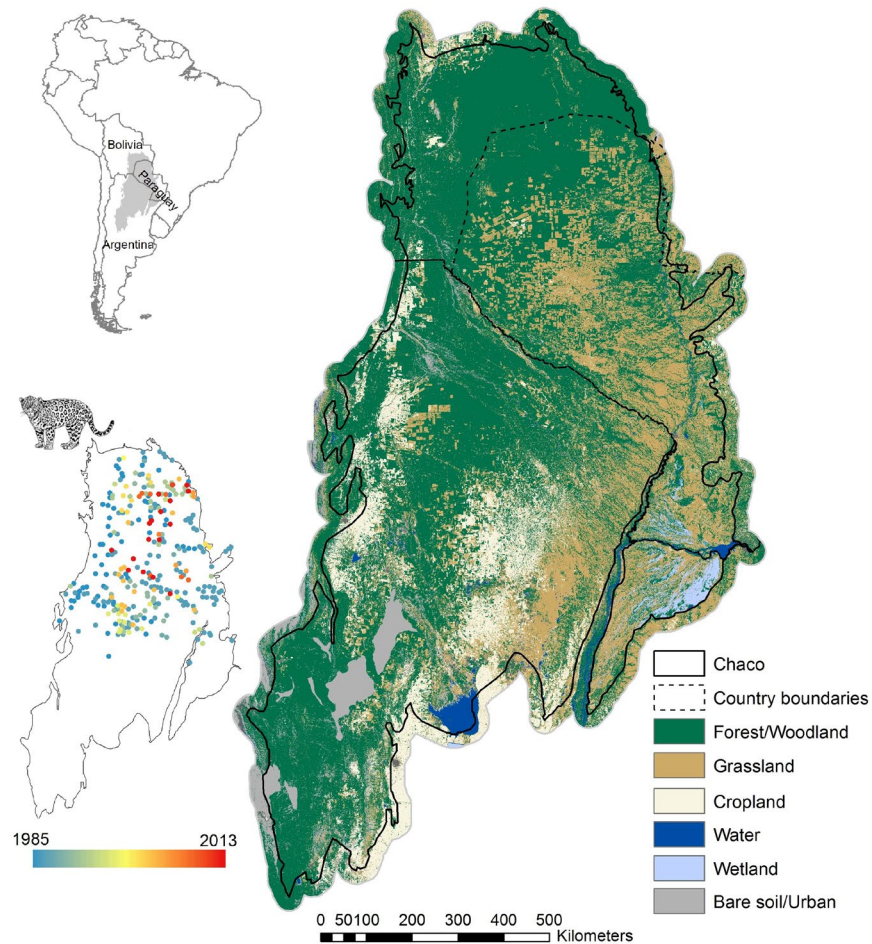


Figure II-1: Gran Chaco ecoregion (plus a 30-km buffer) with the land-use/cover categories of forest/woodland, grazing lands and croplands for the year 2013 (based on Baumann et al. 2017). ‘Grasslands’ include natural grasslands and savannahs and planted pastures. The lower left panel shows colour-coded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

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 (Table SI II-1). To reduce potential sampling bias, we applied spatial filtering by randomly selecting one occurrence record within a radius of 12 km (i.e., 452 km²), 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 II-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 II-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.

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 II-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 (Liu et al. 2013; Bleyhl et al. 2015). We then overlaid the resulting categorical maps for both models to produce core/sink habitat maps for each year (Figure II-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 II-2), and *sinks* (low resources and risky) (Naves et al. 2003; De Angelo et al. 2013; Bleyhl et al. 2015).

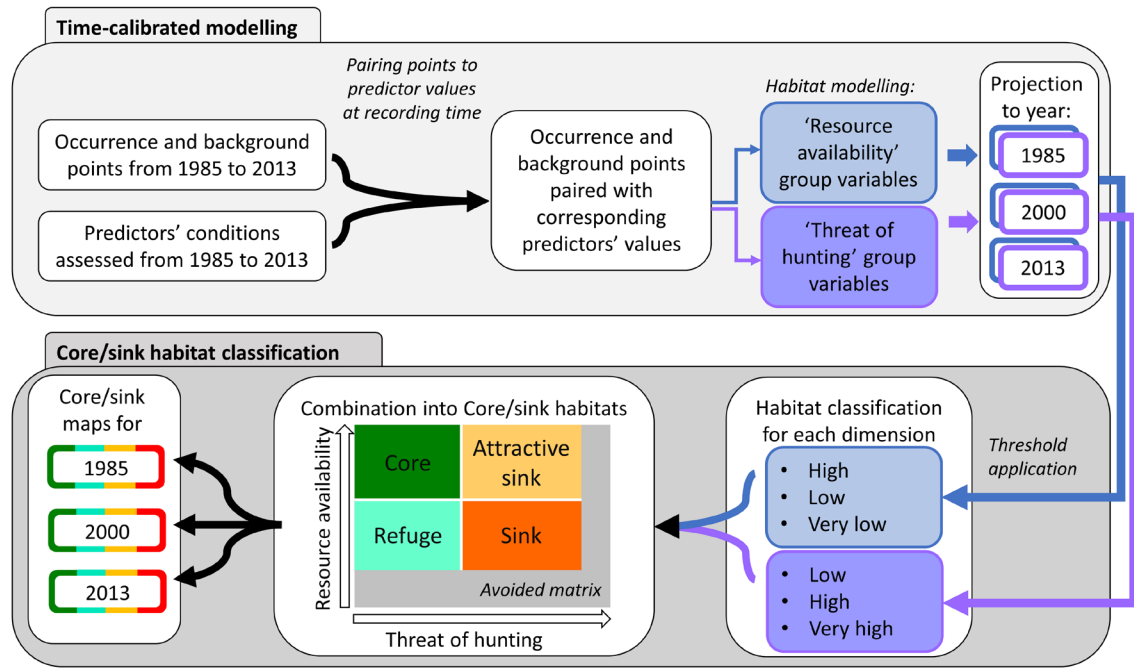


Figure II-2: Flowchart of the habitat modelling approach. We first matched occurrence points with the predictor conditions from when occurrences were recorded. We then ran two time-calibrated habitat models, one characterizing resource availability and one characterizing hunting threat. Projecting these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

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 II-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 (Figure SI II-1).

The final resource-related predictors were %Forests, %Cropland, %Edge_Forest, Annual_Prec, Annual_Temp, and Dist_Water (Table II-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 et al. 2013). The final hunting-threat-related predictors included *Cost_dist*, *Dist_2ryRoads*, *Dens_2ryRoads*, *Dist_ForestBorder* and *%Grassland* (Table II-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; Quiroga et al. 2014; Baumann et al. 2017). 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 II-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-km² 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 km², 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 (Zeller 2007; Rabinowitz & Zeller 2010). 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).

Table II-1: Predictor variables for the two-dimensional habitat modelling for jaguar in the Chaco.

| Variable | Description | Source | Temporal resolution ** | Expected effect | Explanation |
|----------------------------|---|--|------------------------|-----------------|--|
| Resource-related variables | | | | | |
| %Forest * | % forest and open woodland around target cell | Landsat Archive | Yearly | + | Provides resources for food, cover and reproduction for jaguar. |
| %Cropland * | % 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 et al. 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 digitalisation | 1985, 2000, 2013 | – | Indicates concentration of secondary roads, which indicates accessibility to remote areas, while less affected by higher detectability of jaguars. |

Chapter II

| | | | | | |
|-------------------|---|---|------------------|---|--|
| Dist_ForestBorder | Distance to forest border from inside the forest | Landsat Archive | Yearly | + | Indicates both accessibility to the forest by hunters from outside as well as 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 digitalisation 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 * | % of grasslands around target cell | Landsat Archive | Yearly | - | Indicates likelihood of hunting by persecution due to perceived or actual risks of livestock losses to predators. |

* Variables were calculated for different scales (3, 7, 11 km radius).

** Yearly means layers for 1985 and for each year from 2000 to 2013.

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 (Table SI II-2). In the hunting threat model, the most important variable were *Dist_2ryRoads*, positively related to suitability; *Cost_Dist*, positively related, and %*Grassland*, negatively related to habitat suitability (Figure SI II-1). 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 (Table SI II-3).

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 km² (from about 247,400 to 165,100 km²) (Figure II-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 2000-2013 (3,350 km² yr⁻¹) than between 1985-2000 (2,590 km² yr⁻¹). 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 II-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 II-3 and Table SI II-4). The large, continuous patch occupying most of the northern Chaco (169,000 km²) in 1985, split into three main patches by 2013 (with areas of 96,000; 9,300; 5,600 km², Figure II-3), with interspersed attractive sinks and sinks. The key patch in the Central Chaco shrank from 27,500 to 9,800 km² from 1985 to 2013 (Figure II-3). Considering only core area fragments larger than 5,000 km² – an area that may sustain 50 jaguars based on a density of ~1 individual/100 km² estimated in the Bolivian Chaco – suggests an even larger decrease in core area (42% since 1985; Table SI II-4).

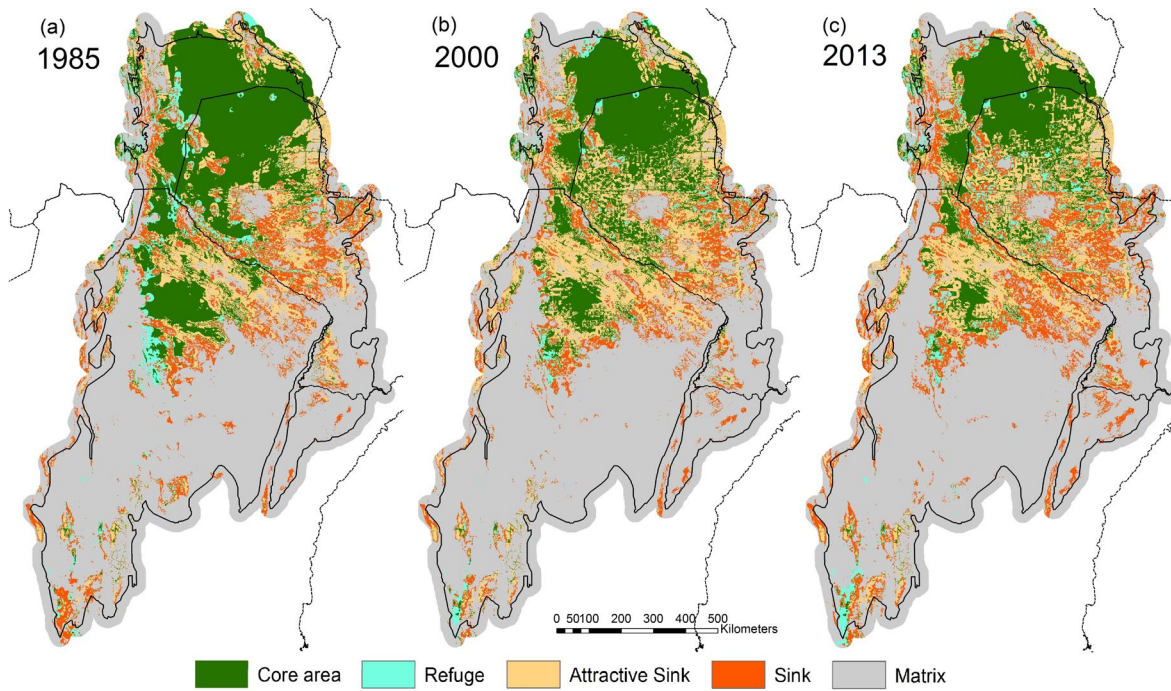


Figure II-3: Source/sink habitat change for jaguars for (a) 1985, (b) 2000 and (c) 2013 in the Gran Chaco ecoregion. Legend of habitat categories and scale apply to all three maps.

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% (0). The areas where both threats acted in synergy (i.e., sinks) covered 22% of all habitats in 1985 and 29% in 2013 (Figure II-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 II-2). Most area (>70%) under low resource availability also overlapped with hunting threats across time (0). The proportion of overlapping threats varied with years and among countries (see Table II-2).

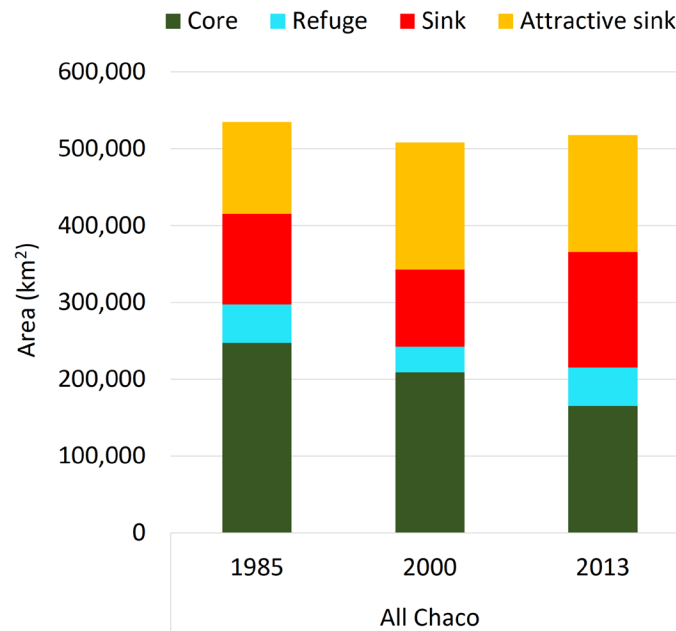


Figure II-4: Area change of the four habitat categories for jaguar for 1985, 2000 and 2013 across the entire Chaco.

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 II-5c). However, Paraguay also lost most core area (35,700 km²) from 1985 to 2013 (31% loss since 1985), while Argentina lost 34,100 km² (54% loss) and Bolivia 12,500 km² (18% loss; Figure II-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 (Figure SI II-2).

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 II-6a,b). Overall, protected areas lost 3,600 km² 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 II-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 km²) of all core jaguar habitat in the Chaco, whilst 68% (111,700 km²) remained unprotected (Figure II-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 II-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 II-6b).

Table II-2: Area covered by (1) high hunting threats, (2) low resource availability, and (3) 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.

| Region | year | Area (km ²) | | | | % of sinks in areas of: | |
|--------------|------|-------------------------|---------------------|---------------------------|---------------------------------|-------------------------|---------------------------|
| | | 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% |

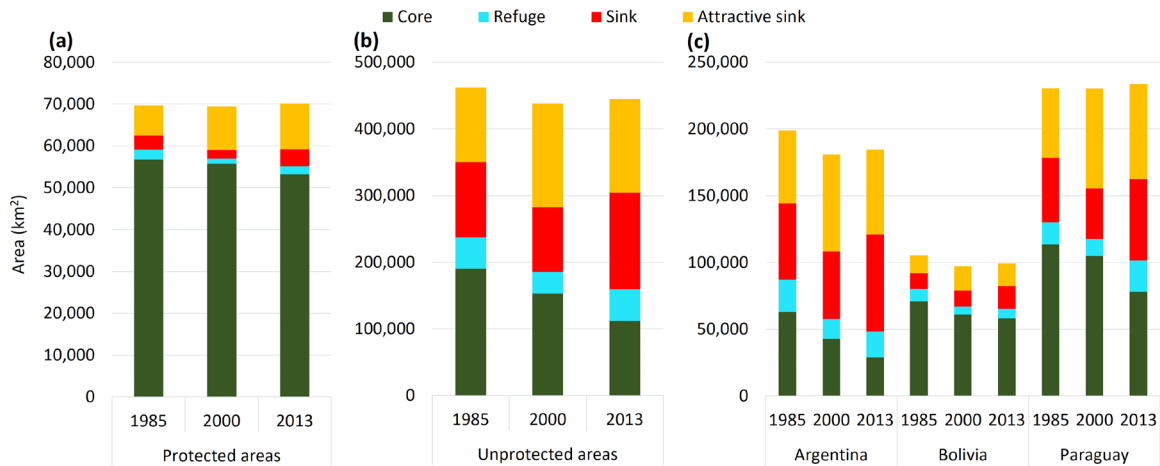


Figure II-5: Area change of the four habitat categories for jaguar in the Chaco for 1985, 2000 and 2013 in (a) protected areas, (b) unprotected areas, and (c) the three Chaco countries.

Core areas inside Jaguar Conservation Units contracted by 10% between 1985 and 2013 (from 82,100 to 74,500 km²) (Figure II-6c), with attractive sinks almost tripling. Core area contraction was faster in the central Chaco unit, where sinks increased five-fold and attractive sinks doubled, than in the larger northern Chaco unit, where sinks increased by 50% and attractive sinks tripled (Figure II-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 II-6c,d).

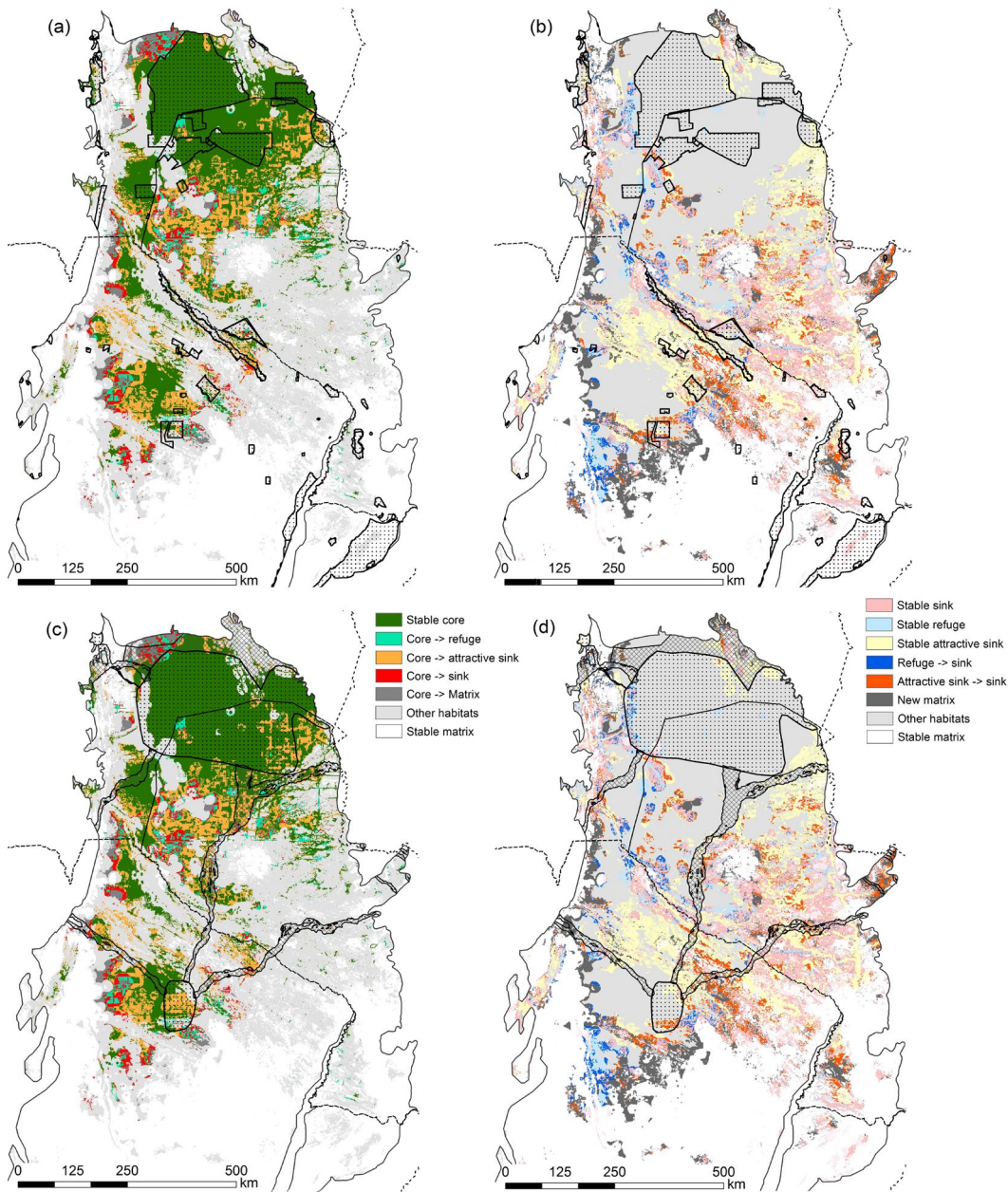


Figure II-6: Transition between jaguar habitat categories between 1985 and 2013 in the Chaco. Left: transitions from core areas to other habitat categories overlapped with the (a) protected areas and (c) with Jaguar Conservation Units and Corridors. Right: transitions among the other habitat categories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

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 to 17 km Figure II-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 II-7, Figure SI II-3). 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 II-7, Table SI II-4).

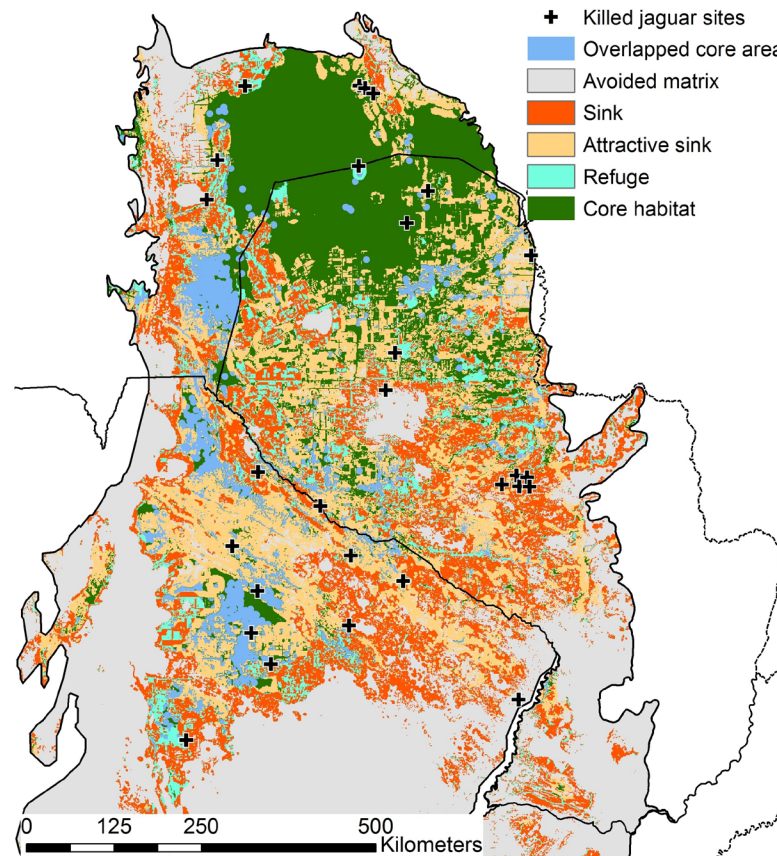


Figure II-7: Smallholder ranches locations plus a 5-km buffer overlapped with core areas for jaguar in the Chaco in 2013 (shown in blue). Such overlap areas may indicate time-delayed effects on jaguars and potential decline by 2013 and they may thus act as attractive sinks. Locations of jaguars killed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

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 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% 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 km² 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 km²). 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 et al. 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 is markedly affected by fragmentation (Haag et al. 2010; Zanin et al. 2015). Furthermore, jaguars in the Chaco exhibit some of the lowest densities and largest home ranges in the Americas (Noss et al. 2012; Quiroga et al. 2014; Giordano 2015; McBride & Thompson 2018). 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 (Naves et al. 2003; Brook et al. 2008). 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; Giordano 2015; Baumann et al. 2017; McBride & Thompson 2018). Similarly, deforestation often accompanies road expansion, which increases hunter accessibility (Piquer-Rodríguez et al. 2015; Benítez-López et al. 2017). Hunting threats expanded faster than deteriorating resource availability and occupied two-thirds of all habitat 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; Paviolo et al. 2016; Jędrzejewski et al. 2017; McBride & Thompson 2018). 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 bonasus*) 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 km² of core area, an area likely to maintain >50 individual jaguars over 100 years (Zanin et al. 2015; Paviolo et al. 2016). 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 (Woodroffe &

Ginsberg 1998; Terborgh et al. 2001; Balme et al. 2010; Laurance et al. 2012; Geldmann et al. 2013).

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 (Gasparri & le Polain de Waroux 2015; Baumann et al. 2017). 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 suggest 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 (Ripple et al. 2014; Paviolo et al. 2016; Benítez-López et al. 2017). 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; Rumiz et al. 2011; Noss et al. 2012; Quiroga et al. 2014; Giordano 2015; McBride & Thompson 2018). 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). While 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 II-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 (Benítez-López 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). Policy makers 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 (TNC et al. 2005; Hansen et al. 2013; Torres et al. 2014; Nori et al. 2016). 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.

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Biosketch

Alfredo Romero-Muñoz is a doctoral researcher at the Conservation Biogeography Group at Humboldt-University Berlin. Alfredo's research focuses on understanding how the rapidly increasing threats driven by agricultural expansion affect mammal distributions and populations in the Chaco. This research can contribute to broad-scale conservation planning for this global deforestation hotspot.

Supplementary Information

Table SI II-1: Sources of occurrence records of jaguars across the Gran Chaco ecoregion.

| Source type | Source |
|-----------------------------|--|
| Publicly available database | Global Biodiversity Information Facility (GBIF) Administration of National Parks of Argentina (APN) |
| Published literature | Sanderson et al. (2002) Torres et al. (2014) Quiroga et al. (2014) Wallace et al. (2010) |
| Unpublished literature | Giordano (2015) |

Table SI II-2: Variable contribution to the resource availability and hunting threats models in Maxent performed for jaguar in the Chaco.

| Model | Variable | Percent contribution | Permutation importance |
|-----------------------|-------------------|----------------------|------------------------|
| Resource availability | %Cropland | 50.8 | 33.1 |
| | %Forest | 23.9 | 9 |
| | Annual_Temp | 14.3 | 32.5 |
| | Dist_Water | 7.1 | 16.8 |
| | Annual_Prec | 3.9 | 8.4 |
| | %Edge_Forest | 0.1 | 0.2 |
| Hunting threats | Dist_2ryRoads | 31.8 | 18.5 |
| | Cost_dist | 26.7 | 17.5 |
| | %Grassland | 16.4 | 29 |
| | Dist_Grass | 8.6 | 17.6 |
| | Dens_2ryRoads | 8.3 | 9.8 |
| | Dist_ForestBorder | 8.2 | 7.6 |

Table SI II-3: Performance of the models incorporating land cover variables' coverage (%Forest, %Cropland, %Forest_Border and %Grassland) sampled at three different radii from the target cell. Performance is based on the AUC (Area Under the Curve) value and is shown for each group of variables

| Sample radius | AUC value |
|-----------------------|-----------|
| Resource availability | |
| 11 km | 0.705 |
| 7 km | 0.695 |
| 3 km | 0.700 |
| Hunting threats | |
| 11 km | 0.699 |
| 7 km | 0.696 |
| 3 km | 0.678 |

Table SI II-4: Frequency and total area of core area patches of different size classes in 1985, 2000, and 2013 for jaguar across the Chaco. The total number and cumulative areas are shown for all fragments and for those larger than 5,000 km². The columns "2013-puestos" show values after subtracting the overlapped area between 2013 core areas and the locations of smallholder ranches ("puestos") plus a 5-km buffer to account for potential time-delayed effects in jaguar decline by 2013.

| Fragment area interval (km ²) | Number of fragments | | | | Total area by fragment class | | | |
|--|---------------------|-------|-------|------------------|------------------------------|---------|---------|------------------|
| | 1985 | 2000 | 2013 | 2013- puestos | 1985 | 2000 | 2013 | 2013- puestos |
| 1 | 2,382 | 3,104 | 2,722 | 1,851 | 2,382 | 3,104 | 2,722 | 1,442 |
| 1-5 | 1,207 | 1,582 | 1,480 | 1,018 | 3,407 | 4,533 | 4,214 | 2,648 |
| 5-10 | 277 | 318 | 330 | 249 | 2,105 | 2,415 | 2,466 | 1,712 |
| 10-50 | 318 | 346 | 373 | 304 | 6,818 | 7,544 | 8,244 | 6,813 |
| 50-100 | 53 | 53 | 67 | 54 | 3,547 | 3,617 | 4,580 | 3,752 |
| 100-200 | 18 | 29 | 39 | 23 | 2,287 | 4,071 | 5,437 | 3,223 |
| 200-500 | 11 | 19 | 23 | 17 | 3,599 | 6,367 | 7,108 | 4,782 |
| 500-1,000 | 6 | 5 | 3 | 5 | 4,164 | 3,243 | 1,773 | 4,092 |
| 1,000-5,000 | 5 | 2 | 5 | 4 | 11,344 | 3,819 | 7,938 | 8,059 |
| 5,000-10,000 | 0 | 1 | 3 | 0 | 0 | 7,430 | 24,700 | 0 |
| 10,000-20,000 | 1 | 1 | 0 | 0 | 11,329 | 17,732 | 0 | 0 |
| 20,000-50,000 | 1 | 0 | 0 | 0 | 27,449 | 0 | 0 | 0 |
| 50,000-100,000 | 0 | 0 | 1 | 1 | 0 | 0 | 95,960 | 85,234 |
| 100,000-200,000 | 1 | 1 | 0 | 0 | 169,069 | 144,857 | 0 | 0 |
| Total | 4,280 | 5,461 | 5,046 | 3,526 | 247,500 | 208,732 | 165,142 | 121,758 |
| Total > 5000 km ² | 3 | 3 | 4 | 1 | 207,847 | 170,019 | 120,660 | 85,234 |

Figure SI II-1: Correlation matrix to test for collinearity among predictor variables. Values for Pearson correlation coefficients shown. When correlation was high (>0.75) we selected the variables with higher contribution according to the Jackknife analysis in preliminary modelling in Maxent (selected variables denoted with an 'x' at the end). 'H' and 'R' at the end of variable names indicate predictor group, as hunting threats, and resource availability groups, respectively. 'pct' = percentage.

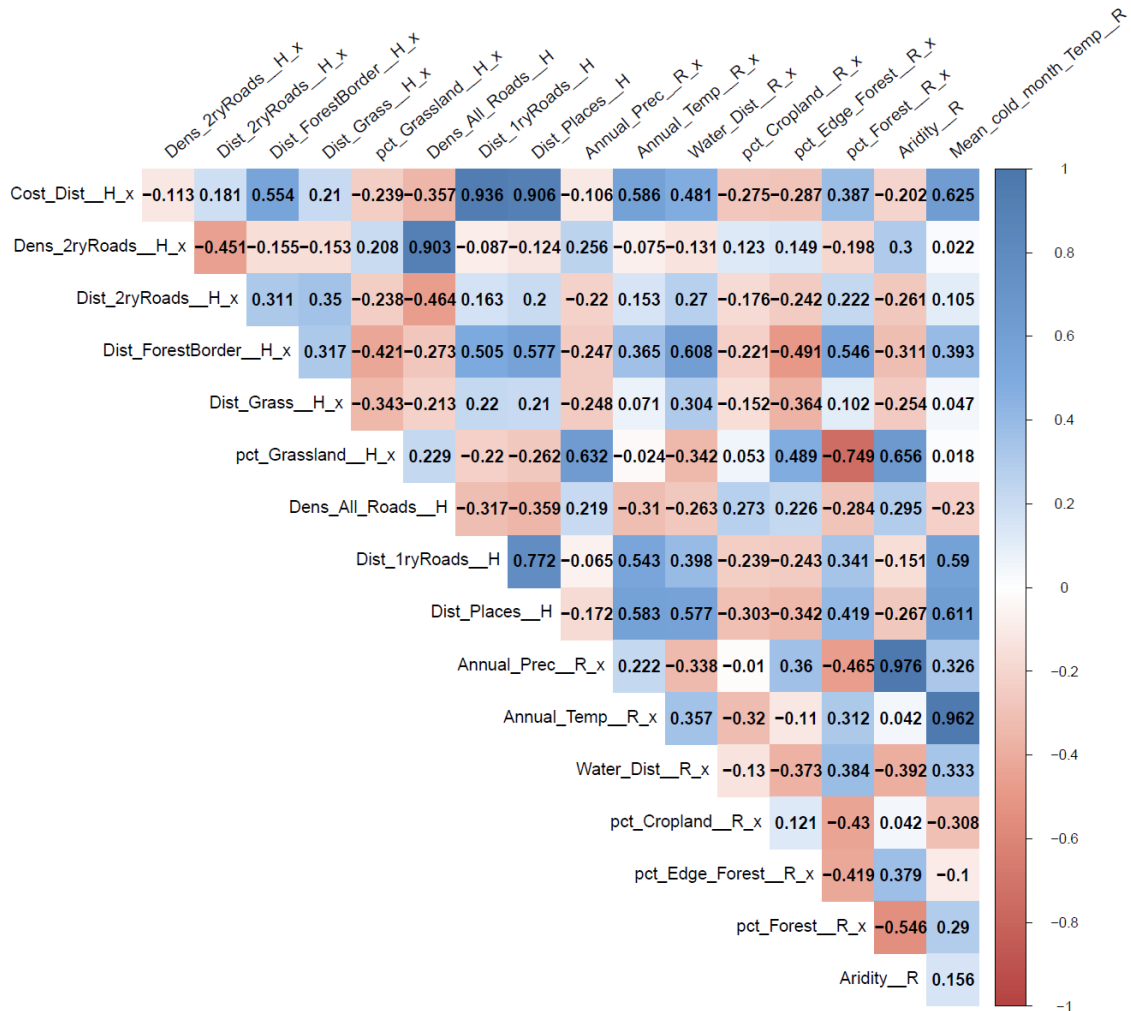


Figure SI II-2: Distance of core area cells for jaguar to the closest international borders in (a) a map of core areas in 2013, and (b) histogram of number of 1-km² core area cells by distance. Median distance to border is 80 km.

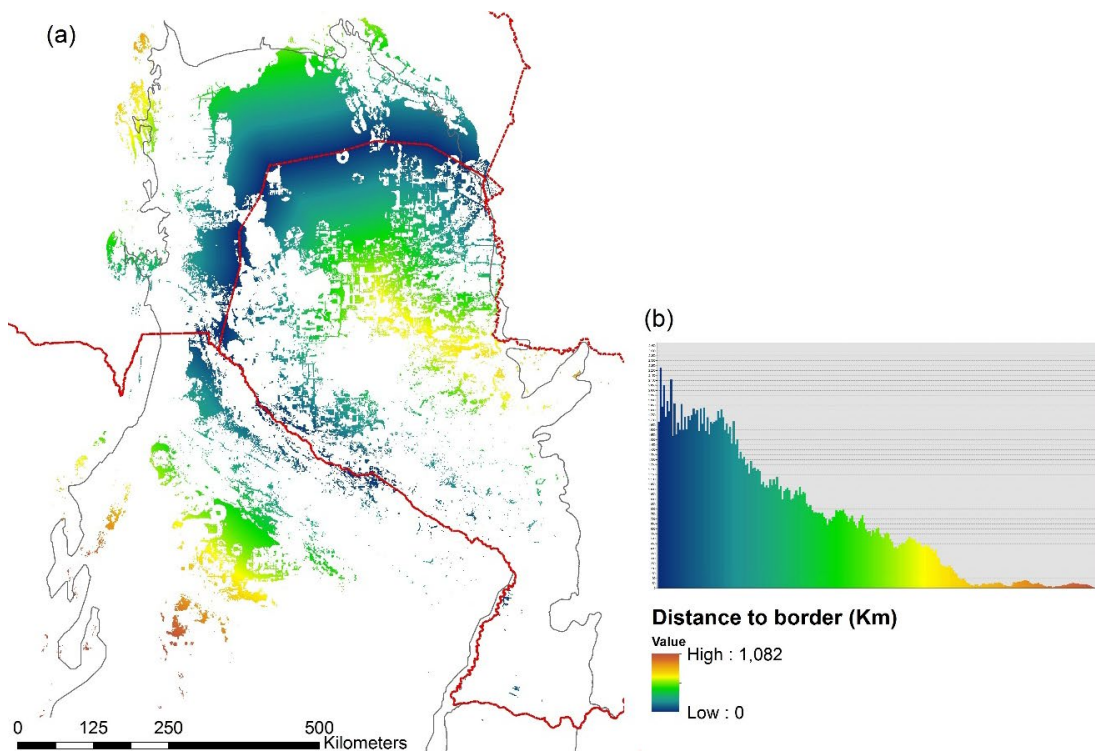
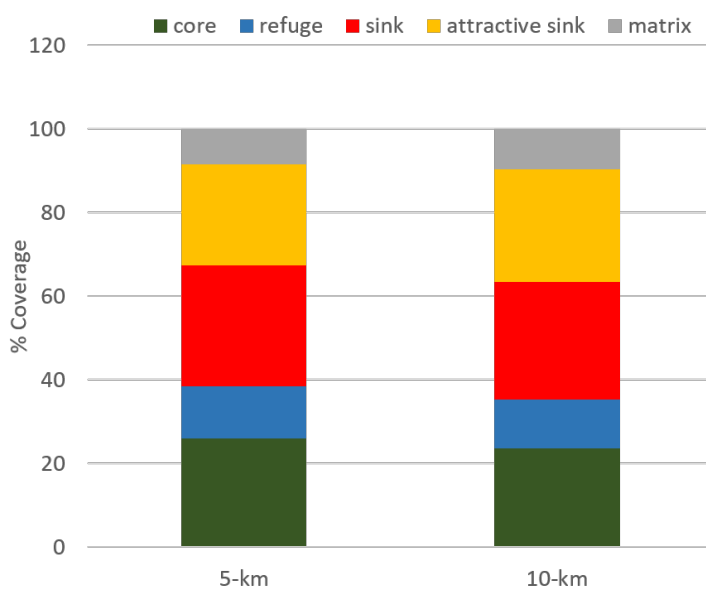


Figure SI II-3: Coverage of habitat categories in areas of 5-km and 10-km buffers around 28 independently collected sites of jaguars killed by humans in the Chaco.



Chapter III:
**Increasing synergistic effects of habitat
destruction and hunting on mammals over
three decades in the Gran Chaco**

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Abstract

Habitat destruction and overexploitation are the main threats to biodiversity and where they co-occur, their combined impact is often larger than their individual one. Yet, detailed knowledge of the spatial footprints of these threats is lacking, including where they overlap and how they change over time. These knowledge gaps are real barriers for effective conservation planning. Here, we develop a novel approach to reconstruct the individual and combined footprints of both threats over time. We combine satellite-based land-cover change maps, habitat suitability models, and hunting pressure models to demonstrate our approach for the community of larger mammals (48 species >1 kg) across the 1.1 million km² Gran Chaco region, a global deforestation hotspot covering parts of Argentina, Bolivia, and Paraguay. This provides three key insights. First, we find that the footprints of habitat destruction and hunting pressure expanded considerably between 1985 and 2015, across ~40% of the entire Chaco – twice the area affected by deforestation. Second, both threats increasingly acted together within the ranges of larger mammals in the Chaco (17% increase on average, $\pm 20\%$ SD, cumulative increase of co-occurring threats across 465,000 km²), suggesting large synergistic effects. Conversely, core areas of high-quality habitats declined on average by 38%. Third, we identified remaining priority areas for conservation in the northern and central Chaco, many of which are outside the protected area network. We also identify hotspots of high threat impacts in central Paraguay and northern Argentina, providing a spatial template for threat-specific conservation action. Overall, our findings suggest increasing synergistic effects between habitat destruction and hunting pressure in the Chaco, a situation likely common in many tropical deforestation frontiers. Our work highlights how threats can be traced in space and time to understand their individual and combined impact, even in situations where data are sparse.

Keywords: Conservation planning, defaunation, deforestation, habitat loss, land-use change, overexploitation

1 Introduction

Habitat destruction and overexploitation are the two main drivers of the unfolding sixth mass extinction, and both threats continue to expand (IPBES 2019). On one hand, growing demands for food, livestock feed, and biofuels trigger widespread land-use changes, including agricultural expansion into remaining natural habitats in the Global South (Kehoe et al. 2017). On the other hand, overexploitation (i.e. the unsustainable hunting, collection of animals and plants, logging, or fishing) (IPBES 2019), expands rapidly as the global human population grows, affluence increases, and demand for wild animals and plants (e.g., meat, live specimens) increases (Benítez-López et al. 2017; Benítez-López et al. 2019). Therefore, understanding the extent of these threats and how they change over time is critically important to inform conservation actions (Wilson et al. 2005; Pressey et al. 2007).

Habitat destruction and overexploitation may synergise where they act simultaneously, exacerbating their individual impacts on biodiversity (Brook et al. 2008). For instance, deforestation increases hunter access to shrinking habitat and formerly remote areas (Peres 2001) as does road infrastructure development related to expanding agriculture (Laurance et al. 2014). Yet, despite these synergistic effects, the interactions among habitat destruction and overexploitation remain weakly understood, and most studies in conservation and ecology continue to study threats in isolation (Brook et al. 2008; Dirzo et al. 2014), because approaches and datasets to jointly study multiple threats are lacking (Wilson et al. 2005; Pressey et al. 2007; Joppa et al. 2016).

Assessing the spatial footprint of threats to biodiversity, how these footprints overlap, where they remain absent, and how they change over time – which we here collectively refer to as the ‘*geographies of threat*’ – can help understand the individual and combined effects of those threats. Understanding geographies of threat is also imperative for guiding conservation planning by identifying where threat-specific conservation actions should take place (Wilson et al. 2005; Pressey et al. 2007; Wilson et al. 2007). However, mapping the geographies of threat is challenging. Few studies have mapped multiple threats at broad scales; typically within the scope of single-species studies (Bleyhl et al. 2015; Romero-Muñoz, Torres, et al. 2019), which has limited value for conservation planning that targets wider biodiversity facets (Nicholson & Possingham 2006). Studies assessing broader groups of species on the other hand, usually rely on IUCN’s expert-based threat categorizations and range maps, thereby assuming that threats impact multiple species

uniformly (e.g. Symes et al. 2018; Allan et al. 2019; Gallego-Zamorano et al. 2020), which is too simplistic. In addition, expert-based range maps contain false presences and vary tremendously in quality, depending on regions and taxa, and their use is therefore limited to very coarse resolutions (Ficetola et al. 2014; Di Marco et al. 2017). Consequently, these approaches are insufficient to inform threat-specific management actions on the ground (Wilson et al. 2005; Tulloch et al. 2015). New approaches to map the species-specific responses to threats for multiple species simultaneously and at resolutions useful for practitioners are urgently needed (Wilson et al. 2005; Pressey et al. 2007; Tulloch et al. 2015).

Recent advances in remote sensing now allow the reconstruction of detailed land-change histories across several decades and large areas (Hansen et al. 2013; Baumann et al. 2017; Song et al. 2018a). This provides opportunities for assessing habitat change dynamically, but few studies to date have made use of these opportunities (Maguire et al. 2015; Oeser et al. 2019; Romero-Muñoz, Torres, et al. 2019). Likewise, new approaches for assessing the impact of hunting in space are developed (Benítez-López et al. 2017). Such hunting pressure models synthesise knowledge across local studies, to describe how species-specific responses to hunting vary across landscapes (Benítez-López et al. 2019). Here, we propose to combine habitat suitability and hunting pressure models for characterising the footprints of habitat destruction and hunting, and how they overlap.

Understanding of the interacting footprints of habitat destruction and hunting is particularly poor in tropical deforestation frontiers, where rapid habitat destruction often couples with high hunting pressure (Peres 2001; Benítez-López et al. 2019). This situation is particularly dire in the world's tropical dry forests, which are vanishing quickly across the globe (Hoekstra et al. 2005; Curtis et al. 2018). However, these systems remain weakly protected (Miles et al. 2006) and under-researched (Blackie et al. 2014). The individual and combined impacts of habitat destruction and hunting on biodiversity in these forests are highly unclear, translating into a real barrier towards implementing conservation planning and action.

At 1.1 million km², the Gran Chaco region (hereafter Chaco) in South America, extending into parts of Argentina, Paraguay and Bolivia, is the largest continuous tropical and subtropical dry forest globally, but it has recently turned into a global deforestation hotspot due to rapid agricultural expansion across the several deforestation frontiers that it encompasses (Baumann et al. 2017; Curtis et al. 2018; Le Polain de Waroux et al. 2018). At

the same time, hunting is very widespread there, causing massive defaunation (Noss et al. 2005; Altrichter 2006; Periago et al. 2014). Together, these threats render the Chaco a global conservation priority (WWF 2015; Kuemmerle et al. 2017). Increasing evidence suggests important interactions between habitat destruction and hunting in this region. For example, large mammals disappear from remaining forest patches soon after the surrounding areas are deforested because they are easily hunted out (Núñez-Regueiro et al. 2015; Semper-Pascual et al. 2019). Likewise, cattle ranchers in areas where pastures expand often persecute large predators over fears of attacks on cattle (Quiroga et al. 2016; Romero-Muñoz, Torres, et al. 2019). Yet, our understanding of how these threats play out and interact in space is very limited.

Here, we reconstruct the individual and combined spatial footprints of habitat destruction and hunting pressure for larger mammals (>1 kg body weight) across the entire Chaco between 1985 and 2015. We combine satellite-based land-use reconstructions with species-specific, time-calibrated habitat suitability models and hunting pressure models. This allows to assess the footprints of habitat destruction and hunting and to identify threat hotspots as well as how they change over time. Specifically, we aimed to answer the following questions:

1. How have the footprints of habitat destruction and hunting pressure on larger mammals changed in the Chaco since 1985?
2. What is the relative importance, in terms of the share of species' ranges affected and their overall footprints, of these two threats acting alone vs. together, and how this has changed over time?
3. How has the distribution of core areas, where threats are absent, changed since 1985, and where are current hotspots of threats and priority areas for conservation?

2 Methods

2.1 Study region

The Chaco region is a highly biodiverse region comprising parts of Bolivia, Paraguay and Argentina (Olson et al. 2001; TNC et al. 2005). The climate ranges from tropical (north) to subtropical (south). Precipitation is seasonal and ranges from >1,200 mm/yr (east) to <400 mm/yr (west and south). Xerophilous forests are the dominant vegetation, interspersed

with gallery forests and savannas (Prado 1993). The Chaco has a long land-use history, with Indigenous Peoples using the area for millennia, and criollo people practicing subsistence ranching for up to 200 years (Camino et al. 2018). Recent expansion of intensified agriculture, mainly driven by large-scale, market-oriented agribusiness, has converted more than 142,000 km² of forests (>20% of the Chaco's forests) to pastures and croplands between 1985 and 2015 (Baumann et al. 2017). Hunting is also widespread (see Extended Methods in Supplementary Information), with many actors hunting for subsistence, commercial, cultural and retaliatory reasons, together producing widespread defaunation across the Chaco (Periago et al. 2014; Torres et al. 2014; Semper-Pascual et al. 2018). Only 9.1% of the Chaco is currently protected (Nori et al. 2016)

2.2 Data preparation

We gathered 27,408 presence locations from local surveys and opportunistic observations for 56 larger terrestrial mammals. These records were collected from 1978 to 2018, partly by the authors, and from public (e.g., GBIF), and governmental and non-governmental organisations' databases (see Table SI III-1 for details). To reduce sampling bias, we spatially filtered presence locations by enforcing a minimum distance of 10 km between presence locations (Kramer-Schadt et al. 2013). We only included species with more than 10 points after applying the spatial filtering, resulting in a final list of 48 species, for which we retained a total of 4,611 presence locations.

As potential predictors for our habitat suitability and hunting pressure models, we generated 11 variables at a 1-km² resolution (Table SI III-2). All variables covered the entire Chaco plus a 30-km buffer to account for potential border effects (Piquer-Rodríguez et al. 2015). For the habitat model, we included four variables characterizing land cover (%Forest, %Cropland, %Grassland, %Pastures), three variables describing habitat structure (%Forest Edge, Distance to Water) and two climate variables (Mean Annual Temperature, Mean Annual Precipitation; Table SI III-2). To assess collinearity among predictors, we calculated Pearson's correlation coefficients for each variable pair and kept the variable with the higher explanatory power for pairs with $r > 0.7$ (Dormann et al. 2013) (Figure SI III-1).

For the hunting-pressure model, we followed Benítez-López et al. (2019) and used three predictors: *Distance to Hunter Access Points*, *Human Population Density* (both indicators of hunting risk), and *Species Body Mass* (an indicator of a species' intrinsic vulnerability to population decline as a result of hunting) (Table SI III-2). We defined spatial features

representing hunter access points for each species separately, based on the regional expertise of the authors (see Table SI III-3). Assessment of subsistence ranches involved screen-digitizing >27,000 individual ranches spread across the Chaco and assessing their persistence over time using high-resolution imagery in Google Earth. Likewise, we reconstructed the evolution of the road network since 1985 based on historic satellite imagery (see Extended methods in the Supporting Information for details).

Modelling habitat destruction and hunting pressure over time

We parameterized (1) a habitat suitability model, characterizing resource availability, and (2) a hunting pressure model, characterizing species-specific population declines due to hunting. By overlaying the two resulting maps, we then identified four habitat categories for each species individually, according to the prevailing threats: core area (good habitat suitability and low hunting pressure), poor habitat-only (poor habitat suitability, but low hunting pressure), hunting pressure-only (high hunting pressure, but good habitat suitability), and both threats together (poor habitat suitability and high hunting pressure). We tracked these habitat categories across time using time-calibrated models for each species, resulting in time series of the individual and combined threat footprints (Figure III-1).

To represent habitat suitability, we used maximum entropy modelling (Phillips et al. 2017). This is a presence-only, non-parametric species distribution modelling algorithm that performs well in predicting habitat suitability, even for small samples (Elith & Leathwick 2009) and for time-calibrated habitat models (Kuemmerle et al. 2012; Sieber et al. 2015; Romero-Muñoz, Torres, et al. 2019). Time-calibrated models have two key advantages: (1) they make use of all available data, across the entire time period studied, and (2) they ensure that observed changes in habitat suitability are solely due to changes in predictor variables, and not due to uneven distribution of points over time or varying sampling bias (Nogués-Bravo 2009; Sieber et al. 2015). We fitted maximum entropy models for each species using Maxent (v3.4.1) (Phillips et al. 2017) using only hinge features to avoid overfitting (Elith et al. 2010). We tested a range of parameterizations and selected a regularisation multiplier of 1 and a prevalence value of 0.5 (Elith et al. 2010).

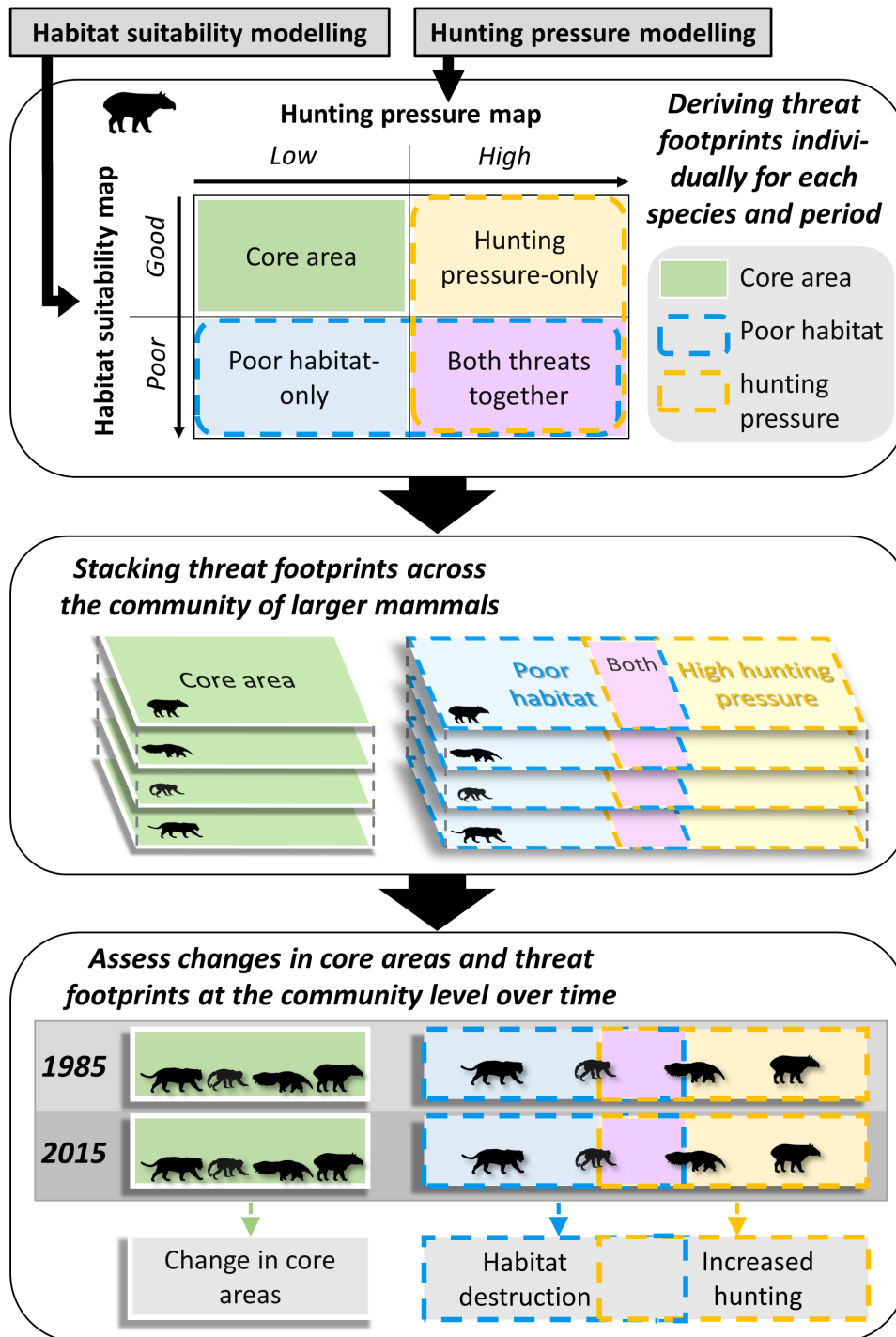


Figure III-1: Framework for reconstructing 'geographies of threat' due to habitat destruction and hunting pressure for 48 larger mammals in the Chaco from 1985 to 2015. We first modelled the spatial footprint of each threat per species, then stacked these footprints across the community, and then used this information to assess how spatial footprints of threats changed over time (including threat overlaps).

As background points, we created sets of points for each species individually to account for differences in species' distribution as well as sampling effort in space and time, which helps to avoid issues arising from sampling biases (Elith et al. 2010; Merow et al. 2013). We used 10,000 background points that we distributed proportionally in time according to the presence points. We then extracted predictor values for each presence and background point from the year each point was sampled (Sieber et al. 2015). This yielded a single, time-calibrated Maxent model per species, which we then projected onto the sets of predictor variables from 1985, 2000, and 2015 (see Extended Methods in the Supporting Information for further details). To assess the robustness of our models, we ran 10-fold cross-validation. We assessed the models' predictive performance with the average area under the curve (AUC) values across the 10 replicates. We defined species' ranges as those areas with habitat suitability values above the 5% quantile in 1985 (Pearson et al. 2004).

To model hunting pressure, we relied on a recently-developed approach to capture hunting-induced defaunation for tropical mammals (Benítez-López et al. 2019). This approach uses a two-stage mixed model that describes a species' population responses to hunting pressure. First, a binomial model was fitted to discriminate extant and locally extinct species. Second, a Gaussian model was fitted to the non-zero response ratios in abundance change due to hunting based on 3,281 abundance estimates in hunted and non-hunted areas studies across the tropics (see Benítez-López et al. 2019) (see Extended methods). This results in a hunting pressure index ranging from 0 (no decline in abundance) to 1 (total local extirpation). We re-fitted the original global model to Neotropical mammals only ($n = 1,945$ abundance ratios) and then evaluated the predictive accuracy with 5-fold cross-validation with an 80%/20% training/testing set. We split our predictions into two categories of high (> 0.3), and low (≤ 0.3) hunting pressure, based on the International Union for Conservation of Nature (IUCN) criterion of 30% population decline due to threats that have not ceased that renders a species threatened (criterion A4, IUCN 2012). We assessed the accuracy of our model for predicting these hunting pressure categories using sensitivity and specificity.

2.3 Mapping the footprints of habitat destruction and hunting pressure

To map the spatial footprints of threats, we first applied thresholds to the habitat suitability maps and the hunting pressure maps to classify good and poor suitability, and high and low hunting pressure (Figure III-1), respectively. For the habitat suitability maps, we used the 'maximum sensitivity plus specificity' threshold (Liu et al. 2013). For the hunting pressure maps, we used the threshold of 0.3 to separate high and low hunting pressure. We then

overlaid the two binary maps to identify the four habitat categories according to threat levels (see Figure III-1).

We stacked the raster maps across all 48 species to obtain per-pixel species counts for each category for the years 1985, 2000, and 2015 (Figure 1). We also calculated for each year the overall area affected by poor habitat and hunting pressure, and the share of each species' ranges affected by either threat alone or by both together. In the habitat model, we kept climate conditions constant for the entire study period (by using 30-year climate averages) but allowed land cover and land use to vary over time. Therefore, expansion of poor habitat over time can only be attributed to impacts of land cover/use change and we refer to this as habitat destruction (Figure III-1). We refer to the increases of hunting pressure over time as 'increasing hunting pressure'.

To identify priority areas (i.e. the most important areas with high-quality habitat and low threat levels) and hotspots of threats (i.e., areas where threats have disproportionately high impacts), we adopted a rarity-weighted richness measure (Kier & Barthlott 2001), which considers both richness (i.e., how many species have their core area in a given cell) and range size (i.e., whether a species has a large or small core area). This approach compares favourably to other prioritisation algorithms (Albuquerque & Beier 2015). Priority areas can guide efforts to expand habitat protection (e.g., via additional protected areas), while threat hotspots can help to spatially target threat-specific conservation action (see Extended Methods in the Supporting Information for further details).

3 Results

Both our habitat suitability models, and hunting-pressure models performed well. Our habitat suitability models had overall high to very high model fit and discrimination values for all 48 modelled species (AUC consistently >0.7 ; Figure SI III-2). For the hunting pressure model, overall sensitivity and specificity were 0.9 and 0.5, respectively, indicating good predictive performance.

In terms of the predicted threat footprints, our habitat suitability models showed that by 2015, poor habitat covered on average 49% ($\pm 20\%$ SD) of the ranges of the species we investigated (Figure III-2A). Similarly, hunting pressure was on average high across 45% ($\pm 30\%$ SD) of species' ranges in 2015 (Figure III-2C). Between 1985 and 2015, large areas of the Chaco became affected by habitat destruction and hunting pressure (38 and 41% of the

region, respectively; Figure III-2B and 2D). For some species, hunting pressure expanded over wide areas and even inside protected areas (Figure III-2D).

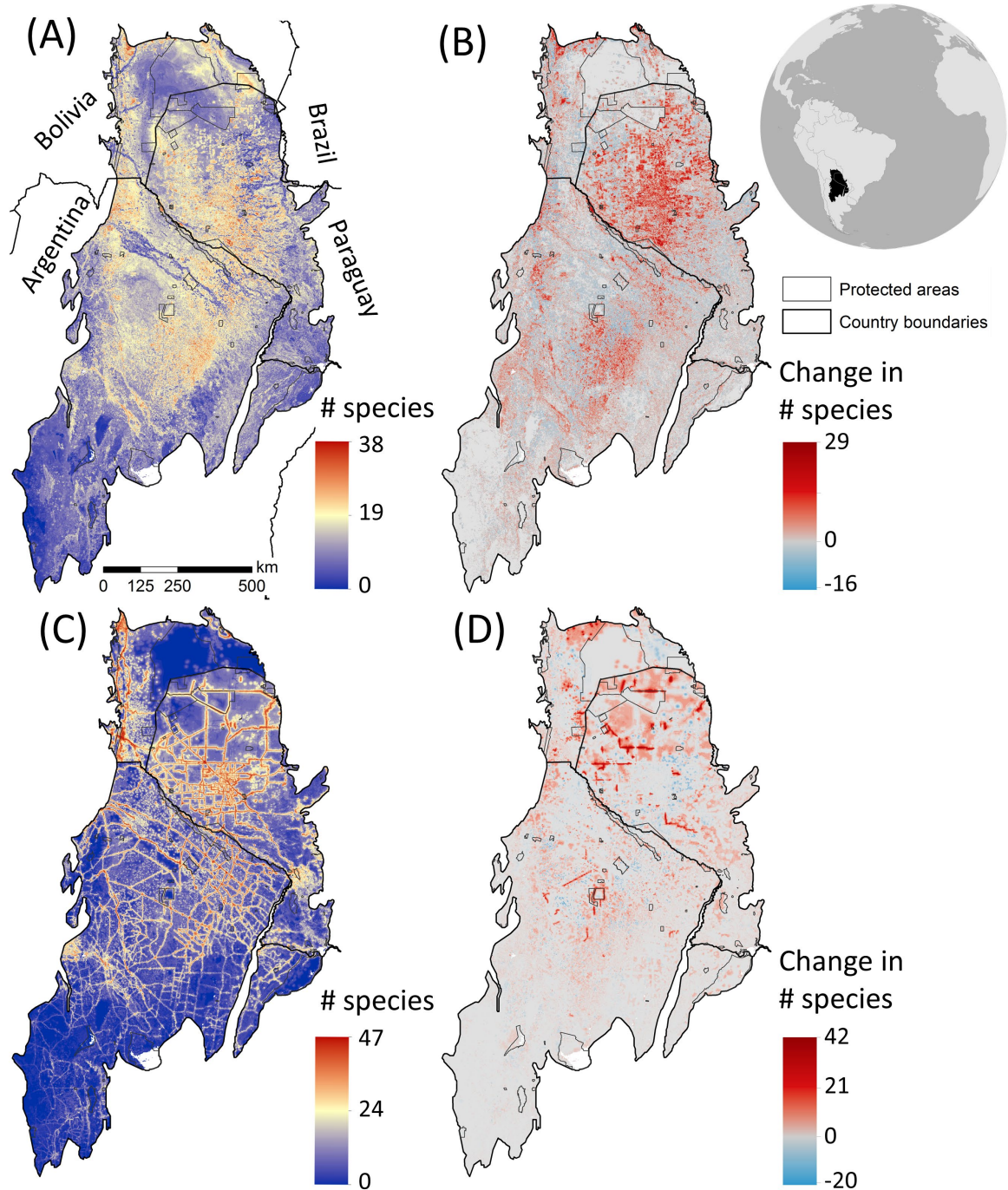


Figure III-2: Spatial footprints of habitat destruction and hunting pressure in the Chaco for 48 larger mammals. Number of species affected by habitat destruction (A) and hunting pressure (C) in 2015. Change in species numbers affected by habitat destruction (B) and hunting pressure (D) between 1985 and 2015.

At the species level, the footprint of habitat destruction showed an average expansion of 9.6% ($\pm 22.7\%$ SD) or 22,000 km² ($\pm 51,000$ km² SD; Figure III-3A). This threat increased for 34 mammals (71%), while it either remained constant or decreased for the remaining 14 species (Figure III-3A). For example, since 1985 land-use change affected over 25% of the high-quality habitat of the jaguar (*Panthera onca*), puma (*Puma concolor*), the white-lipped peccary (*Tayassu pecari*), and the collared peccary (*Pecari tajacu*). In contrast, species such as the maned wolf (*Chrysocyon brachyurus*) or the crab-eating fox (*Cerdocyon thous*) experienced declining pressure from habitat destruction over time (Figure III-3A). Among countries, the footprint of habitat destruction expanded faster in Paraguay than in Bolivia and Argentina (Figure III-3B).

The footprint of hunting pressure expanded on average by 8.4% ($\pm 6.7\%$ SD) or 23,000 km² ($\pm 34,000$ km² SD; Figure III-3A). Generally, this footprint changed more evenly than the footprint of habitat destruction, with increasing hunting pressure for almost all species (i.e., 44 species = 92%). For instance, hunting pressure on the puma, the jaguar, the giant armadillo (*Priodontes maximus*), and the grey brocket deer (*Mazama gouazoubira*) each increased by more than 20%. For some frequently-hunted species, such as the white-lipped peccary and tapir (*Tapirus terrestris*), the footprint of hunting pressure increased only slightly, as this footprint was already large in 1985. Only very few species, such as Geoffroy's cat (*Leopardus geoffroyi*), experienced slightly shrinking hunting pressure (Figure III-3A).

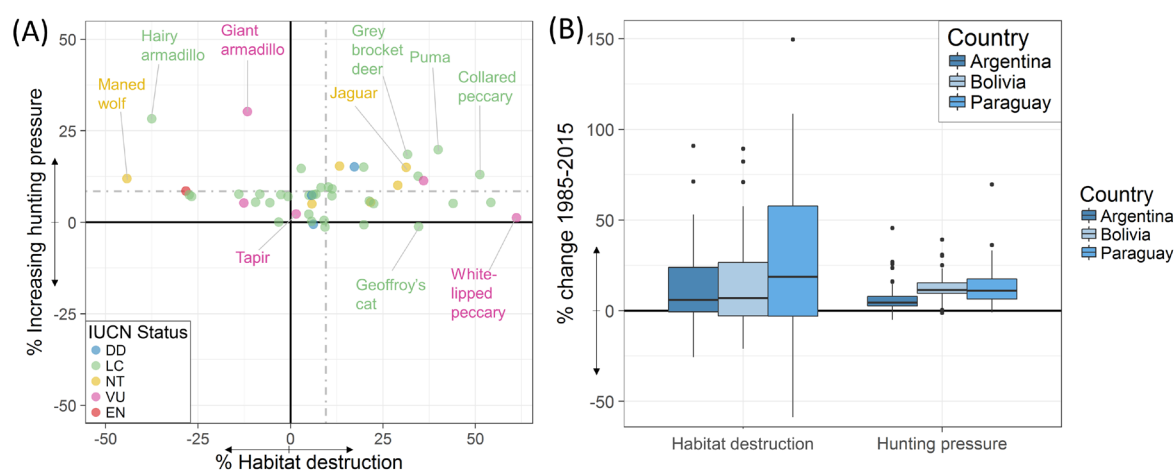


Figure III-3: Expansion in the footprints of habitat destruction and hunting pressure for 48 Chacoan mammals between 1985 and 2015 (as a percentage of their range in 1985). (A) Change in the footprints of habitat destruction vs. that of hunting pressure (see Figure SI III-5 for all species' names). Positive values indicate an expansion and negative values a contraction of threat footprints. Dashed lines indicate averages across all mammals. (B) Relative change from 1985 to 2015 for each threat footprint across the three Chaco countries.

The footprint of hunting pressure expanded faster in Paraguay and Bolivia than in Argentina (Figure III-3B).

In addition to the individual expansion of threat footprints, we found a strong increase between 1985 and 2015 in the area where habitat destruction and hunting pressure overlap (Figure III-4). The cumulative area for all mammals affected by both threats expanded by 465,000 km² (or 43% of the Chaco) between 1985 and 2015 (Figure III-4). In comparison, habitat destruction-only and hunting pressure-only cumulatively expanded by 300,000 km² and 363,000 km² (34% and 28% of the Chaco), respectively (Figure III-4). At the species level, the area of both threats acting together increased by 17% ($\pm 20.2\%$) on average between 1985 to 2015. In contrast, the area where only one threat impacts species decreased (by 39.5% and 6.1%, for habitat destruction and hunting pressure, respectively; Figure III-5).

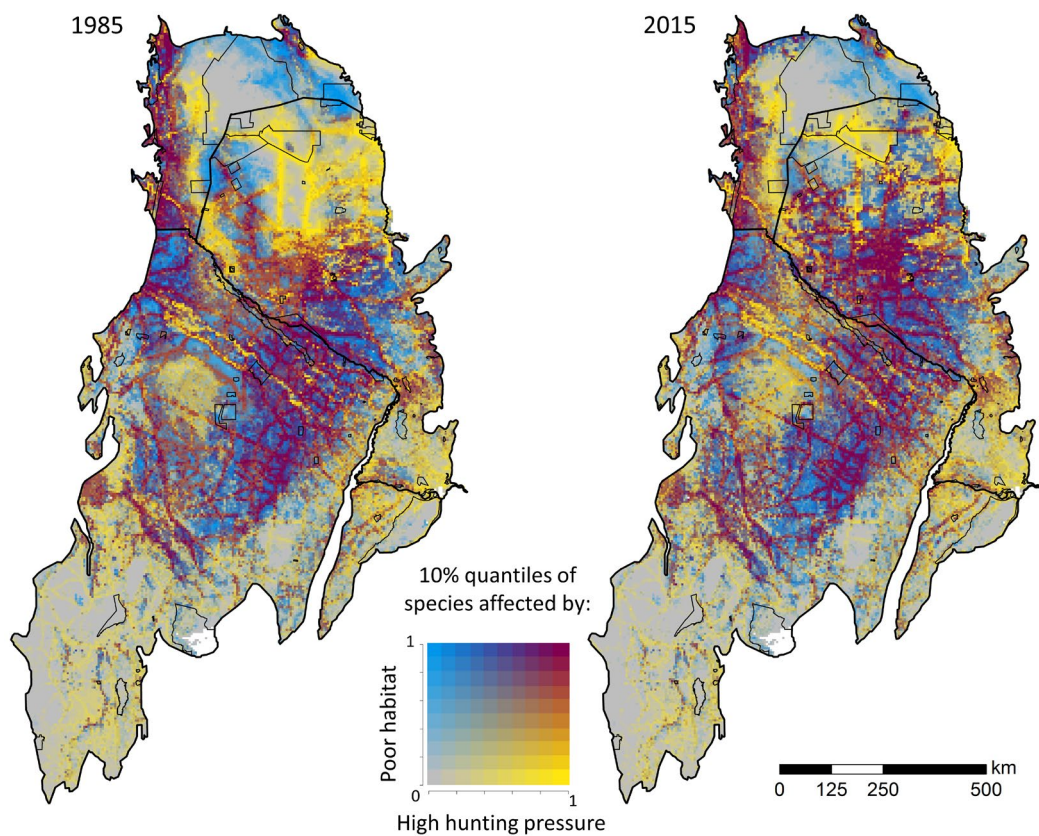


Figure III-4: Numbers of species (in 10% quantiles) affected by poor habitat (blue gradient), high hunting pressure (yellow gradient), or both (grey-to-purple gradient) in 1985 and 2015, for a total of 48 larger mammals. Thick lines represent country limits whereas thin lines denote protected areas in the Chaco

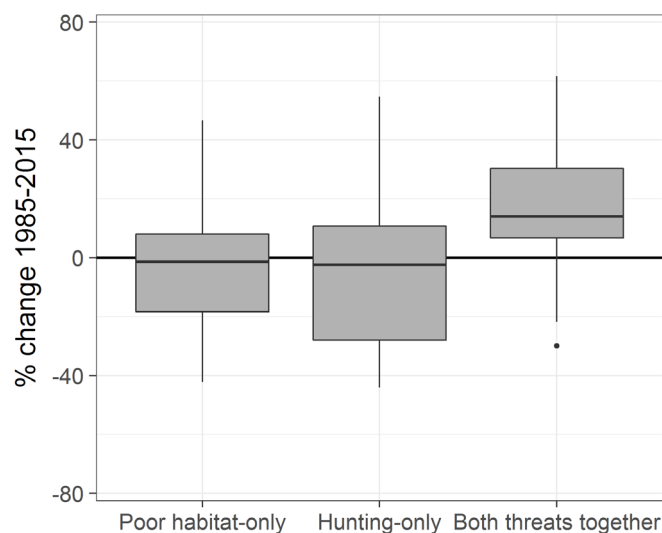


Figure III-5: Relative changes in the footprints of poor habitat and hunting pressure, and areas where both threats acted simultaneously, between 1985 to 2015 in the Chaco

Regarding core areas (i.e., good habitat suitability and low hunting pressure), 36 species (75%) experienced a contraction (on average $38\% \pm 62.2\%$ SD) between 1985 and 2015 (Figure SI III-3). Contractions were particularly common in northern Paraguay and the northernmost Chaco in Bolivia, where up to 34 species lost core areas in some locations (Figure SI III-3). By 2015, remaining core areas were mainly concentrated in southern Bolivia, north-eastern Paraguay, and some smaller areas in northern Argentina (Figure SI III-3). The cumulative core area lost for all species between 1985 and 2015 was 407,000 km².

Our rarity-weighted richness analyses revealed that priority areas for the community of larger mammals as a whole covered large areas of the northern Chaco in 2015, mainly in Bolivia and northern Paraguay, as well as the eastern-most Chaco in Argentina (Figure III-6A). In contrast, hotspots where habitat destruction and hunting pressure acted simultaneously covered broad areas in north-western Paraguay, north-eastern Argentina, and south-western Bolivia (Figure III-6B). Hotspots of habitat destruction-only were spread across central and northern Paraguay, southern Bolivia and the central Chaco in Argentina; whereas hotspots of hunting pressure-only were most common in northern Paraguay, south-western Bolivia, and northern Argentina (Figure III-6B). For comparison, threat hotspots based on species' global ranges were similar to those based on the Chaco ranges. This was different for priority areas, where calculations based on global ranges revealed priority areas in the Bolivian Chaco (as in the analyses using Chaco ranges), but to a lesser

extent in Paraguay and northern Argentina, and not at all in eastern Argentina (Figure SI III-6).

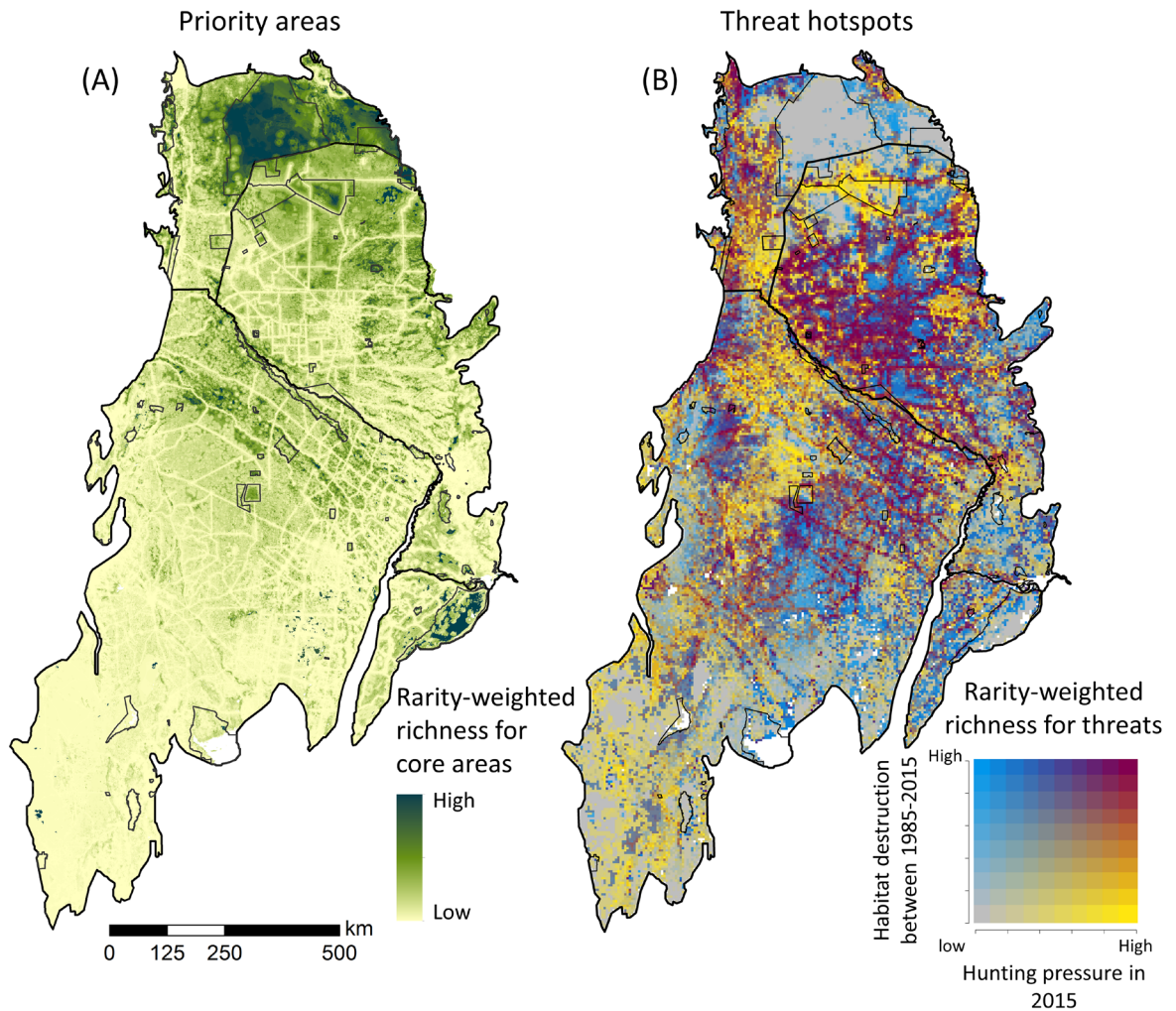


Figure III-6: Priority areas (i.e., the most important areas with high-quality habitat and low threat levels) and hotspots of threats (i.e., areas where threats have disproportionally high impacts) for larger mammals in the Chaco, based on the rarity-weighted richness (i.e., sum of inverse range sizes). (A) Hotspots of core areas in 2015, which represent priority areas for conservation. (B) Bivariate map of hotspots of habitat destruction (1985-2015) and high hunting pressure (2015), which represent priority areas for threat-specific conservation action.

4 Discussion

Understanding the individual and combined effects of different threats to biodiversity is critical for identifying effective conservation interventions to halt biodiversity loss. Yet, we currently lack approaches to map the spatial footprints of threats at resolutions fine enough to be useful for conservation planning. By combining land-cover time series mapped from

satellite imagery, habitat suitability models and hunting pressure models, we reconstructed the footprints of habitat destruction and hunting for the entire community of larger mammals of South America's Gran Chaco, a 1.1 million km² deforestation hotspot. We found that the footprints of both threats expanded considerably — and much more than deforestation alone — across the Chaco over three decades, producing a widespread loss of core areas. In addition, habitat destruction and hunting pressure acted simultaneously over increasing portions of the Chaco over time, suggesting that synergistic effects are becoming the norm. The priority areas and hotspots of threat that we identified point to key areas for larger mammals, where habitat protection and threat-specific management actions should swiftly be implemented to avoid further biodiversity loss. Overall, our findings suggest increasing synergistic effects between habitat destruction and hunting pressure in the Chaco, a situation likely common in many tropical deforestation frontiers around the world. Our work therefore highlights the urgent need to better understanding how these threats act on species in space and time, in other words, the geographies of threat to biodiversity. We here develop an effective and easily transferable approach to do so.

The footprints of habitat destruction and hunting pressure expanded hugely across the Chaco between 1985 and 2015 for almost all mammals we assessed. This is exemplified by the cumulative footprints of threats expanded over more than double the area of forest and natural grassland loss in that period (142,600 and 31,700 km², respectively) (Baumann et al. 2017). The footprint of hunting pressure penetrated even further into remote areas, including protected areas, than habitat destruction. Hunting is the main cryptic disturbance for mammals, and often extends into otherwise 'intact' forests (Peres et al. 2016; Benítez-López et al. 2019). Similarly, the footprint of habitat destruction was also broader than that of deforestation, likely because small fragments are unsuitable for wide-ranging species, and because edge effects decrease resource availability close to deforested areas (Barlow et al. 2016). Only a few forest patches remain in the Chaco that are large enough to be effectively remote from hunter access points and agricultural lands. Other studies in deforestation frontiers have also reported that anthropogenic disturbance can extend over much larger areas than the area undergoing deforestation alone (Peres et al. 2006; Barlow et al. 2016). Together, our results highlight that approximating threats by deforestation footprints alone (Ocampo-Peñuela et al. 2016; Symes et al. 2018; Gallego-Zamorano et al. 2020), or by using fixed distances from roads (Allan et al. 2019) may underestimate the footprints of threats substantially.

The footprint of both threats increased since 1985 across all Chaco countries, but at varied rates. Habitat destruction expanded the most in Paraguay, which reflects Paraguay's rampant conversion of forests into pastures (Baumann et al. 2017). Habitat destruction expanded less in Bolivia, partly because two large protected areas cover large forested regions, and because the main deforestation frontiers in Bolivia are in the Chiquitano forest, just north of the Chaco (Hansen et al. 2013). Hunting pressure expanded more in Paraguay and Bolivia, where human population and road construction increased recently, than in Argentina, where human population density and road density were already high in 1985. In fact, some species, such as Geoffroy's cat, experienced a decreasing hunting pressure in some areas in Argentina. This is likely because subsistence ranchers abandoned some areas as agribusiness expanded (Grau et al. 2008), potentially decreasing hunting pressure but increasing habitat destruction. After 2015, deforestation and forest fires have further advanced in all three countries, most worryingly in some of the last remote areas in northernmost Paraguay (Hansen et al. 2013) and in the northern Bolivian Chaco (Romero-Muñoz, Jansen, et al. 2019). This highlights the urgency for stronger regulation of deforestation and the expansion of roads across all three countries.

The rapid expansion of threats and the massive declines of core areas, predicted for the first time by our maps, signify the defaunation of the larger mammal community across much of the Chaco. Unfortunately, these trends are widespread in deforestation frontiers (Gibson et al. 2011; Barlow et al. 2016). The declines we detected in most species' core areas often contrast with their generally low-threat global conservation status (see Table SI III-3), highlighting the importance of conducting such assessments at the regional level (de la Torre et al. 2018). Given the varied and key ecological roles of larger mammals, their disappearance can disturb ecosystem functioning, including seed dispersal, carbon storage, and nutrient cycling (Dirzo et al. 2014; Periago et al. 2014). This also highlights the importance of the few large remaining core areas for the mammal community as a whole, which are likely to be the last places maintaining the original species assemblage and ecosystem functioning in the Chaco. This reinforces the recognition of the irreplaceable role of 'wilderness' and Indigenous territories in maintaining biodiversity (Ricketts et al. 2010; Gibson et al. 2011). Further, these results underline the importance of halting further agricultural and road expansion into remaining core areas, which could otherwise disappear quickly across the entire Chaco.

A key result of our study was that areas where both threats act together cover increasingly larger portions of the Chaco. This is highly worrying because biodiversity declines even

faster where threats synergise (Brook et al. 2008). Such synergistic effects are particularly likely in the Chaco, because its dense and thorny forests make them very hard to access for hunters unless forests are cleared for roads and agriculture. Hunters often kill mammals crossing such clearings; and workers cutting the forest, building fences, and producing charcoal actively hunt animals in the remaining forest patches (Altrichter 2006; authors' own observations). Accordingly, large mammals tend to disappear from forest strips and smaller forest patches soon after the surrounding areas are deforested (Núñez-Regueiro et al. 2015; Semper-Pascual et al. 2019). Furthermore, in areas already converted to agriculture, ranchers and farmers often persecute carnivores and herbivores thought to cause livestock or crop losses, respectively (Quiroga et al. 2016; Camino et al. 2018). While synergistic effects have been described through non-spatial methods in other deforestation frontiers (Peres 2001), here we provide an approach to map out the individual and combined effect of threats, and thus to track synergistic effects that may be common in deforestation frontiers around the world over time.

Our approach can also provide spatial templates for conservation planning. Our priority areas represent the most important areas for proactive conservation action, such as establishing protected areas. The protected area network currently covers only 9.1% of the Chaco. Extensive priority areas remain unprotected, particularly in northern Paraguay, and northern Argentina, and most are surrounded by threat hotspots. These areas are excellent candidate regions for expanding the existing protected area network and our analyses can serve to update previous prioritization exercises (TNC et al. 2005; Nori et al. 2016). Further, efforts should be directed to ensure Indigenous Peoples' land rights as many of these lands harbour priority areas and are thus important for Chacoan biodiversity.

Our threat hotspots overlapped extensively with previously prioritized areas (TNC et al. 2005; Nori et al. 2016), particularly in the central Chaco. This highlights the need for swift reactive threat management. In hotspots of habitat destruction, potential actions include (1) stopping further agricultural expansion and enforcing existing regulations, (2) securing Indigenous People's rights to land, (3) promoting culturally acceptable livelihoods that encourage sustainable land use, and (4) fostering forest recovery. In hotspots of hunting pressure, specific actions include (1) careful planning of new roads and other land changes that foster access for hunters; (2) educational programs and improved management to lower or avoid conflicts with wildlife; (3) enforcing bans on recreational and commercial hunting, and (4) ensure the sustainability of Indigenous People subsistence hunting. Several of these recommendations are in agreement with different Indigenous and

smallholders visions in the Bolivian and Argentinean Chaco (Noss & Cuellar 2001; Camino et al. 2016). Where both threats co-occur, they must be managed simultaneously. Implementing such complementary management actions is more likely to produce conservation gains than addressing single threats alone (Wilson et al. 2007).

Our work represents, to our knowledge, the first spatially explicit and high-resolution mapping of the footprints of multiple threat at the community level. Thereby it advances previous analyses assessing single threats (Ocampo-Peñuela et al. 2016; Benítez-López et al. 2019), threat interactions for individual species (Bleyhl et al. 2015; Romero-Muñoz, Torres, et al. 2019), and coarse-grained overlays of multiple threats based on species range maps (e.g. Symes et al. 2018; Allan et al. 2019; Gallego-Zamorano et al. 2020). Our study is also the first to reconstruct changes in multiple threats over long time periods, by combining satellite-based land-cover change maps with longitudinal datasets of road networks and over 27,000 subsistence ranches. Still, our work contains some limitations. First, although we gathered the largest occurrence dataset ever collected for the larger mammal community of the Chaco, presence points were scarce for some species in some regions, particularly the northern and southern Chaco for the 1980's. Second, our maps depend on thresholds for classifying threat levels, and we applied common criteria to define them. Still, other thresholds would change our maps. Finally, we used the human population density layers for 2000 also for 1985, because a comparable dataset for 1985 was missing. Although human population has likely not changed markedly in 1985-2000, we may have underestimated changes in hunting pressure for this period. This highlights the importance of long-term human population timeseries to transfer approaches such as ours to other regions (Lloyd et al. 2017).

Mapping the spatial footprints of habitat destruction and overexploitation has been hard, constituting a real barrier towards better understanding their individual versus combined impacts, and for targeting threat-specific conservation planning. Here, we pioneer a new approach to reconstruct the changing footprints of main threats to biodiversity (see Figure III-1). Applying this approach to the 1.1 million km² Gran Chaco, a global deforestation hotspot, we find that the footprints of habitat destruction, hunting pressure, and the areas where they synergize, are rapidly expanding. Such trends are likely common across other deforestation frontiers in Latin America, Africa and South-East Asia and our approach should therefore be broadly applicable to assess the geographies of threat in these regions. Our approach also allows to identify the remaining priority areas for biodiversity and to pinpoint to where threat-specific conservation actions to halt biodiversity declines

should be implemented. Overall, our study highlights the importance of understanding and addressing the combined effects of major threats to biodiversity in order to better tackle biodiversity loss.

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Supplementary information

Extended Methods

Role of hunting in the study region

Hunting of larger mammals is carried out by a wide range of actors in the Chaco (Noss et al. 2005; Altrichter 2006). Indigenous People and subsistence ranchers typically hunt to enrich their diets (Noss et al. 2005; Altrichter 2006; Camino et al. 2018). Ranchers and crop farmers also kill some species in response to the perceived risk of livestock losses (e.g. jaguars, pumas) or crop damages (e.g., peccaries, plains vizcachas) (Altrichter 2006; Quiroga et al. 2016; Camino et al. 2018). Additionally, both local people and outsiders hunt for sport, and to sell skins, bushmeat, or live animals (Altrichter 2006; Periago et al. 2014). The combination of habitat destruction and hunting causes widespread declines of mammals across the Chaco (Periago et al. 2014; Camino et al. 2018; Romero-Muñoz, Torres, et al. 2019). Remaining natural habitats are often fragmented (Piquer-Rodríguez et al. 2015) and are used for forest ranching, charcoal production, or logging (Rueda et al. 2015).

Preparation of predictor variables

We used land-cover/use maps for 1985, 2000 and 2015 (Baumann et al. 2017). In order to increase the temporal resolution to annual land-cover/use layers between 2000 and 2015 we assigned the year of deforestation from Hansen et al. (2013) to the land-cover/use category of 2015 from Baumann et al. (2017). We generated %Edge_Forest through a Morphological Spatial Pattern Analysis (MSPA) considering a 1-km forest edge (Soille & Vogt 2009). Species with different mobility levels may judge land cover suitability at different scales (Wilman et al. 2014; Romero-Muñoz, Torres, et al. 2019) (Table SI III-2). Therefore, we calculated the proportional shares of forest, grasslands, croplands, pastures, and edge forest within buffers of 1km, 3km and 7km radius from the target cell (i.e., areas of 1, 28, and 154 km²). We assigned the radius for each species individually, depending on their respective home range size (see Table SI III-2). We calculated climate predictors (mean annual temperature and mean annual precipitation) as climate normals (i.e. three-decade averages) between 1981 and 2010 using the ClimateSA v1.0 database (Hamann et al. 2013).

Due to the lack of comparable human population density layers for 1985, we used the 2000 layer for both 1985 and 2000 (Lloyd et al. 2017), which is reasonable since human

population did not change dramatically in the Chaco in that period. We reconstructed historical road networks based on current national road maps and comparisons with historical imagery in Google Earth. We also screen-digitized >27,000 subsistence ranches for 1985, 2000 and 2015 using historical imagery in Google Earth. Finally, we used pastures and croplands from the land cover maps.

Presence and background data preparation for the habitat suitability models

Spatial sampling bias is a common phenomenon in occurrence data, particularly in inaccessible area such as the Gran Chaco (Elith et al. 2010; Kramer-Schadt et al. 2013). Sampling bias thus needs to be accounted for when modelling species' distributions (Kramer-Schadt et al. 2013). To eliminate or mitigate the potential impact of sampling bias, we implemented two procedures. First, we randomly filtered presence records to only one within a 10 km radius to generate an input dataset of presence records for our habitat suitability models. To rarefy presence records, we matched occurrence data collected at a given time with the corresponding temporal predictor variables for the years 1985 and 2000-2015. To avoid losing earlier locations, which were scarcer, we applied this filtering independently for the time periods 1978-1992, 1993-2007 and 2008-2018 (i.e., periods centred around the years 1985, 2000, 2015).

Second, we created sets background points that accounts for the distribution of a species and the spatial sampling bias. Maxent requires these background data to describe the overall distribution of predictor values across the study area. We first gathered species with similar distributions of presence points into seven groups, based on visual examination. For each group and time period (1985, 2000 and 2015), we produced kernel-density maps of the presence points and used the resulting probability maps to spatially weight a random sample of background points (Elith et al. 2010).

Modelling hunting pressure

We modelled hunting pressure using a two-stage modelling process that consisted of a binomial model, which included locally extant and extirpated species due to hunting, and a Gaussian model that included abundance changes (expressed as non-zero response rations) due to hunting compared with control areas (Benítez-López et al. 2019). To parameterize this hunting pressure model, we used three predictors: *Distance to Hunter Access Points*, *Human Population Density* (both indicators of hunting risk), and *Species Body*

Mass (an indicator of a species' intrinsic vulnerability to population decline as a result of hunting) (Table SI III-2).

Once parameterized, we projected the hunting pressure model in space, accounting for each species' characteristics, socio-economic variables, and spatially explicit determinants of hunting pressure. Specifically, we specified as random effects *Country*, *Study*, and *Species* to account for between-country variation in hunting laws and policies, culture, taboos, and traditions, as well as to control for non-independence in the data from the same study or species (Benítez-López et al. 2019). The final model was selected through a model selection procedure based on the Bayesian Information Criterion (BIC) by Benítez-López et al. (2019). Our projections were based on the taxonomic identity of the species (captured by the random-effect intercept *Species*), the country where it was located (random-effect intercept *Country*"), and its weight (*Body mass*, an indicator capturing the vulnerability of a species to hunting pressure at the population level), combined with the distribution of context-dependent drivers of hunting pressure (*Distance to settlements*, and *Human population density*) within the species range. This results in a defaunation index ranging from 0 (no decline in abundance) to 1 (total local extirpation), which we interpret as a hunting pressure index. We re-fitted the original global model to Neotropical mammals only ($n = 1,945$ abundance ratios).

Identifying hotspots of core areas and hotspots of threats

To identify hotspots per habitat category, we adopted an approach used to derive rarity-weighted species richness. This approach calculates shares of species' ranges within a gridcell, and then sums these shares across all species present in a gridcell. Thus, rarity-weighted richness is a measure of the overall importance of a gridcell for representing the entire community of species considered, accounting for both the number of species (higher values for gridcells with high numbers of species) and how widespread they are (higher values for gridcells with many small-ranged species) (Kier & Barthlott 2001). We applied this approach separately to each habitat category to create measures of importance for each category. For example, to assess a gridcell's importance in providing core areas to the species assessed here, we summed the weighted core area share across all species. These areas can be directly interpreted as priority areas for conservation, because rarity-weighted-richness approaches have been shown to compare favourably to other prioritisation algorithms for such prioritization (Albuquerque & Beier 2015).

We used the same approach to identify hotspots of habitat destruction and hunting at a resolution of 5 km². Threat hotspots are areas where a threat exerts disproportionate pressure, either on many species or on rarer species. Threat hotspots therefore represent the most important areas where to concentrate actions to mitigate the impact of that threat. To calculate threat hotspots, we first weighted for each species and gridcell the area assigned to a threat by the total area of that threat plus the core area for that species. This accounts for the overall distribution, giving higher weight to species with a higher share of their range under threat. Second, we then summed the weighted threat footprints across the larger mammal community per gridcell. To identify threat hotspots for 2015, we used species' maps of hunting pressure in 2015, but habitat destruction over time (1985 to 2015). We did so to separate marginal habitat (e.g., due to poor climatic conditions, see above) from habitat destruction. As a sensitivity analysis, we repeated these hotspot analyses using species' global range extents (IUCN 2018) instead of their Chaco range. This emphasises the global importance of the species whereas our base analysis emphasises the regional importance.

Table SI III-1: Sources of presence locations for the 48 mammal species from across the Chaco ecoregion.

| Source type | Source |
|-----------------------------|--|
| Publicly available database | Global Biodiversity Information Facility (GBIF) |
| | Administration of National Parks of Argentina (APN) |
| | Museo Noel Kempff Mercado, Universidad Autónoma Gabriel René Moreno, Santa Cruz, Bolivia |
| Published literature | Rumiz (2012) |
| | Sanderson et al. (2002) |
| | Torres et al. (2014) |
| | Quiroga et al. (2014) |
| | Wallace et al. (2010) |
| Unpublished literature | Giordano (2015) |

Table SI III-2: Description of predictor variables used in the habitat suitability and hunting pressure models. All variables covered the entire study region and were generated at a resolution of 1 km² (see Supporting Information for details).

| Variable name | Description | Data source | Time period | Rational |
|----------------------------------|---|---|--|---|
| Habitat suitability models | | | | |
| %Forest * | % woodland cover around target cell (at buffers of 1km, 3km and 7km) | Baumann et al. (2017) and Hansen et al. (2013) | 1985 and yearly maps from 2000 to 2015 | Provides resources in terms of food and shelter for most of our species |
| %Cropland * | % cropland cover around target cell | Romero-Muñoz, Torres, et al. (2019) | See above | Indicates a lack of resources for most species, and resource availability for some others (e.g., peccaries) |
| %Grassland * | % natural grasslands around target cell | See above | See above | Captures open, natural vegetation that several species depend on |
| %Pastures * | % implanted, intensified pastures around target cell | See above | See above | Indicates resource depletion compared to natural woodlands and natural grasslands |
| %Forest Edge | % of Edge Forest around target cell | See above | See above | Captures edge effects, which can be positive or negative for the species studied |
| Distance to Water | Distance to water | See above | See above | Characterizes access to water, which is critical for all species |
| Mean Annual Temperature | Annual Average Temperature | ClimateSA v1.12 | 1981-2010 average | Captures temperature limitations (particularly hot temperatures) |
| Mean Annual Precipitation | Annual precipitation | ClimateSA v1.12 | 1981-2010 average | Indicates vegetation productivity and water availability |
| Hunting pressure model | | | | |
| Distance to Hunter Access Points | Hunter access points may include roads, towns, agricultural land or smallholder ranches | National road atlas; Open Street map; land-cover / use maps as above; Onscreen digitization | 1985, 2000, 2015 | Characterizes for each species whether a location is accessible for hunters and is therefore an indirect proxy for hunting pressure |

| | | | | |
|--------------------------|---|--|------------|---|
| | | (see SI for details) | | |
| Human Population Density | Human population density at 1-km resolution | WorldPop Population Dataset (www.worldpop.org) | 2000, 2015 | Hunting pressure often increases with the density of people living in an area due to increasing meat demand and/or human-wildlife conflicts |
| Body Mass | Species body mass | Trait database (Wilman et al. 2014) | | Captures intrinsic hunting risk as large-bodied species are more vulnerable due to (1) being rarer, (2) reproducing more slowly, and (3) being often preferred by hunters |

Table SI III-3: Characteristics of the 48 larger mammals analysed.

| <i>Species</i> | No. location points | IUCN Status | Body mass (g) | Distribution group | Scale group- km radius | Hunting access points * |
|--------------------------------------|---------------------------|----------------|---------------------|-----------------------|---------------------------------|---|
| <i>Alouatta caraya</i> | 40 | LC | 5862 | Northeast | 3 | Towns, roads, rivers |
| <i>Aotus azarae</i> | 33 | LC | 930 | Northeast | 1 | Towns, roads |
| <i>Blastocerus dichotomus</i> | 18 | VU | 86666 | East | 3 | Towns, roads, cropland, Pastures, puestos |
| <i>Cabassous chacoensis</i> | 34 | NT | 1490 | Dry Chaco | 1 | Towns, roads, puestos |
| <i>Callicebus pallescens</i> | 40 | LC | 800 | Northernmost | 1 | Towns, roads |
| <i>Calyptophractus retusus</i> | 15 | DD | 130 | North | 1 | Towns, roads |
| <i>Catagonus wagneri</i> | 94 | EN | 35566 | Dry Chaco | 3 | Towns, roads, cropland, Pastures, puestos |
| <i>Cerdocyon thous</i> | 168 | LC | 5240 | North and center | 1 | Towns, roads |
| <i>Chaetophractus vellerosus</i> | 91 | LC | 1030 | Dry Chaco | 1 | Towns, roads, cropland, puestos |
| <i>Chaetophractus villosus</i> | 98 | LC | 4540 | Dry Chaco | 1 | Towns, roads, cropland, puestos |
| <i>Chrysocyon brachyurus</i> | 60 | NT | 23250 | East | 3 | Towns, roads, Pastures, puestos |
| <i>Coendou prehensilis</i> | 22 | LC | 4400 | Northernmost | 1 | Towns, roads |
| <i>Conepatus chinga</i> | 140 | LC | 1918 | All | 1 | Towns, roads |
| <i>Cuniculus paca</i> | 7 | LC | 8173 | Northeast | 1 | Towns, roads, puestos |
| <i>Dasyprocta azarae</i> | 62 | DD | 2310 | Northeast | 1 | Towns, roads, puestos |
| <i>Dasypus novemcinctus</i> | 118 | LC | 4204 | North and center | 1 | Towns, roads, puestos |
| <i>Didelphis albiventris</i> | 71 | LC | 904 | North and center | 1 | Towns, roads |
| <i>Dolichotis salinicola</i> | 88 | LC | 1600 | Dry Chaco | 1 | Towns, roads, puestos |
| <i>Eira barbara</i> | 56 | LC | 3910 | North and center | 3 | Towns, roads |
| <i>Euphractus sexcinctus</i> | 132 | LC | 4783 | North and center | 1 | Towns, roads, puestos |
| <i>Galictis cuja</i> | 52 | LC | 1000 | North and center | 1 | Towns, roads |
| <i>Galictis vittata</i> | 6 | LC | 3200 | Northeast | 1 | Towns, roads |
| <i>Hydrochoerus hydrochaeris</i> | 63 | LC | 48145 | North and center | 1 | Towns, roads, puestos, rivers |
| <i>Lagostomus maximus</i> | 50 | LC | 4648 | Dry Chaco | 1 | Towns, roads, cropland, puestos |

Chapter III

| | | | | | | |
|--------------------------------|-----|----|--------|------------------|---|---|
| <i>Lama guanicoe</i> | 12 | LC | 142500 | Dry Chaco | 3 | Towns, roads, cropland, puestos |
| <i>Leopardus geoffroyi</i> | 232 | LC | 5158 | All | 1 | Towns, roads, puestos |
| <i>Leopardus pardalis</i> | 78 | LC | 11900 | North | 3 | Towns, roads, puestos |
| <i>Leopardus wiedii</i> | 11 | NT | 3250 | Northeast | 3 | Towns, roads |
| <i>Lontra longicaudis</i> | 24 | NT | 6555 | East | 3 | Towns, roads |
| <i>Lycalopex gymnocercus</i> | 202 | LC | 4543 | All | 1 | Towns, roads |
| <i>Mazama americana</i> | 22 | DD | 22800 | Northeast | 1 | Towns, roads, cropland, Pastures, puestos |
| <i>Mazama gouazoubira</i> | 220 | LC | 16633 | All | 1 | Towns, roads, cropland, Pastures, puestos |
| <i>Mico melanurus</i> | 7 | LC | 336 | Northernmost | 1 | Towns, roads |
| <i>Myocastor coypus</i> | 21 | LC | 6937 | East | 1 | Towns, roads |
| <i>Myrmecophaga tridactyla</i> | 175 | VU | 22333 | North and center | 3 | Towns, roads |
| <i>Nasua nasua</i> | 49 | LC | 3794 | North and center | 1 | Towns, roads |
| <i>Panthera onca</i> | 403 | NT | 100000 | North | 7 | Towns, roads, Pastures, puestos |
| <i>Pecari tajacu</i> | 192 | LC | 21267 | All | 1 | Towns, roads, cropland, Pastures, puestos, rivers |
| <i>Priodontes maximus</i> | 56 | VU | 45360 | North | 1 | Towns, roads, Pastures, puestos |
| <i>Procyon cancrivorus</i> | 118 | LC | 6950 | North and center | 1 | Towns, roads |
| <i>Puma concolor</i> | 399 | LC | 51600 | All | 7 | Towns, roads, Pastures, puestos |
| <i>Puma yagouaroundi</i> | 153 | LC | 6875 | All | 3 | Towns, roads, puestos |
| <i>Sapajus cay</i> | 18 | LC | 2687 | Northeast | 1 | Towns, roads |
| <i>Sylvilagus brasiliensis</i> | 112 | LC | 950 | North and center | 1 | Towns, roads, puestos |
| <i>Tamandua tetradactyla</i> | 92 | LC | 5515 | All | 1 | Towns, roads |
| <i>Tapirus terrestris</i> | 123 | VU | 207501 | North | 3 | Towns, roads, puestos, rivers |
| <i>Tayassu pecari</i> | 120 | VU | 32234 | North | 3 | Towns, roads, cropland, puestos, rivers |
| <i>Tolypeutes matacus</i> | 214 | NT | 1200 | Dry Chaco | 1 | Towns, roads, cropland, puestos |

* "Puestos" are subsistence ranches

Figure SI III-1: Correlation matrix of the predictor variables of resource availability.

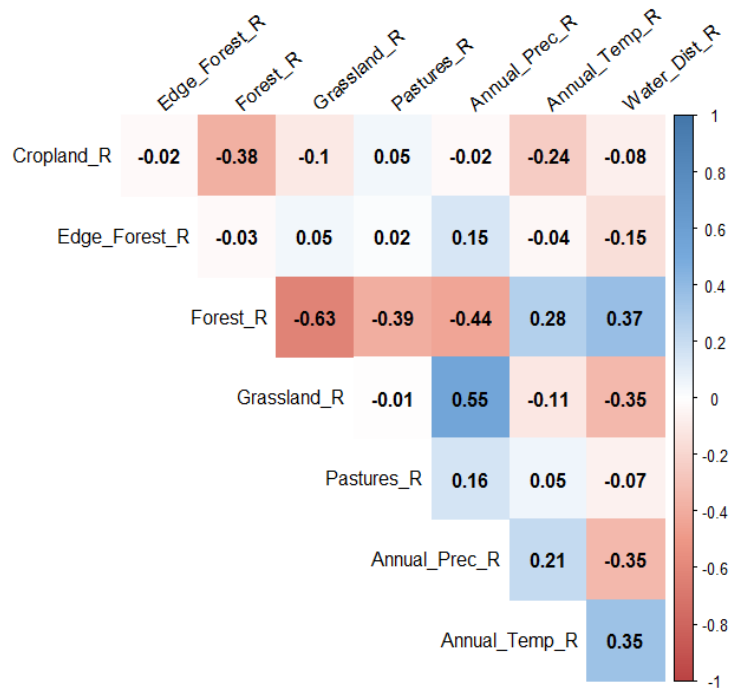


Figure SI III-2: Average Training Area Under the Curve scores for the habitat suitability models for the resource-related models for the mammals of the Chaco

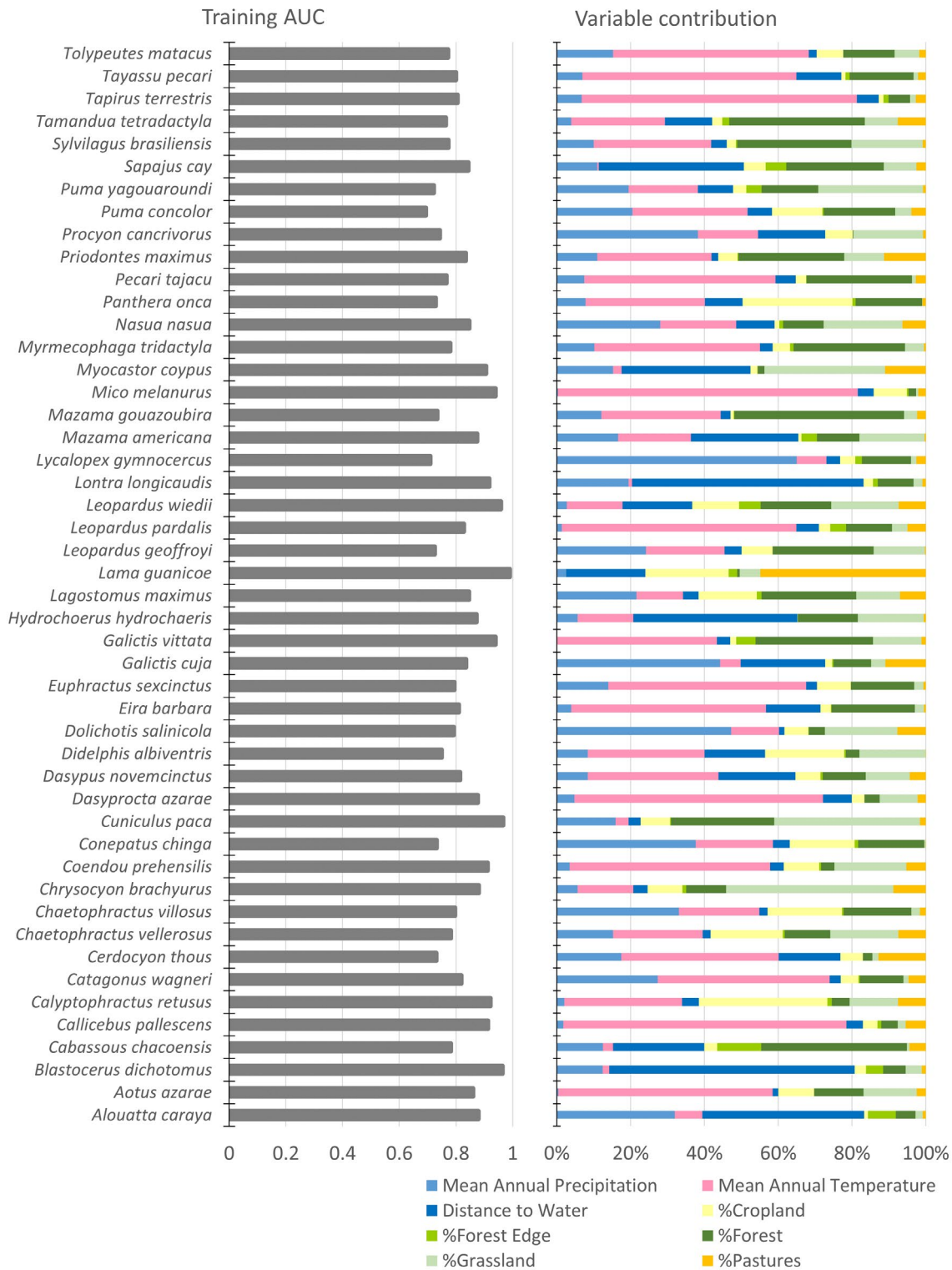


Figure SI III-3: Number of core areas – where both threats are low – of the 48 larger mammals of the Chaco in 2015 (left) and their change between 1985 and 2015 (right). On the right, red = loss of core areas, grey = stable, blue = gain of core areas). Thick lines represent country limits whereas thin lines denote protected areas in the Chaco.

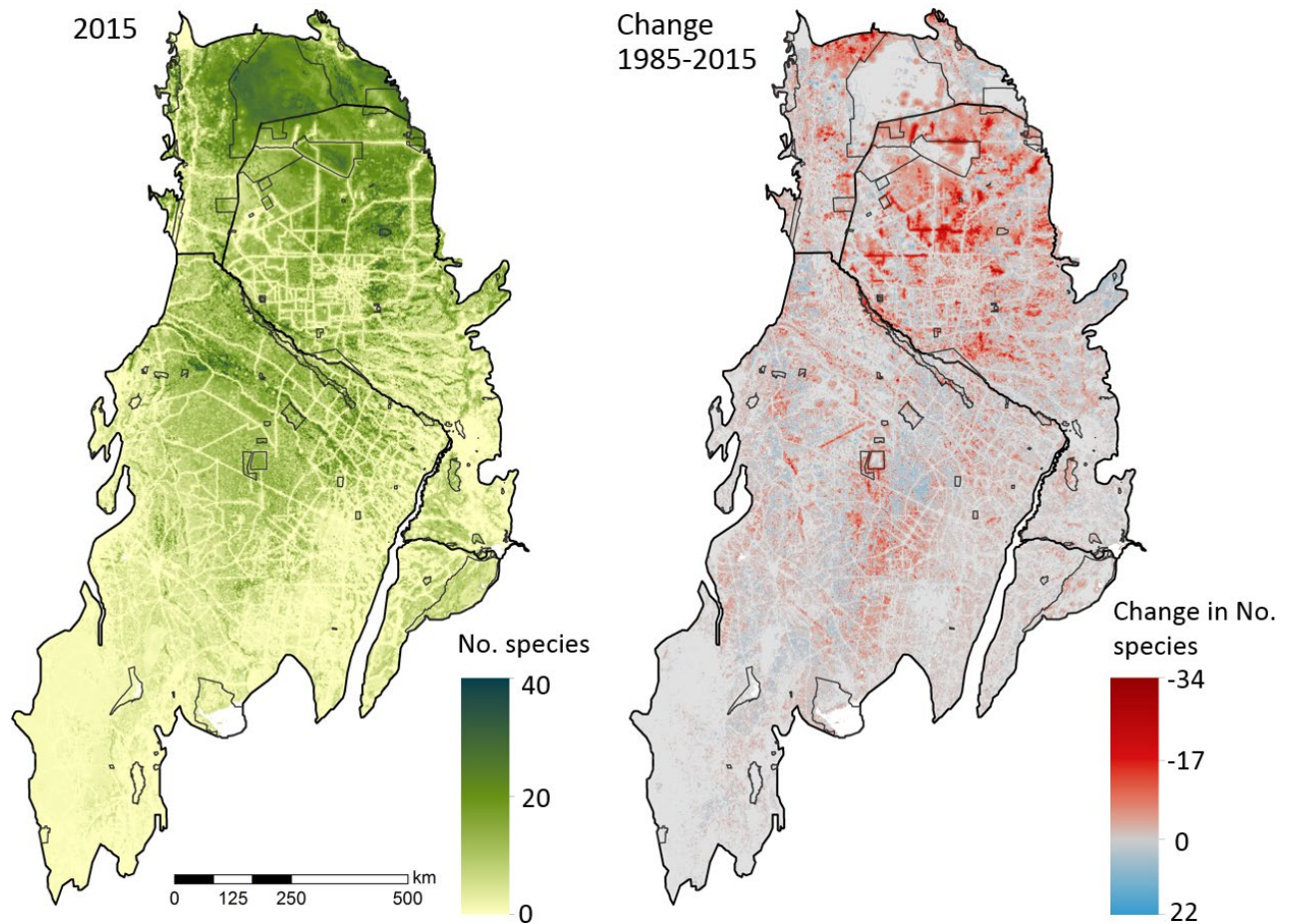


Figure SI III-4: Habitat destruction and hunting pressure change over time inside and outside protected areas from 1985 to 2015 (A). (B) Area change (in km²) of threats inside and outside protected areas. (C) Change in % core area change among Chaco countries and (D) between protected and unprotected areas across Chaco countries.

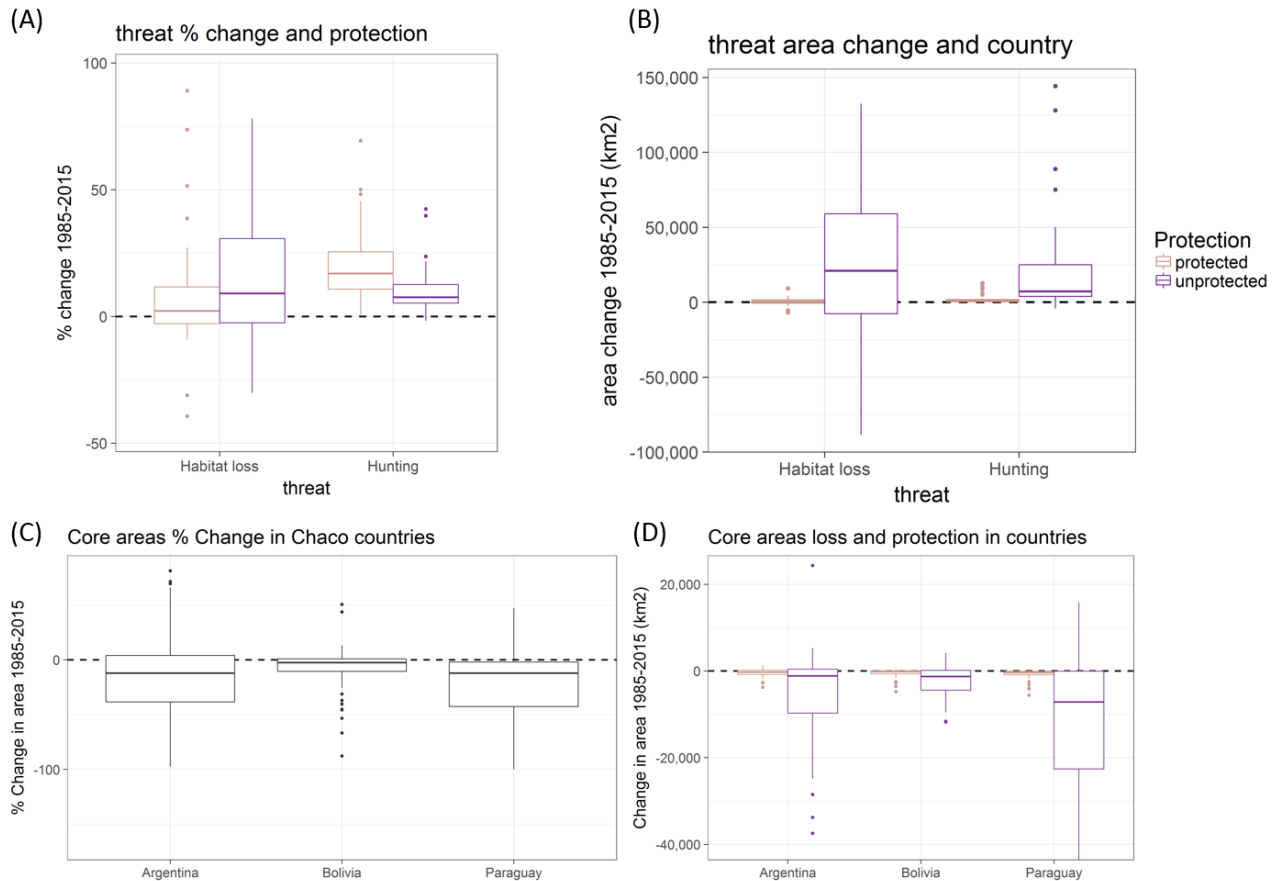


Figure SI III-5: Expansion in the footprints of habitat destruction and hunting pressure for 48 Chacoan mammals between 1985 and 2015 (as a percentage of their range in 1985) with the species names for all evaluated mammals. Change in the footprints of habitat destruction vs. that of hunting pressure, where positive values indicate an expansion of that threat. The grey dashed line indicates the average change per threat for all mammals.

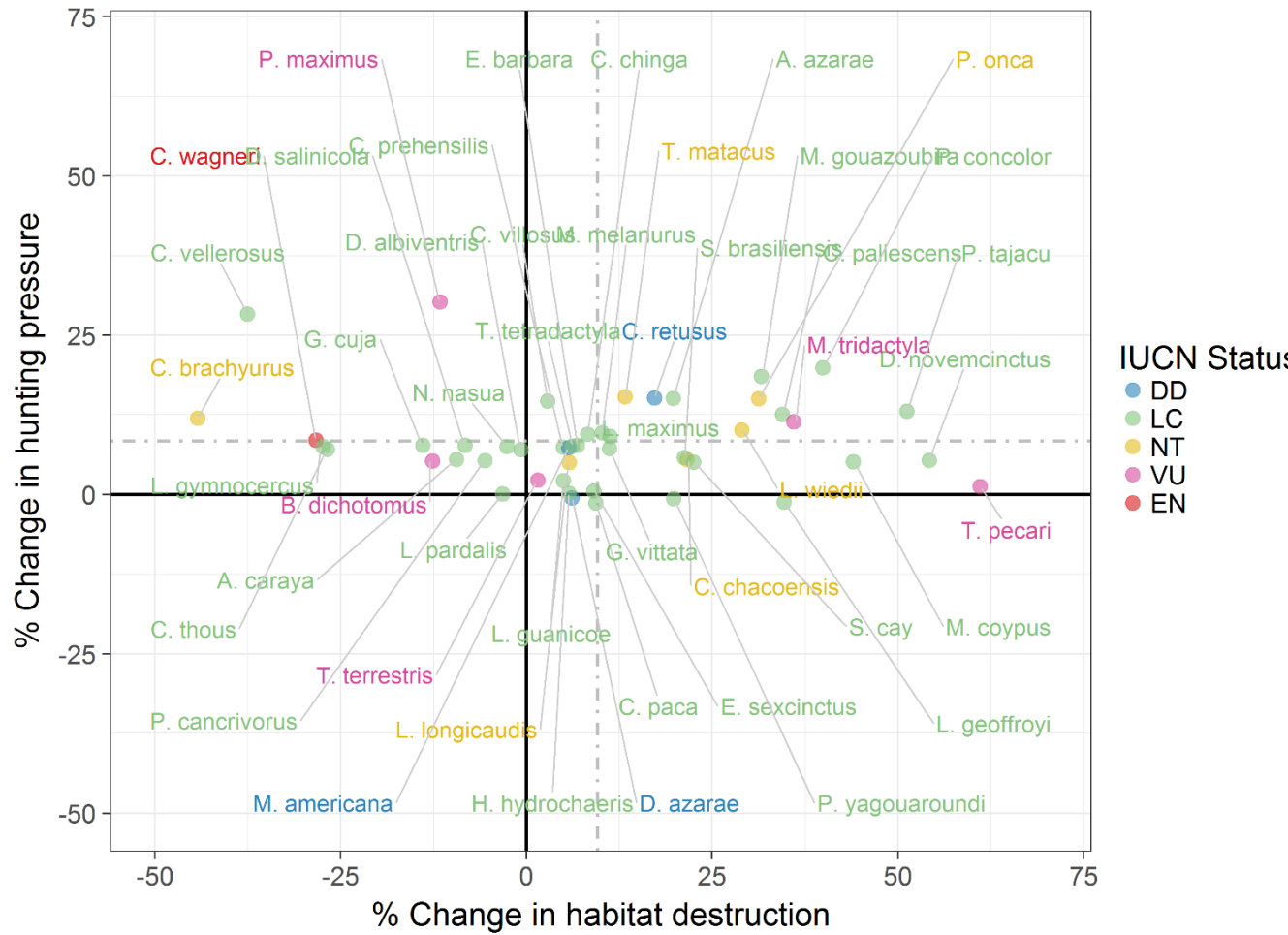
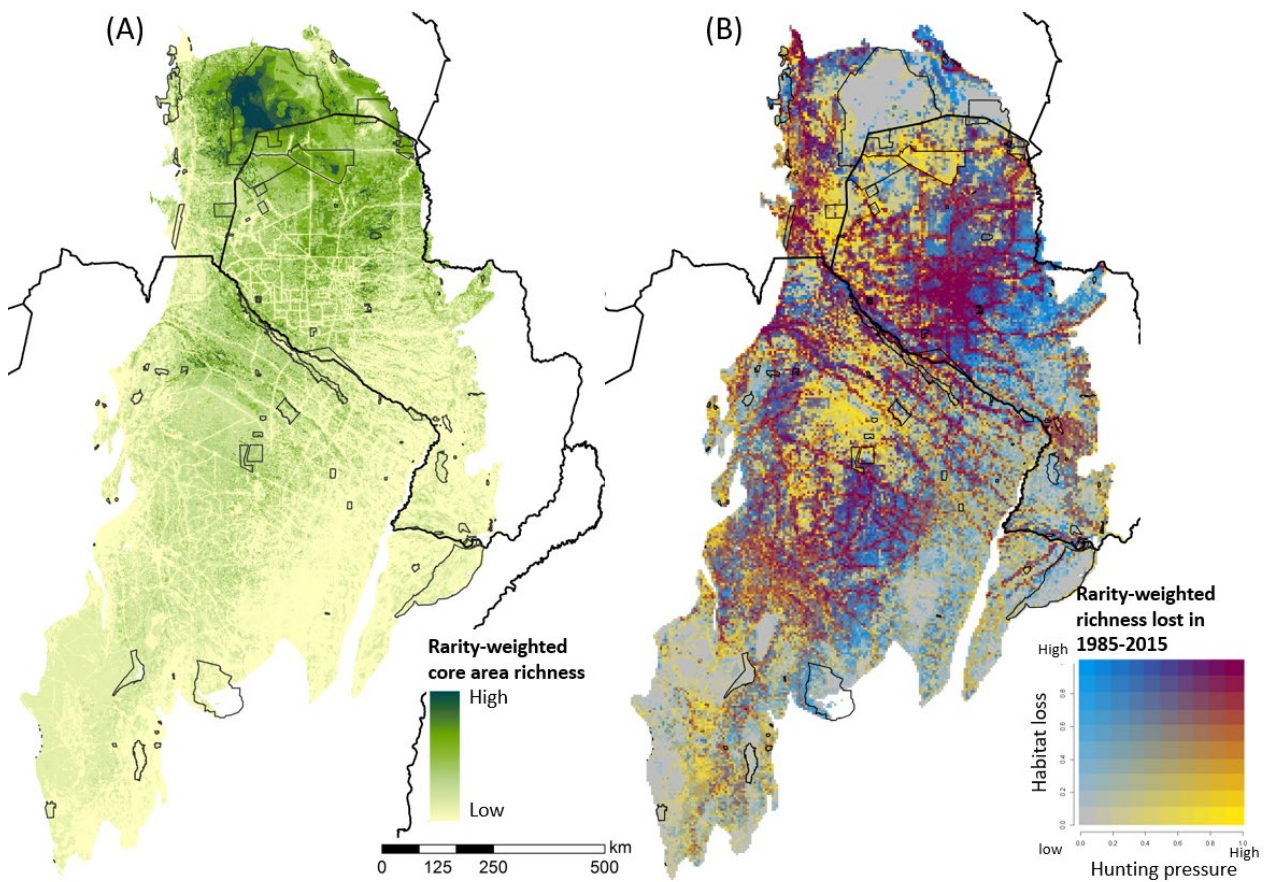


Figure SI III-6: Hotspots of core areas and of habitat destruction and hunting pressure for the Chaco larger mammals in a global context, based on the rarity-weighted richness considering the global extent of species ranges from IUCN. (A) Hotspots of core area in 2015, where high values indicate more species that have small core areas. (B) Bivariate map of hotspots of habitat destruction (1985-2015) and high hunting pressure (2015), where higher scores mean more species that have small overall area of their core area + the area under each threat.



Chapter IV:

**Habitat destruction and overexploitation
drive widespread declines in all facets of
mammalian diversity in the Gran Chaco**

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Abstract

Global biodiversity is under high and rising anthropogenic pressure. Yet how the taxonomic, phylogenetic, and functional facets of biodiversity are affected by different threats over time is unclear. This is particularly true for the two main drivers of the current biodiversity crisis, habitat destruction and overexploitation. We provide the first long-term assessment of multifaceted biodiversity changes caused by these threats for any tropical region. Focussing on larger mammals in South America's 1.1 million km² Gran Chaco region, we assessed changes in multiple biodiversity facets between 1985 and 2015, determined which threats drive those changes, and identified remaining key areas for all biodiversity facets. Using habitat and threat maps, we found, first, that between 1985 and 2015 taxonomic (TD), phylogenetic (PD) and functional (FD) diversity all declined drastically across over half of the area assessed. FD declined about 50% faster than TD and PD, and these declines were mainly driven by species loss, rather than species turnover. Second, habitat destruction, hunting, and both threats together contributed ~57%, ~37%, and ~6% to overall facet declines, respectively. However, hunting pressure increased where TD and PD declined most strongly, whereas habitat destruction disproportionally contributed to FD declines. Third, just 23% of the Chaco would have to be protected to safeguard the top 17% of all three facets. Our findings uncover a widespread impoverishment of mammal species richness, evolutionary history, and ecological functions across broad areas of the Chaco due to increasing habitat destruction and hunting. Moreover, our results pinpoint key areas that should be preserved and managed to maintain all facets of mammalian diversity across the Chaco. More generally, our work highlights how long-term changes in biodiversity facets can be assessed and attributed to specific threats, to better understand human impacts on biodiversity and to guide conservation planning to mitigate them.

Keywords: biodiversity facets, extinction drivers, functional diversity, functional richness, overhunting, phylogenetic diversity, taxonomic diversity, traits

1 Introduction

Human activities are driving the global biodiversity crisis, and the two biggest threats are habitat destruction and overexploitation (Hooper et al. 2012b; Díaz et al. 2019; IPBES 2019). Assessing patterns of biodiversity change due to these threats is therefore crucial for conserving biodiversity and achieving sustainability goals (Cardinale et al. 2012; Díaz et al. 2019; IPBES 2019). Most efforts assessing biodiversity change across broad spatial scales have focused on taxonomic diversity and have not connected those changes to multiple threats (e.g. Kerbiriou et al. 2009; Tingley & Beissinger 2013; Dornelas et al. 2014). Yet a focus on taxonomic diversity neglects evolutionary history and long-term evolutionary potential (Winter et al. 2013). Likewise, taxonomic diversity overlooks the diverse ecological functions of species in ecosystems (Cadotte et al. 2011; Winter et al. 2013), which maintain ecosystem integrity and functioning and ultimately provide nature's contributions to people (Cadotte et al. 2011; Cardinale et al. 2012; Díaz et al. 2019). Therefore, assessing how different threats contribute to long-term changes in all three biodiversity facets, taxonomic (TD), phylogenetic (PD), and functional (FD) diversity, is crucial for a more comprehensive understanding of human impacts on nature. Likewise, this understanding is also vital to develop conservation strategies that better account for all biodiversity facets.

The varied and widespread change across biodiversity components is better understood through temporal assessments – rather than space-for-time substitutions – particularly across rapidly changing regions (Damgaard 2019). Long-term studies have reported decreasing (Tingley & Beissinger 2013), increasing (Kerbiriou et al. 2009) or no net change of TD (Dornelas et al. 2014). Likewise, the few studies focusing on more than one biodiversity facet have reported both similar (Jarzyna & Jetz 2017) or different (Villéger et al. 2010; Monnet et al. 2014) temporal trends among facets. Only two studies, focusing on birds across France (Monnet et al. 2014) and the USA (Jarzyna & Jetz 2017), have simultaneously assessed the long-term changes of all three biodiversity facets at broad scales. All facets increased in both studies, except for FD in France, which remained stable.

In contrast, the long-term multifaceted changes of biodiversity in the tropics - where the overwhelming majority of Earth's biodiversity resides, and where their main threats are expanding the fastest (Bradshaw et al. 2009; Barlow et al. 2018) - remain largely unexplored. The downward trends of TD and of natural habitats reported in the tropics (Hansen et al. 2013; Barlow et al. 2016; Romero-Muñoz et al. 2020) suggest that

biodiversity trends likely differ substantially from those reported from temperate regions. Recent advances in remote sensing and ecological modelling allow us to reconstruct detailed land-use change histories, as well as the distributions of species and the spatial footprints of threats for multiple species across several decades and large regions (Baumann et al. 2017; Benítez-López et al. 2019; Romero-Muñoz et al. 2020). Together with increasingly available trait and phylogenetic information, these developments open the opportunity to assess long-term changes in multiple biodiversity facets across rapidly changing regions.

Habitat destruction and overexploitation are the leading drivers of global biodiversity decline (Maxwell et al. 2016; IPBES 2019). Both threats are rapidly expanding into previously natural areas across the tropics due to the increasing human demand for agricultural products, such as beef, soy (predominantly used as livestock feed), and palm oil (Laurance et al. 2009; Kehoe et al. 2017). Yet these threats affect species differently (Ripple et al. 2017; Romero-Muñoz et al. 2020), and therefore may affect biodiversity facets differently. For instance, habitat destruction and degradation through land-use change may disproportionately affect species within specific phylogenetic lineages (Frishkoff et al. 2014; Nowakowski et al. 2018) or with specific traits (Wordley et al. 2017; Newbold et al. 2020). Likewise, species from some lineages (D'agata et al. 2014; Davis et al. 2018), or with certain traits, like large body size (Ripple et al. 2017; Benítez-López et al. 2019), are more vulnerable to overexploitation.

Habitat destruction and hunting pressure are widespread in tropical regions (Gallego-Zamorano et al. 2020; Romero-Muñoz et al. 2020) and, where these threats co-occur, they exacerbate biodiversity loss even more than either threat alone (Peres 2001; Brook et al. 2008; Mouillot et al. 2013). Despite the importance of assessing and mapping the combined impact of these major threats, previous studies have focused either on individual threats, usually only habitat modification, when assessing changes in several biodiversity facets (e.g. Frishkoff et al. 2014; Wordley et al. 2017; Chapman et al. 2018), or on multiple threats for single species (Romero-Muñoz, Torres, et al. 2019) or only on TD (Romero-Muñoz et al. 2020). The contribution of the individual vs. combined effects of threats to changes in multiple biodiversity facets remains so far unexplored.

This is unfortunate, as learning how the three biodiversity facets are impacted by threats in space and time would enable more effective conservation planning, through threat-specific targeting of conservation actions (Devictor et al. 2010; Pollock et al. 2017). Although

conservation planning often assumes that one facet also represents others, recent studies found considerable spatial mismatches among facets (Devictor et al. 2010; Safi et al. 2011; Mazel et al. 2018). Therefore, conservation planning could benefit from identifying the most important areas for each biodiversity facet, as well as where those areas overlap. However, current methods to map facets are not ideal, because most rely on expert-based species range maps, which represent single snapshots in time, contain errors, and are built at a coarse scale (Ficetola et al. 2014). As threats are expanding and intensifying (Benítez-López et al. 2017; Kehoe et al. 2017; Allan et al. 2019), there is an urgent need to map the spatial congruence of all three biodiversity facets at resolutions fine enough to inform conservation planning.

This is particularly urgent in tropical deforestation frontiers, which are global hotspots of biodiversity loss (Hoekstra et al. 2005; Bradshaw et al. 2009; Barlow et al. 2018). Many such frontiers, particularly those in tropical dry forests, are weakly protected (Hoekstra et al. 2005; Kuemmerle et al. 2017). The Gran Chaco (hereafter ‘Chaco’) in South America, is one of the most at-risk regions globally, due to rapid expansion of cattle ranching and soy cultivation (WWF 2015; Kuemmerle et al. 2017). The region is a global hotspot of habitat conversion and defaunation (Baumann et al. 2017; Romero-Muñoz et al. 2020), yet despite calls for assessing the facets of biodiversity in this region (Periago et al. 2014), no such assessment exists.

Here, we provide the first assessment of TD, FD, and PD for the large- and medium-sized mammals (>~ 1 kg, hereafter ‘larger mammals’) in the Chaco, a global deforestation hotspot. These species represent a phylogenetically diverse group, including some lineages endemic to the Chaco, such as those represented by the Chacoan peccary (*Catagonus wagneri*), the Chacoan mara (*Dolichotis salinicola*), and several armadillo species (Nori et al. 2016). The enormous variation in size and morphology among larger mammals in the Chaco also translates into a high diversity of ecological roles and resource uses. Several ecosystem functions are unique to larger mammals, such as dispersing the seeds of the largest trees or regulating the populations of other large animals (Lacher et al. 2019). Such roles have significant effects on nutrient cycling and energy flows, and in structuring ecological communities and thus promoting high biodiversity and ecosystem stability (Terborgh 2015; Lacher et al. 2019). In turn, larger mammals provide various contributions to people directly, such as by being sources of protein for local communities, and indirectly, such as by enhancing forest regeneration and carbon storage capacity (Noss et al. 2004; Bello et al. 2015). Many larger mammals in the Chaco are highly vulnerable to habitat

destruction and hunting (Semper-Pascual et al. 2018; Romero-Muñoz et al. 2020) and their declines threaten to erase unique evolutionary histories, affect ecosystem integrity, and negatively impact nature's contributions to people.

Here we aim to assess 30 years of change in the three facets of mammalian diversity in the Chaco and explore how habitat destruction and overexploitation contributed to these changes. To our knowledge this represents the first assessment of this kind for (a) mammals, (b) the tropics, and (c) in relation to multiple, interacting threats. Specifically, we aim to answer:

1. How has the taxonomic, phylogenetic, and functional diversity of larger mammals in the Chaco changed between 1985 and 2015?
2. How have the individual and combined effects of habitat destruction and hunting contributed to changes in these three facets?
3. Where are the priority areas for conserving each facet of mammalian diversity in the Chaco and where do they overlap?

2 Methods

2.1 Study region

The Gran Chaco region extends across 1.1 million km² in Argentina, Paraguay, and Bolivia, and is the largest tropical and subtropical dry forest in the world. Xeric forests are the dominant vegetation formation, with interspersed mosaics of natural savannas and gallery forests. The climate ranges from tropical in the north to subtropical in the centre and south. Precipitation ranges from 1400 mm in the east to 400 mm in the west and south. The Chaco is rich in biodiversity, with over 150 mammal species, 500 birds, and over 3000 plant species (TNC et al. 2005). Over the last decades the Chaco has become a global deforestation hotspot, losing 20% of its forests since 1985 due to the expanding croplands, mainly in Argentina, and livestock ranching, mainly in Paraguay and Bolivia (Baumann et al. 2017). These pressures are likely impacting ecosystem functioning over large scales (Periago et al. 2014), although this has not been yet quantified. Despite these pressures, only about 9% of the Chaco is currently protected (Nori et al. 2016).

3 Datasets used

We produced maps of the habitats and the footprints of habitat destruction and hunting pressure separately for 48 larger mammals between 1985 and 2015 at a 1km² resolution in an earlier study (Romero-Muñoz et al. 2020). This was done using habitat suitability models to track habitat suitability across space and time and hunting pressure models to do the same for the hunting risk. We performed separate multi-temporal habitat suitability models and hunting pressure models for each species.

To assess habitat suitability we used the largest database of presence records of larger mammals ever collected for the Chaco, containing occurrences from 1985 to 2015, which we analysed using maximum entropy modelling (Maxent v3.4.1; Phillips et al. 2017). Maxent predicts a species' occurrence' by comparing the locations of recorded presences to the overall distribution of environmental predictors for a study region, which are sampled through background points (Phillips et al. 2017). We generated seven predictors related to habitat suitability for mammals for 1985 and 2015, at a 1km² resolution: % forest, % pastures, % cropland, % forest edge, distance to water, mean annual temperature, and mean annual precipitation. All Maxent models were parameterized using only hinge features to avoid overfitting, a regularisation multiplier of 1, and a prevalence value of 0.5, and we controlled for sampling bias in our occurrence and background datasets. We cross-validated all models using averaged area under the curve (AUC) values across the replicates. Our models generally had a high discriminative power (AUC >0.7) (see Romero-Muñoz et al. 2020).

We applied the method developed by Benítez-López et al. (2019) to model hunting pressure as the declines in each species' abundance due to hunting. The hunting pressure model is based on 3281 abundance estimates of larger mammals systematically comparing hunted and non-hunted sites across the Tropics (Benítez-López et al. 2019). To accommodate for both local extirpations and abundance declines, a two-stage mixed model is fitted, including a binomial model to discriminate extant and locally extinct species, and a Gaussian model to assess abundance change due to hunting (Benítez-López et al. 2019). We refitted the original global model to Neotropical mammals only (n=1,974 abundance changes). We included the *distance to hunter's access points* and *human population density* as spatial predictors of hunting risk, and *species' body mass* as predictor of species-specific vulnerability to population decline due to hunting (Benítez-López et al. 2019). The result of

our hunting pressure model is a hunting pressure index ranging from 0 (no decline in abundance) to 1 (local extirpation) (see Romero-Muñoz et al. 2020).

We projected the habitat suitability and hunting pressure models to 1985 and 2015 (Romero-Muñoz et al. 2020). For each year, we classified the maps resulting from the habitat suitability model into good and poor habitat suitability using the maximum sensitivity plus specificity threshold (Liu et al. 2013). Similarly, we classified the hunting pressure maps for each species into low and high hunting pressure. We used a 30% abundance decline as threshold to classify a species as threatened (here representing high hunting pressure), following the IUCN Red List criteria (IUCN 2012). Overlapping these classified, binary habitat suitability and hunting pressure maps per species highlighted four areas differently affected by threats at each time step: (1) areas with good habitat suitability and low hunting pressure (hereafter: core areas); (2) areas with good habitat suitability but high hunting pressure (hunting pressure); (3) poor habitat suitability but low hunting pressure (poor habitat); and (4) poor habitat and high hunting pressure (co-occurring threats). Furthermore, we considered the change from core area in 1985 to 'poor habitat' in 2015 as 'habitat destruction' and from core to 'hunting pressure' as increasing hunting pressure (hereafter simply 'hunting pressure'), because such increasing threats can be solely attributed to anthropogenic impacts during this period.

We then calculated the three biodiversity facets at a 5 x 5 km² resolution, where each gridcell represents a community of mammals. The 25 km² gridcell size is meaningful in our case as it allows for integrating across species with a wide range of home range sizes (mean = 9.7 km², SD = ±22.2; gathered from Jones et al. (2009)), while being fine enough for regional conservation planning. To aggregate our species-level, 1km² resolution maps to the 5-km grid, we assigned the most frequent habitat or threat category at the 1km grids. We considered a species present in a grid cell if it had core area in it.

4 Depicting biodiversity facets

We calculated metrics for each of the three facets for the years 1985 and 2015 individually (Figure IV-1). We derived taxonomic diversity as species richness (i.e., number of species per gridcell). In addition, we assessed the change in community composition over time, (i.e., temporal community dissimilarity) and the contribution of its components (Baselga 2010). Changes in the species composition of a community result from changes in species

richness and the replacement of some species by others (i.e., turnover), or a combination of both (Baselga 2010). Measures of total dissimilarity, such as the Sørensen dissimilarity index, can thus be decomposed into its turnover and species richness change components (Baselga 2010). While the Sørensen index measures total dissimilarity, the Simpson dissimilarity index accounts only for the turnover component. Thus, the difference between both indices accounts for the species richness change component of dissimilarity (Baselga 2010). We assessed the temporal community dissimilarity only for TD, as equivalent methods have not yet been developed for the other biodiversity facets (Baselga & Orme 2012). We determined the contribution of species richness change and turnover to total dissimilarity change between 1985 and 2015 for each community using the *beta.temp* function in the R package *betapart* v1.5.1 (Baselga & Orme 2012).

For measuring phylogenetic diversity, we used Faith's PD index, which represents the minimum total length of the phylogenetic tree's branches of the species within each community (Faith 1992). To account for phylogenetic uncertainty, we extracted an average tree for the entire set of species from a set of 1000 trees available in the PHYLACINE database (Faurby et al. 2018) using the function *averageTree* in the *phytools* package (Revell 2012). Based on this phylogenetic tree, we calculated the PD index using the *Picante* package in R (Kembel et al. 2010).

As our measure of FD, we calculated functional richness (also known as 'FRic') (Villéger et al. 2008). This index represents the amount of multidimensional functional space occupied by all the species in the community (Villéger et al. 2008). We chose this index instead of the commonly used dendrogram-based index (Petchey & Gaston 2002), because the latter has been shown to produce biased estimates of FD, leading to inaccurate biogeographical patterns (Maire et al. 2015). We first gathered a database of traits related to resource use (Table S1), assessed the collinearity among traits through a Pearson's correlation test, to ensure that traits had $r < 0.5$ to and therefore non-redundant (Villéger et al. 2008) (Figure SI IV-1). Our final list included seven traits: *diet*, *use of forest strata*, *use of day/night*, *home range size*, *body mass*, *generation length*, and *number of offspring per year*, gathered from several sources (Table S1) (Jones et al. 2009; Tacutu et al. 2012; Wilman et al. 2014; Myers et al. 2019). To calculate FD, we used a distance-based framework, based on the Gower distance among traits (Laliberté & Legendre 2010). We weighted traits equally and applied a Principal Coordinates Analysis (PCoA) ordination based on the distance matrix to build a multidimensional functional space. We calculated FD using the *FD* package v1.0-12 in R (Laliberté & Legendre 2010).

The quality of the functional space used to calculate FD (i.e. how well it represents the initial trait values) depends on the number of dimensions of the multidimensional functional space spanned by the PCoA axis (Maire et al. 2015). We compared the quality of functional spaces produced by two to seven dimensions by calculating the mean squared deviation (mSD) metric (Maire et al. 2015). This metric assesses the degree of consistency between the initial and final functional distances (the closer mSD is to 0, the higher the quality of the functional space). As can be expected (Maire et al. 2015), functional space quality increased with the number of dimensions (Figure SI IV-2a). However, there is trade-off between functional space quality and the spatial comprehensiveness of our analyses, as FD can only be calculated for communities with more species than the number of dimensions (Villéger et al. 2008). Therefore, the more dimensions are used to calculate FD, the higher the number of gridcells that will be dropped from the analyses (Figure SI IV-2b). Aiming to produce a high-quality functional space that still allows us to estimate FD across a large portion of our regions, we opted for a four-dimensional functional space in our case (mSD = 0.023). About 50% of all gridcells had less than five species in either 1985 or 2015 and were therefore not included in our FD analyses. These areas mainly occurred in the southern Chaco (Figure SI IV-2c), where anthropogenic pressures caused substantial defaunation before our study period, meaning that threat levels remained relatively static during 1985-2015.

To facilitate comparisons across facets, we calculated all three facets for the same set of communities (i.e. gridcells with ≥ 5 species in both 1985 and 2015) and standardised the values for all three facets by expressing them as the percentage of the maximum value per facet (i.e. the total TD; the entire length of branches for the full tree for PD; and the entire functional space for all species for FD) (Kembel et al. 2010; Laliberté & Legendre 2010). We assessed changes over time for each facet as the difference between 1985 and 2015 (e.g., $\Delta FD_{1985-2015} = FD_{2015} - FD_{1985}$). As the rate and extent of land-use change has varied across space (Baumann et al. 2017), we assessed the change in biodiversity facets for the entire region as well as within countries and inside vs. outside protected areas. We included all designated national-level protected areas from UNEP-WCMC and IUCN (2019).

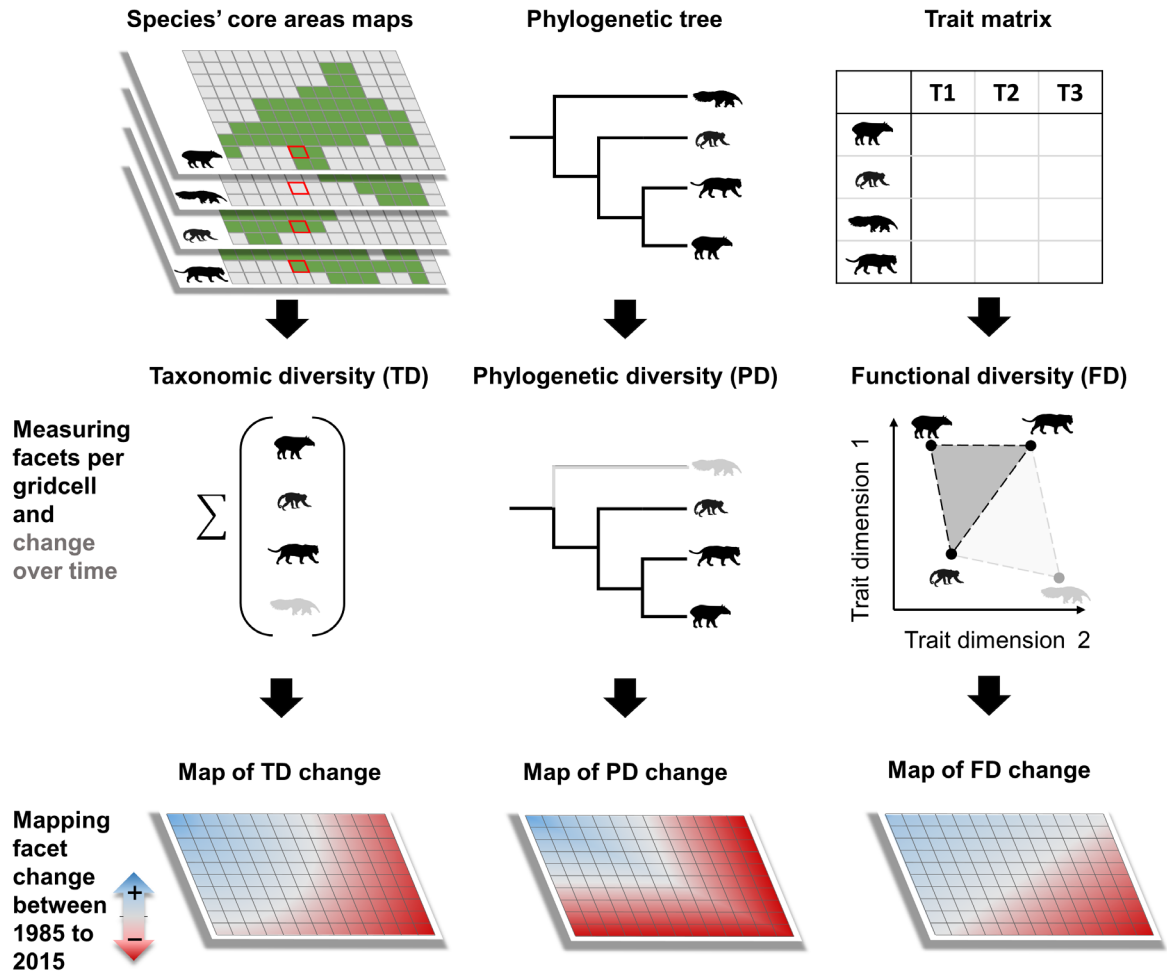


Figure IV-1: Framework to quantify and map changes in the three facets of mammalian diversity (taxonomic, phylogenetic, and functional diversity) across our study region.

4.1 Threat effects on biodiversity facets

A challenge in assessing the impacts of multiple threats on multiple biodiversity facets is the attribution of community-level declines in facets to particular threats, because different threats can affect species differently in different areas. We addressed this challenge using newly developed measures for assessing species' functional and phylogenetic distinctiveness within communities (Violle et al. 2017; Cadotte & Tucker 2018). Specifically, we assessed the relative importance of habitat destruction and hunting pressure on the decline of each facet by first assessing which species lost core areas in a given gridcell (i.e., one or both threats became prevalent for that species in that gridcell), and second summing up threats responsible for that loss (habitat destruction, hunting, or co-occurring threats) while weighting species according to their distinctiveness.

Distinctiveness is defined as the mean distance in the diversity measure used to the N other species within each community (Violle et al. 2017). For TD, these distances between species are always 1. For FD and PD, we calculated distinctiveness per species for the community in 1985 – here considered as the baseline year – using the ‘distinctiveness’ function in the *funrar* package v1.4.1 in R (Grenié et al. 2017). A species’ taxonomic, phylogenetic, or functional distinctiveness is calculated according to:

$$Di = \frac{\sum_{j=1, i \neq j}^N d_{ij}}{N - 1}$$

where N is the number of species within the community, and d_{ij} is the taxonomic, functional, or phylogenetic distance between species i and j . We scaled d_{ij} between 0 and 1 using a minmax transformation (Violle et al. 2017).

We used this approach to calculate the relative importance of habitat destruction, hunting pressure, or co-occurring threats for biodiversity loss, separately for each of our three facets. To assess whether the relative importance of threats changed at higher values of facet loss, we repeated this procedure at different thresholds of loss per facet (e.g. for the top 75%, 50% and 25% of the gridcells with the highest losses per facet). We also assessed the spatial congruence among the three biodiversity facets for 2015 by measuring the pairwise correlation of facet values across all gridcells. We then mapped the gridcells with the top 5%, 10%, 17% and 25% values per facet (Brum et al. 2017). We assessed the overlap of the top 17% gridcells among facets – the minimum surface recommended for protection by the Convention on Biological Diversity’s Aichi target 11 (Tittensor et al. 2014).

5 Results

We assessed taxonomic diversity (TD), functional diversity (FD) and phylogenetic diversity (PD), and their change from 1985 to 2015, for a total of 21,462 communities (i.e., gridcells of 5x5 km²) with five or more species, representing 536,550 km². TD, PD, and FD declined considerably between 1985 and 2015, across 52%, 56% and 53% of the area assessed, respectively. In areas of decline, TD declined on average by -7.3% ($\pm 6.11\%$ SD) of the maximum TD value for the entire Chaco, while PD and FD decreased on average by -6.5% ($\pm 5.8\%$ SD) and -11.2% ($\pm 12.15\%$ SD), respectively. Considering the entire area assessed, TD declined on average by -2.8% ($\pm 6.8\%$ SD) on average, while PD and FD decreased on average by -2.6 ($\pm 6.8\%$ SD) and -4.2% ($\pm 12.7\%$ SD), respectively. The areas excluded from this comparison (< 5 species) were predominantly located in southern Chaco. For

comparison, we also assessed the change in TD and PD (but not FD) across the entire Gran Chaco (43,941 communities; 1.1 million km²). This revealed very similar trends than for areas with ≥ 5 species, but smaller average changes (Figure SI IV-6).

Among countries, Bolivia held higher values for all biodiversity facets in 1985, followed by Paraguay and Argentina (Figure IV-2a). Between 1985 and 2015 Paraguay lost substantially more mammalian diversity in all three facets (TD= -5.2%, PD= -4.4%, FD= -6.8%, and on average), than Bolivia (and -2.4%, -2.1%, and -2.8%, respectively), and Argentina (-0.9%, -1.2%, and -2.6%, respectively; Figure IV-2b). All biodiversity facets decreased more in unprotected areas (TD: -2.9%, PD: -2.6%, and FD: -4.5%) than in protected areas (-2.2%, -2.1%, and -2.3%, respectively; Figure SI IV-3).

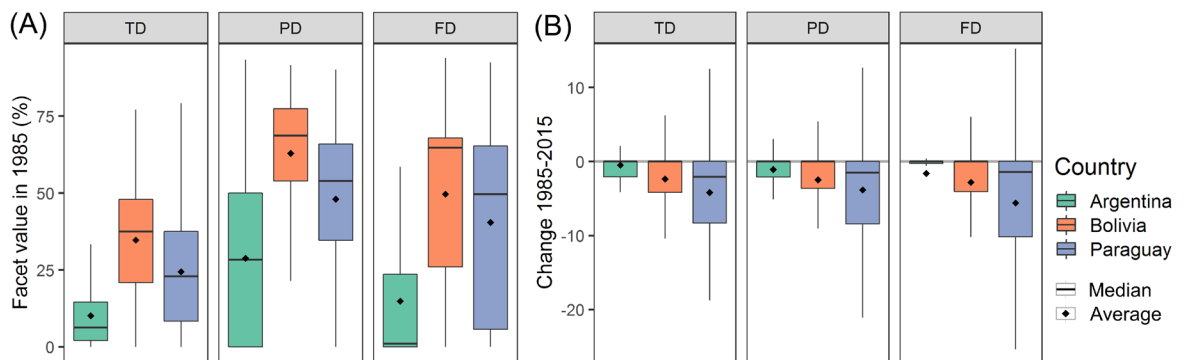


Figure IV-2: Change in the three facets of mammalian diversity of the Chaco between 1985 and 2015. (a) Standardized facet values (percentage of maximum values) per country for the baseline year of 1985. (b) Changes in standardized facet values between 2015 and 1985 across 21,462 communities (5x5 km² gridcells).

The geographical patterns of change of the three biodiversity facets over time showed some similarities, but also marked differences (Figure IV-3). The geographical patterns of change were similar for TD and PD, with the areas of highest loss concentrated mainly in northern Paraguay (Figure IV-3). Losses in FD were highest in north-western Paraguay and the north-western Chaco in Bolivia. In contrast, we identified areas with low positive changes in TD, PD, and FD in the central and southern Chaco. Overall, changes over time in TD and PD were more correlated (Spearman's $\rho = 0.87$), than the changes in FD and TD ($\rho = 0.73$), and FD and PD ($\rho = 0.68$).

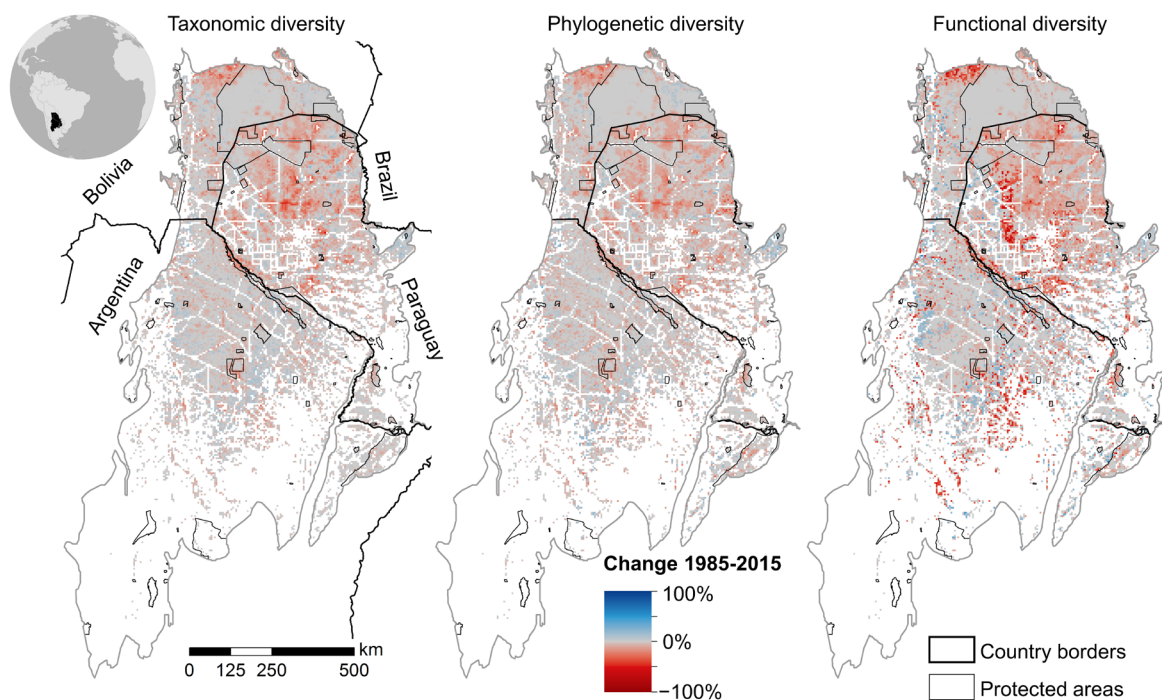


Figure IV-3: Changes in the taxonomic, phylogenetic, and functional facets of mammalian diversity in the Chaco from 1985 to 2015, assessed for communities with ≥ 5 species in both 1985 and 2015. Red areas represent communities with higher losses, blue with higher increases, and grey no change. In white we represent all communities that were not assessed because they had ≤ 4 species in either 1985 or 2015. All facets are standardized so that 100% represents the diversity of this facet for the full Chacoan community of 48 larger mammals.

Regarding the overall community composition change over time, the contribution of species richness change was larger (mean = 0.11 ± 0.14 SD; median = 0.06) than that of turnover (0.09 ± 0.18 SD; median = 0.00) to total Sørensen temporal dissimilarity (mean = 0.20 ± 0.21 SD; median = 0.16) (Figure SI IV-4). These differences were highly significant (Wilcoxon signed ranks test, $V = 217830000$, $P < 0.001$). Among communities that changed, species richness change (and here specifically species loss) was a larger contributor to dissimilarity than turnover (61% vs. 39% of communities).

The expansion of habitat destruction and hunting pressure between 1985 and 2015 contributed strongly to declines in all biodiversity facets. The overall area of expansion of habitat destruction, hunting pressure, and co-occurring threats between 1985 and 2015 covered 42%, 24%, and 8% (448,900, 261,000, and 84,600 km²) of the entire Chaco, respectively (Figure SI IV-5). The cumulative area experiencing habitat destruction and hunting pressure extended to over 51% of the Gran Chaco (563,500 km²). In terms of their

contributions to declines in facets' distinctiveness, when considering all areas experiencing facet loss, habitat destruction was by far the most important threat (57%), followed by hunting pressure (37%), and co-occurring threats (6%; Figure IV-4a). Focussing on those areas experiencing highest loss in a facet revealed some interesting differences compared to the region-wide results. When considering the 25% of gridcells with highest loss per facet, the relative importance of hunting increased (to 38 and 39% for TD and PD, respectively), whereas the relative importance of habitat destruction increased to 64% for FD. In addition, the relative importance of co-occurring threats increased slightly for all facets when focusing on those areas experiencing highest loss in a facet (Figure IV-4b). The contributions of threats to facet declines were practically identical for the entire Chaco and the areas of the Chaco with communities with 5 or more species (Figure SI IV-7).

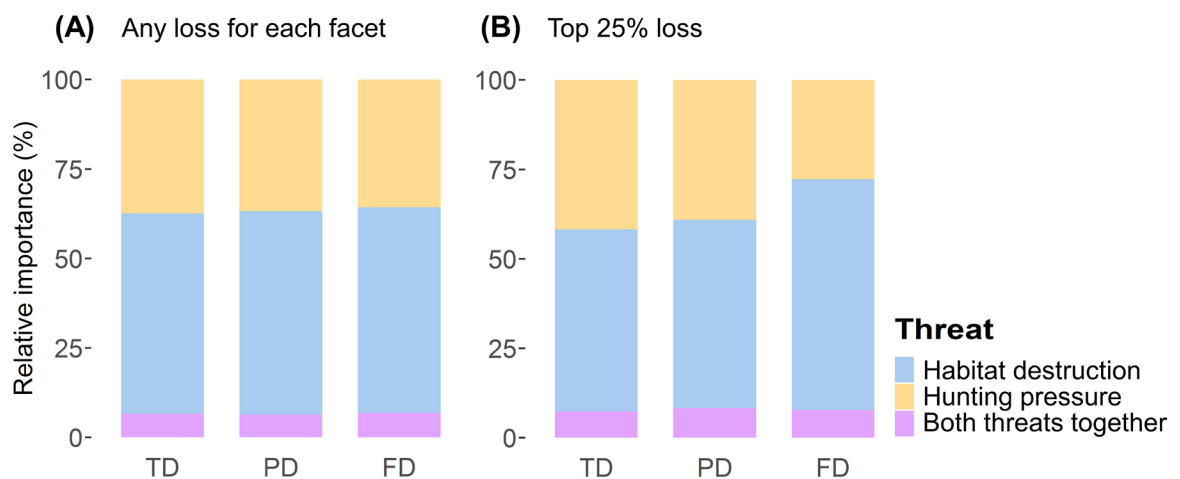


Figure IV-4: Relative importance of threats for losses in biodiversity facets between 1985 and 2015. Relative importance is measured by attributing a threat category to each species lost from a community, and weighting species by their distinctiveness in the community. (a) Relative importance of threats across all cells that experienced facet decline. (b) Relative importance of threats in the top 25% of cells with highest declines per facet.

The spatial patterns of gridcells with highest facet values in 2015 were roughly similar among facets. The top 5%, 10%, 17%, and 25% of gridcells per facets were concentrated in the northern Chaco in southern Bolivia and northern Paraguay, and to a lesser extent in north-eastern Argentina (Figure IV-5). However, while the top 5% of cells for TD and PD were concentrated mainly in Bolivia, for FD the top-ranking cells also occurred in north-eastern Argentina, and in easternmost Argentinean Chaco in the 'Bañados del Iberá' area.

Similarly, while the top 25% cells of TD and PD were scattered over large areas of the central Chaco, for FD they were mainly distributed in northern Paraguay and north-western Chaco in Bolivia (Figure IV-5). TD and PD were generally more spatially correlated (Spearman's $\rho = 0.84$) than PD and FD ($\rho = 0.83$), and FD and TD ($\rho = 0.75$).

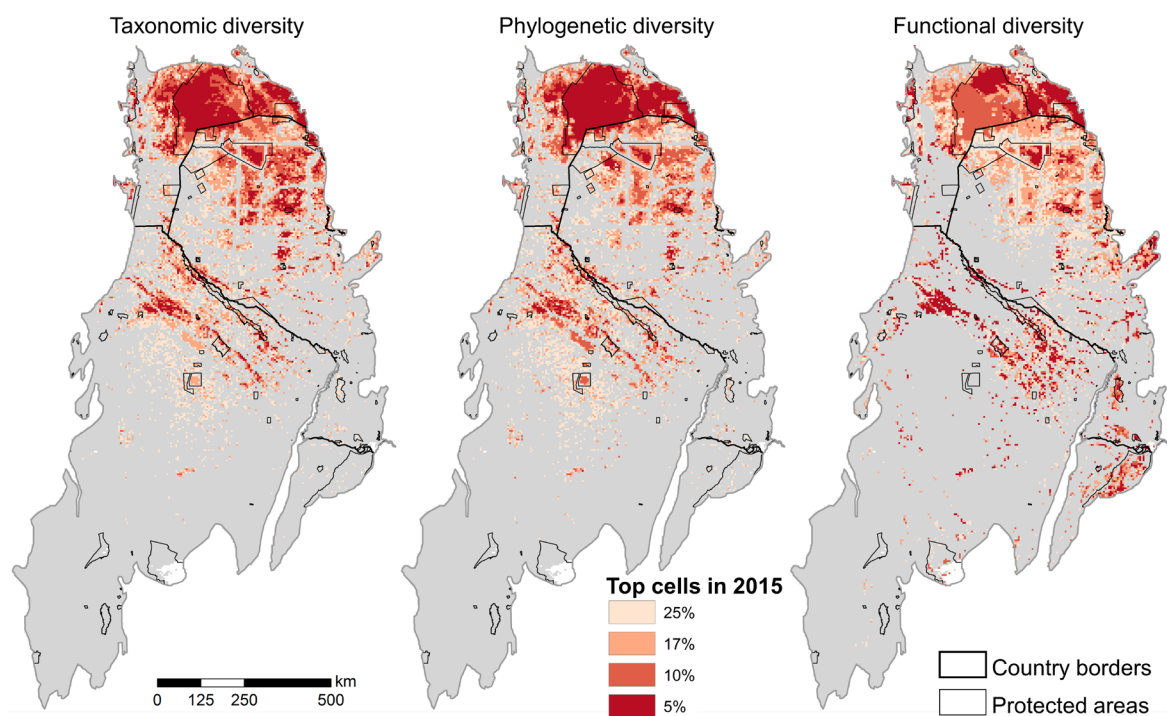


Figure IV-5: Top 25%, 17%, 10% and 5% of gridcells for each facet of mammalian diversity in the Chaco in 2015.

Considering the top 17% of gridcells per facet, all three facets overlapped across 12% of the Chaco, particularly in the northern Chaco in Bolivia and Paraguay, as well as to some extent in northern Argentina. However, between 1985 and 2015 the overlap among all three facets decreased by 3% of the 1985 value, particularly in northernmost Chaco in Bolivia, and several areas in Northern Paraguay. In 2015, TD and PD overlapped most strongly (on 16% of gridcells, with only about 1% of gridcells across the Chaco uniquely important for one facet). This was very different for FD, which overlapped less and where almost 4% of the Chaco was uniquely important for this facet (Figure IV-6). Overall, the cumulative area of the top 17% of all three facets of the mammalian diversity covered 23% of the entire Chaco. About a quarter (51,275 to 55,200 km²) of the top 17% areas for each facet were inside protected areas (TD: 26%, PD: 27%, FD: 30%).

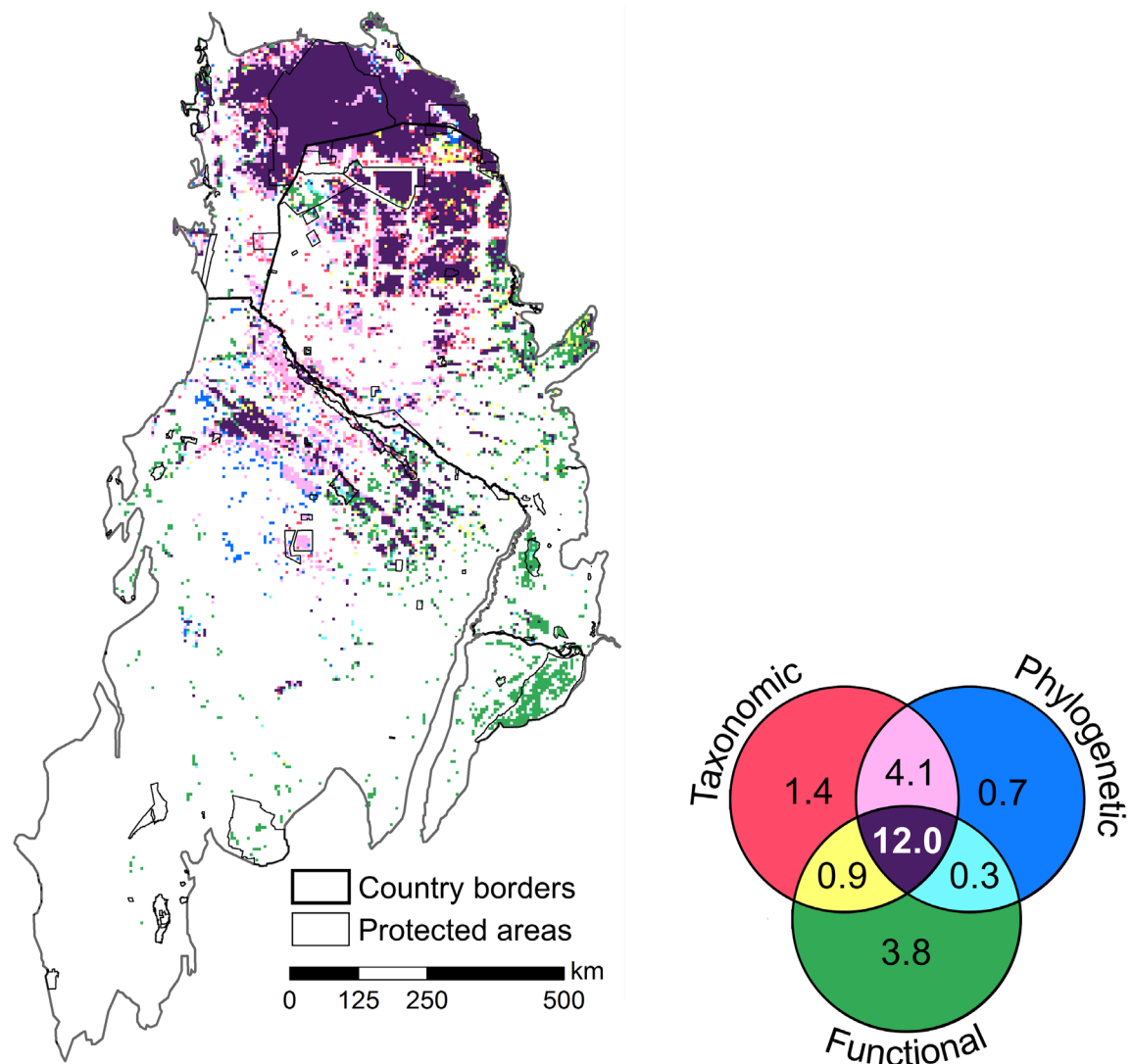


Figure IV-6: Overlap among the 17% of gridcells with the highest values for each of the three facets of mammalian diversity in the Chaco in 2015. Colours indicate facet overlap. The legend also indicates the percent of the total Chaco area inside each combination of facets.

6 Discussion

To better understand the impacts of people on nature, we need to learn how different facets of biodiversity change in response to anthropogenic threats. Here, we provide the first multi-decadal, broad-scale assessment of changes in all three biodiversity facets caused by specific threats. Furthermore, this is to our knowledge the first assessment of changes in multiple biodiversity facets for mammals and in the tropics. Using habitat maps for 48 larger mammals and the spatial footprints of habitat destruction and hunting, we assessed how these threats, individually and jointly, drive changes in mammalian diversity over 30 years across the 1.1 million km² Chaco. Our analyses reveal a general biotic

impoverishment. This is illustrated by the rapid and widespread changes in mammalian communities, resulting in declines across all biodiversity facets. These changes were mainly driven by defaunation rather than by species turnover. Habitat destruction was the main threat responsible for declines across facets, partly because it expanded over larger areas than did hunting pressure. However, hunting pressure became increasingly important where taxonomic and phylogenetic diversity declined the most, because hunting expanded especially into remote areas where these facets were still high. Although the most important remaining areas across the three facets showed moderate spatial congruence in 2015, some areas were uniquely important, particularly for functional diversity. As a result, 23% of the Chaco would have to be protected in order to safeguard the top 17% of all three facets. Yet, only about a quarter are currently protected. This corresponds to about 5% of the Chaco, which is even lower than the 9% of the Chaco under protection overall. Our work advances the understanding of where and how different threats drive changes in the facets of biodiversity. Such an understanding can inform conservation planning, in order to spatially target threat-specific actions to maintain all biodiversity facets.

The decline across biodiversity facets since 1985 reveals a generalized and widespread impoverishment of species numbers, evolutionary history, and ecological roles filled by larger mammals across the Chaco. The loss of phylogenetic diversity (PD) includes the declines of lineages endemic to the Chaco, such as that of the Chacoan peccary and the Chacoan naked-tailed armadillo (*Cabassous Chacoensis*) (Romero-Muñoz et al. 2020). Functional diversity (FD) decreased more drastically than other facets, as a result of the decline of mammals with key ecological roles, such as seed dispersers (e.g. maned wolf *Chrysocyon brachyurus* and tapir *Tapirus terrestris*), or top predators (e.g. jaguar *Panthera onca* and puma *Puma concolor*) (Romero-Muñoz et al. 2020). Such declines in FD can have important implications for ecosystem functioning, such as forest regeneration and the regulation of herbivore and mesopredator abundances (Bello et al. 2015; Terborgh 2015).

Temporal changes in species composition were mainly driven by changes in species richness, whereas species replacement played a smaller role. These findings strongly suggest that the overall dominance of changes in total richness, specifically species loss, also explains the downward trends we found for phylogenetic and functional diversity. Nevertheless, although turnover was less important, the replacement of some species with distinctive functions (e.g. the Azaras's capuchin monkey *Sapajus cay*) or phylogeny (e.g. the Chacoan naked-tailed armadillo) by less distinctive species may drive PD and FD declines

in some communities. Our finding of the dominance of species loss contrasts with reported global trends, where species richness has been on average relatively stable over time across local studies, and turnover has been the main driver of community changes (Dornelas et al. 2014; Blowes et al. 2019). However, it is unclear what proportion of the communities assessed at global scale are under similarly high pressure from habitat destruction and hunting as communities in the Chaco.

The varying rates and spatial patterns of decline in biodiversity facets that we found suggest that trends observed for a single facet may conceal how other facets change. For instance, the higher similarity in the spatial patterns of decline of taxonomic diversity (TD) with PD than with FD suggests that TD is an imperfect surrogate for changes in other facets – although this is often assumed (Dornelas et al. 2014; McGill et al. 2015). Despite varying geographical patterns of decline, on average all facets declined. This adds further evidence that change in biodiversity facets is context-specific, as exemplified for birds, where all facets changed in parallel in the USA (Jarzyna & Jetz 2017), but not in France (Monnet et al. 2014). This also could imply that recently reported observations of long-term stability of local species richness, but high species turnover across the world (Dornelas et al. 2014; Blowes et al. 2019) may conceal important trends in other facets. Our work, the first from the tropical and subtropical biomes, thus reinforces calls based on studies from temperate regions (Monnet et al. 2014; Jarzyna & Jetz 2017) to assess long-term change of all facets of biodiversity.

Our results advance the previously limited understanding of the downward trends of biodiversity facets in tropical deforestation frontiers. Although the calculation of FD and the comparison of temporal changes among facets were limited to communities with five or more species (see *Methods*), these communities, mainly located in the northern half of the Chaco, faced most of the changes in land use and threat levels over the last three decades (Baumann et al. 2017; Romero-Muñoz et al. 2020). In contrast, areas in the southern Chaco for which FD could not be calculated remained largely stable since 1985 (Baumann et al. 2017; Romero-Muñoz et al. 2020). Overall, the changes we report represent considerable declines in one or more facets of mammalian diversity for tens of thousands of mammal communities. These troubling widespread declines across biodiversity facets may be common in deforestation frontiers, highlighting the urgency of assessing them in such regions. Furthermore, our work provides spatially-explicit, fine-scale trends of change of biodiversity facets for individual communities in the Chaco.

A major advance of our approach is the ability to attribute declines in biodiversity facets to specific threats. The greater contribution of habitat destruction to declines across all facets is partly due to habitat destruction expanding over a ~41% larger area than hunting pressure. However, in the 25% of gridcells with the highest declines per facet, hunting pressure contributed more to TD and PD declines. This 25% of gridcells includes many remote and highly diverse areas. In total, over half the Chaco is currently impacted by one or the other threat, with co-occurring threats contributing much less to declines in all facets. This is partly because we only considered changes from core areas to areas under threat over time; when Romero-Muñoz et al. (2020) considered changes from one threat to multiple threats for TD, the importance of synergistic threats was substantial. Furthermore, it is important to note that we focus on core areas, whereas species could remain outside them. Yet outside core areas species are affected by one or more threats, and may in many cases be locally functionally extinct, or committed to local extinction in the near future (Semper-Pascual et al. 2018). Overall, these results uncover the substantial and mutually amplifying importance of habitat destruction and overexploitation in deteriorating all facets of mammalian diversity.

Such large and widespread impacts of habitat destruction and hunting pressure on biodiversity facets may be common across tropical and subtropical deforestation frontiers. This is corroborated by various studies reporting negative effects of habitat modification on biodiversity facets (e.g. Frishkoff et al. 2014; Wordley et al. 2017; Chapman et al. 2018). However, only studies focusing on TD have assessed the relative impact of multiple threats. In such studies, habitat destruction contributed more than overexploitation to TD declines in tropical mammals and birds, but with wide variation among species (Symes et al. 2018; Gallego-Zamorano et al. 2020; Romero-Muñoz et al. 2020), implying that responses in to threats may differ between TD and other facets.

Indeed, while habitat destruction was the main contributor to decline across facets in our case as well, it was particularly important for declines in FD. In turn, hunting pressure was particularly prevalent where TD and PD declined the most. Such differences are likely due to different susceptibility of species to different threats as well as the different spatial footprints of threats. For instance, habitat destruction affected many species across much of the Chaco, whereas hunting pressure typically affected larger species more strongly and increased mainly in more remote areas (Figure SI IV-5). Our work therefore highlights the importance of simultaneously assessing the impact of multiple threats on multiple biodiversity facets and provides a novel framework to do so.

The three biodiversity facets we mapped showed moderate spatial congruence across the Chaco in 2015, with FD being more distinct than TD and PD (which were more congruent). This pattern appears to be mainly driven by FD being high in the ‘Bañados del Iberá’ area in easternmost Chaco, likely because a few species with unique trait combinations, such as the marsh deer *Blastoceros dichotomus* or river otter *Londra longicaudis*, concentrate in this savannah wetland (Romero-Muñoz et al. 2020). Our finding that FD had a more distinct spatial distribution than TD and PD at the regional scale corroborates patterns found for terrestrial birds and mammals (Pollock et al. 2017), and for marine mammals (Albouy et al. 2017) at the global scale. This underlines the importance of considering functional diversity in biodiversity assessments.

Our work contributes to conservation planning by detecting and mapping priorities for all facets of biodiversity at fine spatial resolutions. Identifying the most valuable areas per facet can help us to identify protection gaps and to prioritise areas for closing these gaps, which is important given that most conservation planning exercises have focused only on TD, but largely ignored PD and FD (Pressey et al. 2007). Furthermore, our approach allows us to map which threats affect different biodiversity facets and where. This can identify the best locations to implement threat-specific management actions, such as promoting forest recovery, fostering sustainable hunting (including the preferential targeting of hunting-resilient species such as rodents), through culturally-appropriate education or sensitisation programs, or ensuring the land rights of Indigenous Peoples (Ripple et al. 2016). Such threat-specific actions are an increasingly important focus of conservation planning, yet have so far not focussed on multiple facets of biodiversity (Pressey et al. 2007; Tulloch et al. 2015). Our work illustrates how this can be achieved using the Chaco, a severely under-protected region in need of conservation planning, as a demonstration case (Periago et al. 2014).

In conclusion, our study reveals a widespread impoverishment in mammalian diversity, including in overall richness, evolutionary history, and ecological functions, across large areas in the Chaco since 1985. Our approach linking changes in biodiversity facets with specific threats allowed us to uncover how habitat destruction and hunting pressure individually and jointly drive declines across all biodiversity facets in this global deforestation hotspot. Our approach, along with the resulting indicators and maps, can inform conservation planning by governments and conservation organizations by identifying priority areas for facet protection and for threat-specific management

interventions. Overall, our study advances the understanding of where and how multiple biodiversity facets change over time in response to different extinction drivers.

Acknowledgements

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Supplementary information

Table SI IV-1: Species, traits and trait values for each species in the Chaco. Abbreviations: Ar = Arboreal, G = Ground dwelling, S = Scansorial; invert = invertebrates, vert = vertebrates.

| Species | Forest strata | Activity periods | | Home Range (km ²) | Diet | | | | | Body Mass (g) | Generation length (d) | Offspring per year |
|----------------------------------|---------------|------------------|---------|-------------------------------|--------|------|-------|------|-------|---------------|-----------------------|--------------------|
| | | Nocturnal | Diurnal | | invert | vert | fruit | seed | plant | | | |
| <i>Alouatta caraya</i> | Ar | 0 | 1 | 0.2 | 0 | 0 | 40 | 0 | 60 | 5862.5 | 3750.6 | 1.0 |
| <i>Aotus azarae</i> | Ar | 1 | 0 | 0.1 | 20 | 10 | 20 | 20 | 20 | 929.6 | 3047.8 | 1.0 |
| <i>Blastocerus dichotomus</i> | G | 1 | 0 | 48.0 | 0 | 0 | 0 | 0 | 100 | 86666.3 | 1825.0 | 1.0 |
| <i>Cabassous chacoensis</i> | G | 1 | 0 | 1.0 | 100 | 0 | 0 | 0 | 0 | 1490.0 | 1859.1 | 1.0 |
| <i>Callicebus pallescens</i> | Ar | 0 | 1 | 0.2 | 20 | 0 | 50 | 0 | 30 | 800.0 | 2920.0 | 1.0 |
| <i>Calyptophractus retusus</i> | G | 1 | 0 | 0.0 | 100 | 0 | 0 | 0 | 0 | 130.0 | 1460.0 | 1.0 |
| <i>Catagonus wagneri</i> | G | 0 | 1 | 7.0 | 0 | 0 | 0 | 30 | 70 | 35566.4 | 1471.0 | 2.4 |
| <i>Cerdocyon thous</i> | G | 1 | 0 | 1.4 | 50 | 40 | 0 | 0 | 0 | 5240.0 | 1530.2 | 7.6 |
| <i>Chaetophractus vellerosus</i> | G | 1 | 1 | 0.0 | 50 | 20 | 0 | 0 | 30 | 1030.0 | 1460.0 | 1.5 |
| <i>Chaetophractus villosus</i> | G | 1 | 1 | 0.0 | 50 | 20 | 0 | 0 | 30 | 4540.0 | 1460.0 | 2.0 |
| <i>Chrysocyon brachyurus</i> | G | 1 | 0 | 21.4 | 10 | 70 | 10 | 0 | 10 | 23249.8 | 2032.3 | 2.5 |
| <i>Coendou prehensilis</i> | Ar | 1 | 0 | 0.1 | 0 | 0 | 30 | 0 | 70 | 4400.0 | 3032.0 | 1.0 |
| <i>Conepatus chinga</i> | G | 1 | 0 | 2.0 | 80 | 10 | 10 | 0 | 0 | 1917.5 | 1317.7 | 2.5 |
| <i>Cuniculus paca</i> | G | 1 | 0 | 0.0 | 0 | 0 | 20 | 30 | 50 | 8172.6 | 2097.5 | 1.5 |
| <i>Dasyprocta azarae</i> | G | 0 | 1 | 0.0 | 10 | 0 | 40 | 0 | 50 | 2310.0 | 1891.0 | 1.9 |
| <i>Dasypus novemcinctus</i> | G | 1 | 0 | 0.0 | 100 | 0 | 0 | 0 | 0 | 4203.8 | 1825.0 | 4.0 |
| <i>Didelphis albiventris</i> | S | 1 | 0 | 0.0 | 20 | 30 | 0 | 0 | 20 | 904.0 | 419.6 | 5.0 |
| <i>Dolichotis salinicola</i> | G | 0 | 1 | 9.7 | 0 | 0 | 0 | 0 | 100 | 1600.0 | 1675.8 | 1.5 |
| <i>Eira barbara</i> | G | 1 | 1 | 11.4 | 0 | 90 | 10 | 0 | 0 | 3910.0 | 2686.6 | 2.0 |
| <i>Euphractus sexcinctus</i> | G | 1 | 1 | 0.7 | 50 | 0 | 0 | 0 | 50 | 4782.9 | 1825.0 | 2.0 |
| <i>Galictis cuja</i> | G | 1 | 1 | 1.0 | 20 | 60 | 20 | 0 | 0 | 1000.0 | 1262.0 | 3.0 |

Chapter IV

| | | | | | | | | | | | | |
|----------------------------------|----|---|---|-------|-----|-----|----|----|-----|----------|--------|------|
| <i>Galictis vittata</i> | G | 1 | 1 | 4.2 | 20 | 60 | 20 | 0 | 0 | 3200.0 | 1262.0 | 2.0 |
| <i>Herpailurus yagouaroundi</i> | G | 0 | 1 | 52.4 | 10 | 80 | 10 | 0 | 0 | 6875.0 | 2250.6 | 4.0 |
| <i>Hydrochoerus hydrochaeris</i> | G | 0 | 1 | 0.1 | 0 | 0 | 10 | 0 | 90 | 48144.9 | 2030.4 | 6.0 |
| <i>Lagostomus maximus</i> | G | 1 | 0 | 0.0 | 0 | 0 | 0 | 40 | 60 | 4647.5 | 1328.2 | 3.6 |
| <i>Lama guanicoe</i> | G | 0 | 1 | 28.0 | 0 | 0 | 0 | 0 | 100 | 142500.0 | 4064.1 | 0.5 |
| <i>Leopardus geoffroyi</i> | G | 1 | 0 | 3.0 | 0 | 100 | 0 | 0 | 0 | 5157.9 | 2827.9 | 2.6 |
| <i>Leopardus pardalis</i> | G | 1 | 0 | 5.1 | 0 | 100 | 0 | 0 | 0 | 11900.1 | 3011.9 | 2.0 |
| <i>Leopardus wiedii</i> | S | 1 | 0 | 8.5 | 0 | 80 | 20 | 0 | 0 | 3250.0 | 2190.0 | 1.5 |
| <i>Lontra longicaudis</i> | G | 1 | 0 | 7.0 | 10 | 90 | 0 | 0 | 0 | 6555.0 | 3442.6 | 2.5 |
| <i>Lycalopex gymnocercus</i> | G | 1 | 1 | 1.5 | 0 | 50 | 30 | 0 | 20 | 4542.7 | 1717.8 | 2.5 |
| <i>Mazama americana</i> | G | 1 | 1 | 1.0 | 0 | 0 | 0 | 20 | 80 | 22799.8 | 2017.4 | 1.3 |
| <i>Mazama gouazoubira</i> | G | 1 | 1 | 1.5 | 0 | 0 | 30 | 20 | 50 | 16633.2 | 2158.1 | 1.0 |
| <i>Mico melanurus</i> | Ar | 0 | 1 | 2.9 | 20 | 0 | 40 | 0 | 20 | 335.6 | 2200.5 | 4.0 |
| <i>Myocastor coypus</i> | G | 1 | 0 | 0.0 | 0 | 0 | 0 | 0 | 100 | 6937.5 | 1311.7 | 13.8 |
| <i>Myrmecophaga tridactyla</i> | G | 1 | 1 | 4.0 | 100 | 0 | 0 | 0 | 0 | 22333.2 | 4124.5 | 1.2 |
| <i>Nasua nasua</i> | S | 0 | 1 | 2.0 | 10 | 20 | 70 | 0 | 0 | 3793.9 | 2778.4 | 4.0 |
| <i>Panthera onca</i> | G | 1 | 1 | 52.6 | 0 | 100 | 0 | 0 | 0 | 100000.0 | 3581.7 | 1.0 |
| <i>Pecari tajacu</i> | G | 1 | 0 | 1.4 | 10 | 20 | 10 | 0 | 60 | 21266.7 | 3102.9 | 4.0 |
| <i>Priodontes maximus</i> | G | 1 | 0 | 8.0 | 90 | 10 | 0 | 0 | 0 | 45359.7 | 1979.2 | 0.5 |
| <i>Procyon cancrivorus</i> | G | 1 | 0 | 1.0 | 50 | 30 | 10 | 10 | 0 | 6949.9 | 2192.0 | 3.0 |
| <i>Puma concolor</i> | G | 1 | 1 | 129.9 | 0 | 100 | 0 | 0 | 0 | 51600.0 | 2693.8 | 1.1 |
| <i>Sapajus cay</i> | Ar | 0 | 1 | 1.0 | 20 | 10 | 40 | 0 | 10 | 2687.2 | 5475.0 | 0.5 |
| <i>Sylvilagus brasiliensis</i> | G | 1 | 0 | 0.1 | 0 | 0 | 0 | 0 | 100 | 950.0 | 969.9 | 1.9 |
| <i>Tamandua tetradactyla</i> | S | 1 | 1 | 2.7 | 100 | 0 | 0 | 0 | 0 | 5515.1 | 1854.7 | 1.4 |
| <i>Tapirus terrestris</i> | G | 1 | 0 | 4.6 | 0 | 0 | 0 | 0 | 100 | 207500.9 | 4015.0 | 0.4 |
| <i>Tayassu pecari</i> | G | 1 | 0 | 41.0 | 10 | 10 | 30 | 30 | 20 | 32233.7 | 3177.4 | 2.0 |
| <i>Tolypeutes matacus</i> | G | 1 | 1 | 0.1 | 80 | 0 | 20 | 0 | 0 | 1200.0 | 4288.0 | 1.0 |

Figure SI IV-1: Correlation matrix among traits and trait levels (see Table SI IV-1) used to calculate Functional diversity.

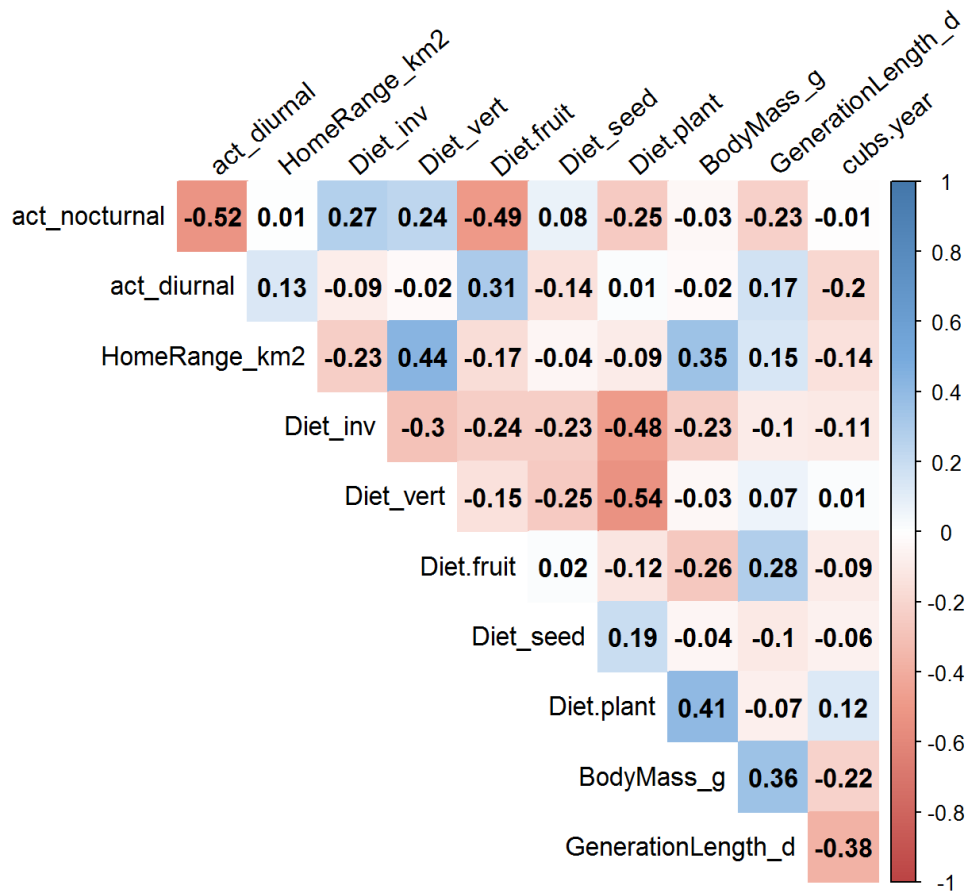


Figure SI IV-2: Quality of the functional space and the trade-off between number of dimensions included and the area excluded from the functional diversity (FD) calculation. (A) Quality of the functional space assessed with the mean squared deviation (mSD) resulting from the use of two to seven PCoA dimensions (2D to 7D; the lower the mSD value, the more accurately the functional space represents the initial trait values). (B) Area of the Gran Chaco (total area = 1,100,000 km²) that would be excluded from the FD calculation for each number of dimensions, and the associated minimum species number required per community to calculate FD (e.g., when using four dimensions, FD can be calculated only for communities with five or more species). (C) Area of the Chaco for which FD can be included (blue) and area excluded (grey) when using four dimensions.

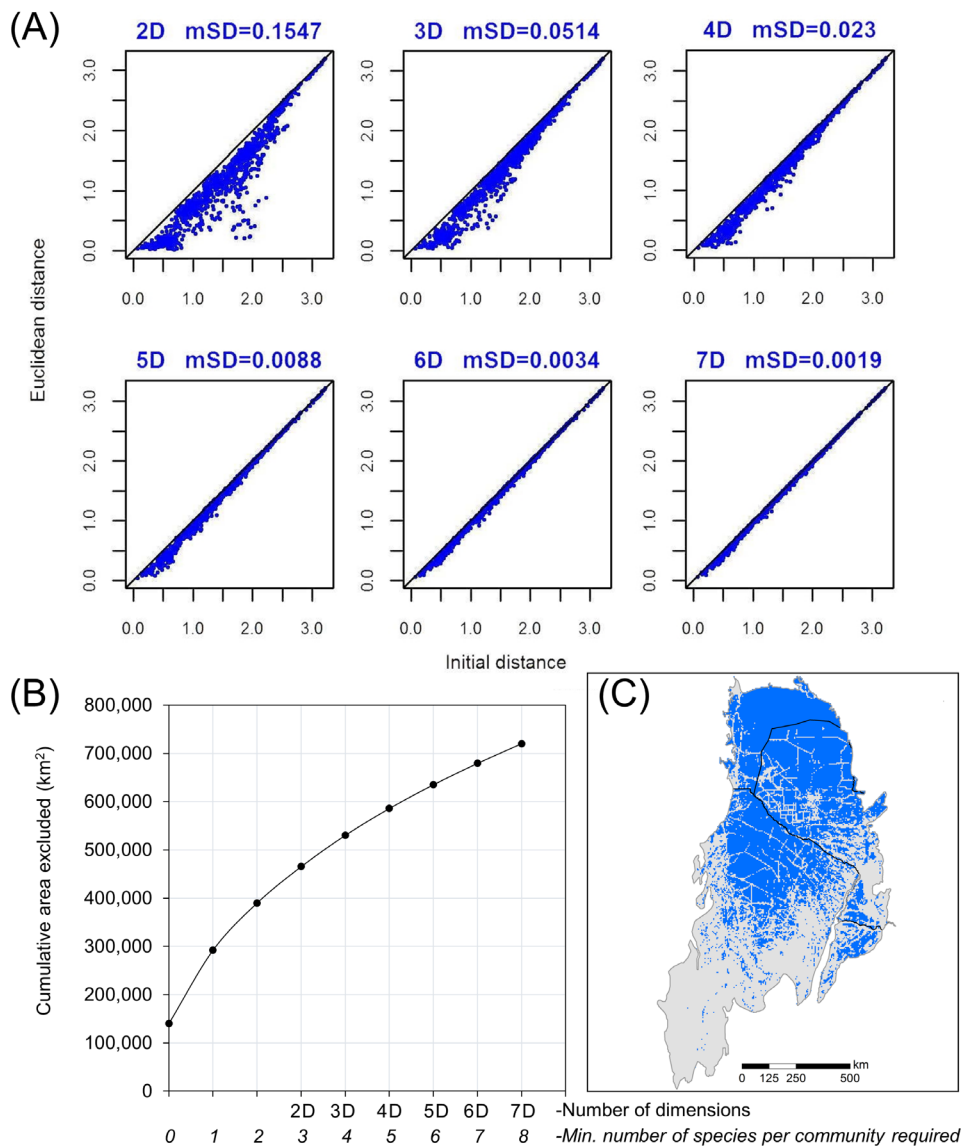


Figure SI IV-3: Change in the metrics for biodiversity facets within and outside protected areas across communities with ≥ 5 larger mammal species in the Chaco region.

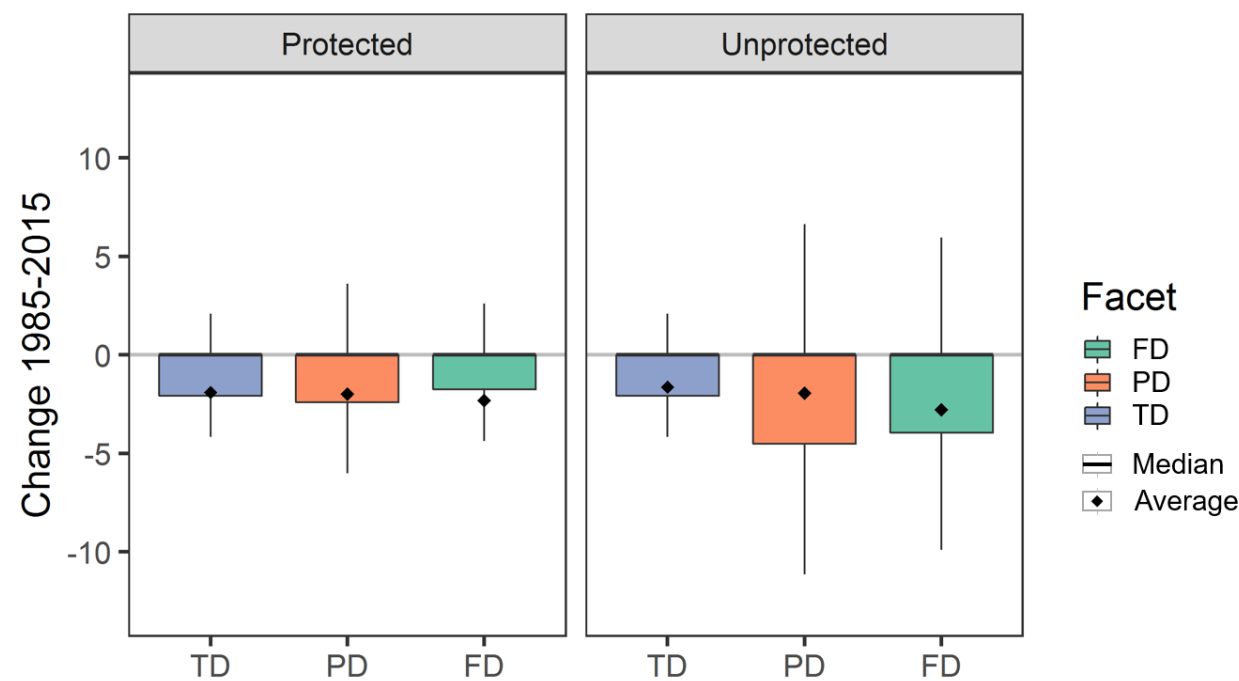


Figure SI IV-4: Decomposition of the temporal community dissimilarity between 1985 and 2015 in the Gran Chaco into its species richness change and turnover components based on the Sorensen dissimilarity index. (A-C) maps of each component and of total dissimilarity in the Gran Chaco. (D) boxplots of the values of each component.

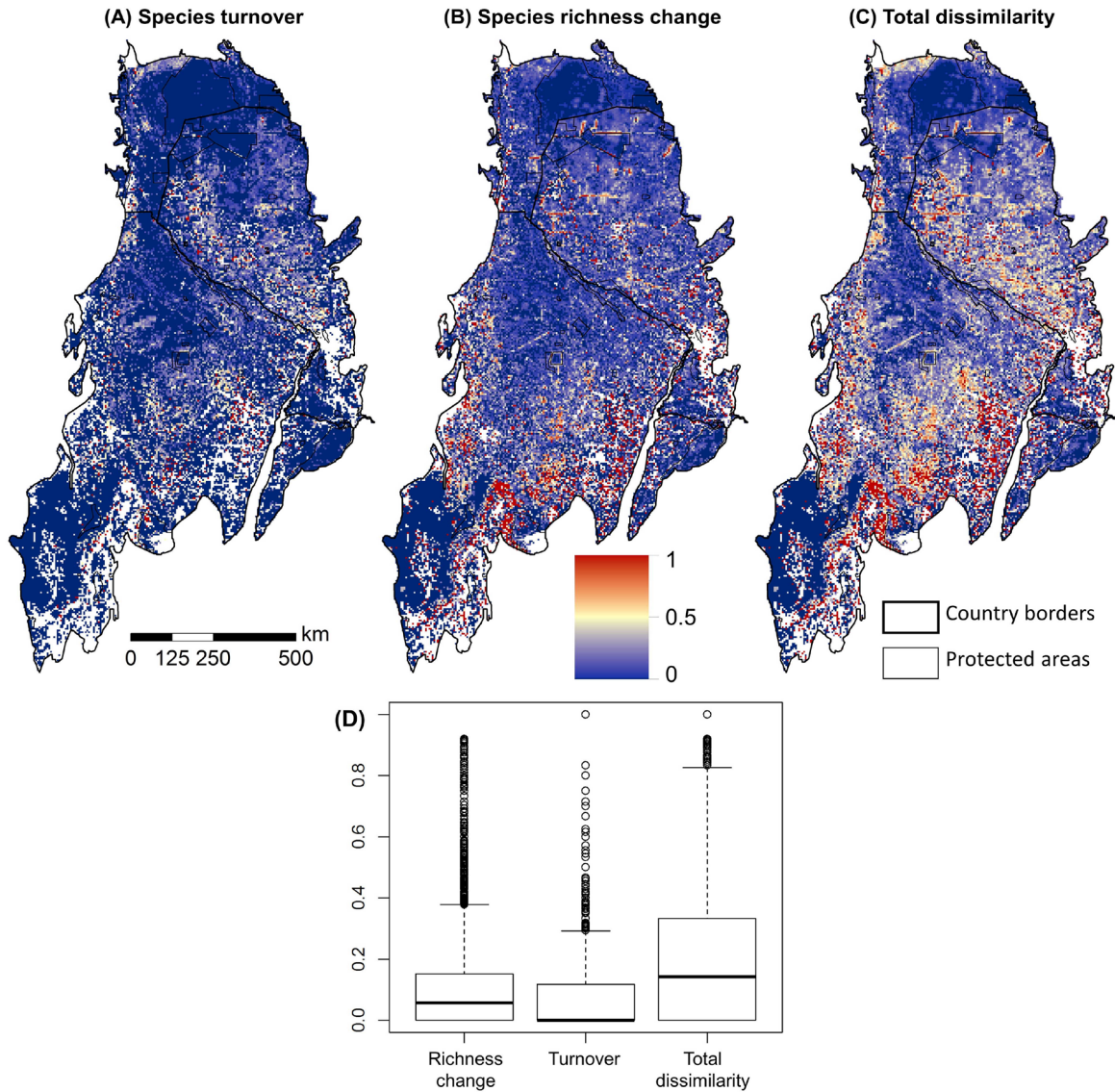


Figure SI IV-5: Values of the taxonomic, phylogenetic, and functional distinctiveness of the species that became affected by single or co-occurring threats between 1985 and 2015 across the Gran Chaco region.

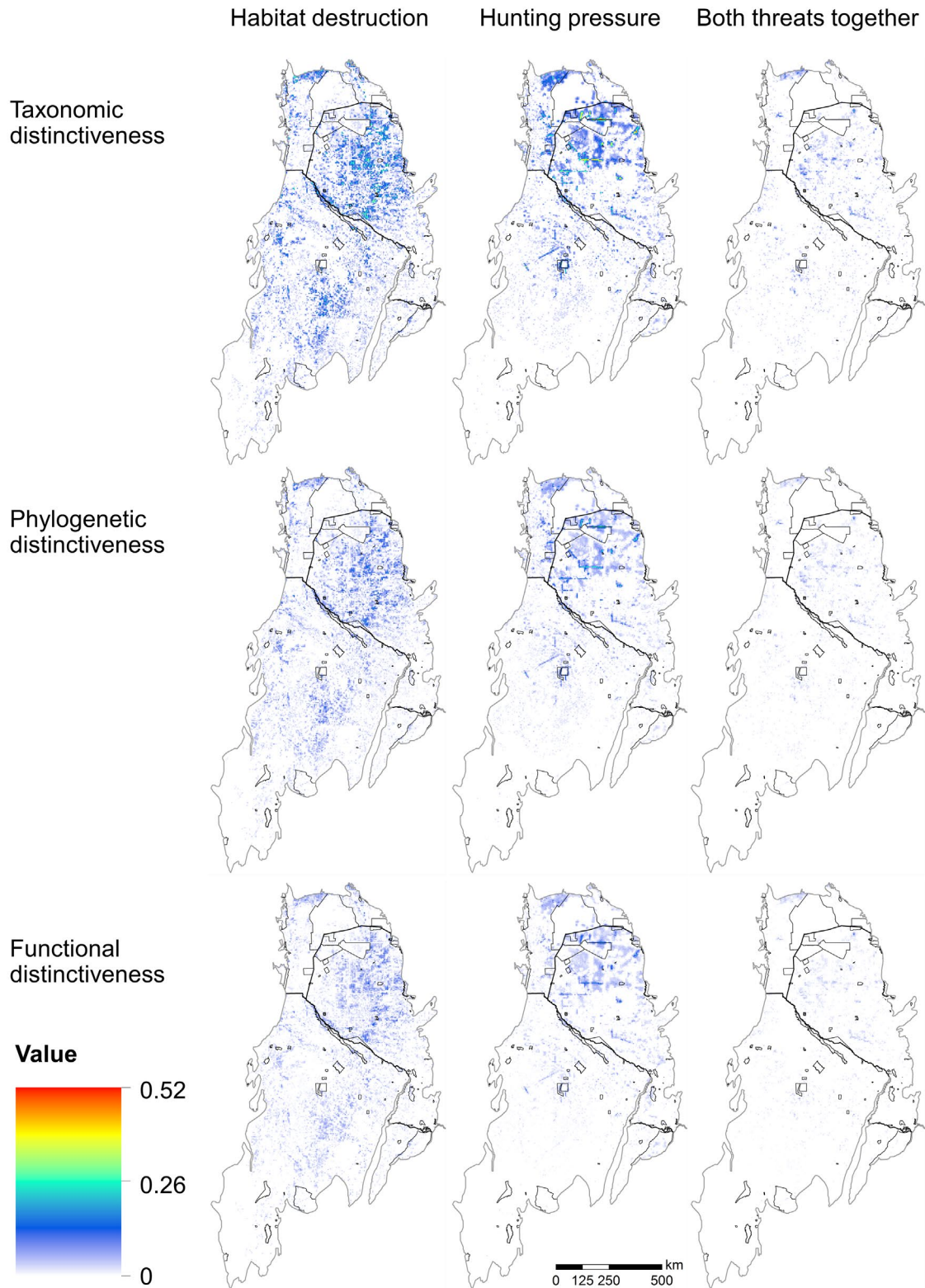


Figure SI IV-6: Change in the taxonomic and phylogenetic facets of mammalian diversity across the entire Chaco from 1985 to 2015 (43,941 communities). (A) Maps of change of taxonomic and phylogenetic diversity across the Chaco. Red areas represent communities with higher losses. Facets are standardized so that 100% represents the diversity of this facet for the full Chacoan community of 48 larger mammals. (B) Boxplot of the change in the two facets across Chaco countries.

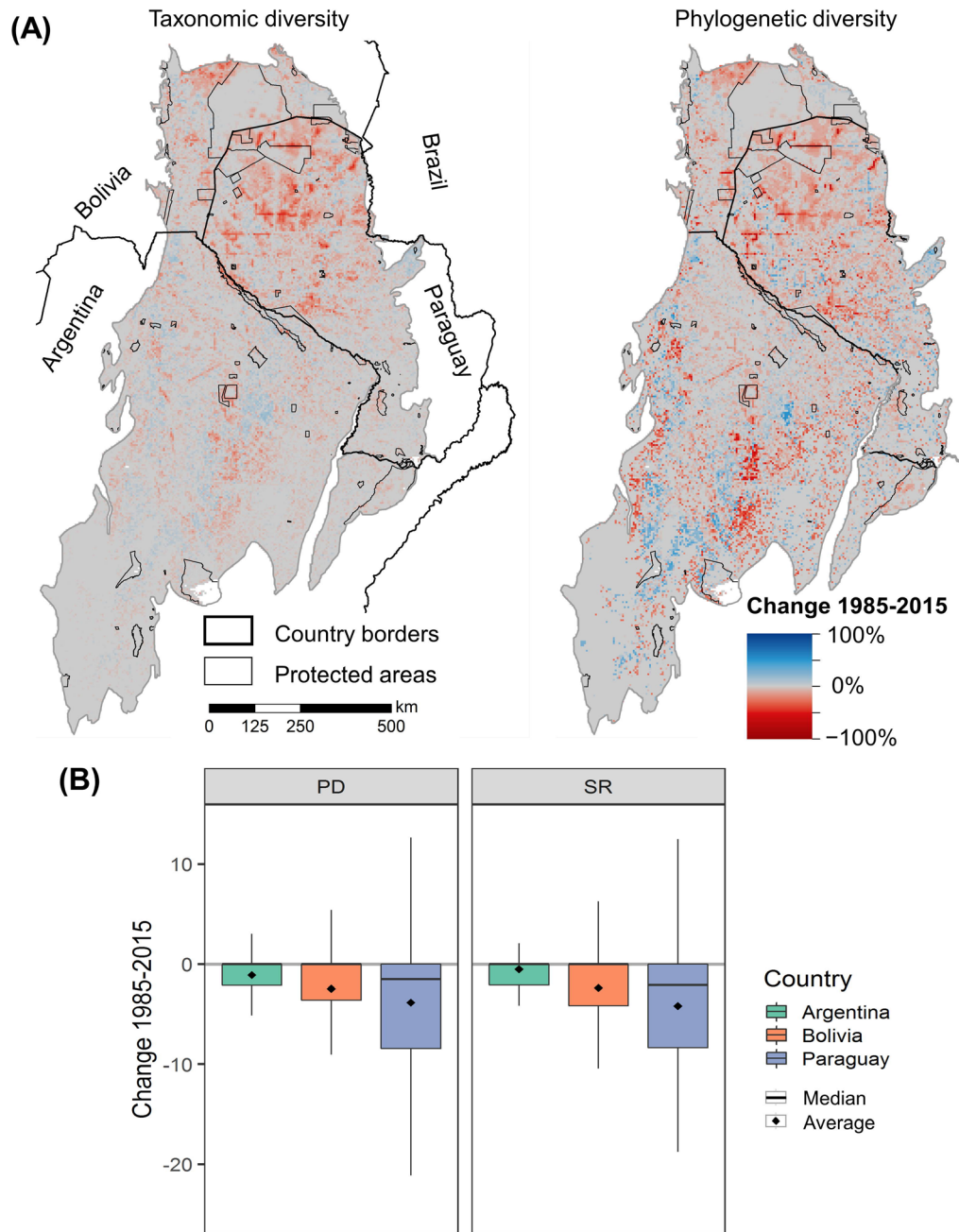
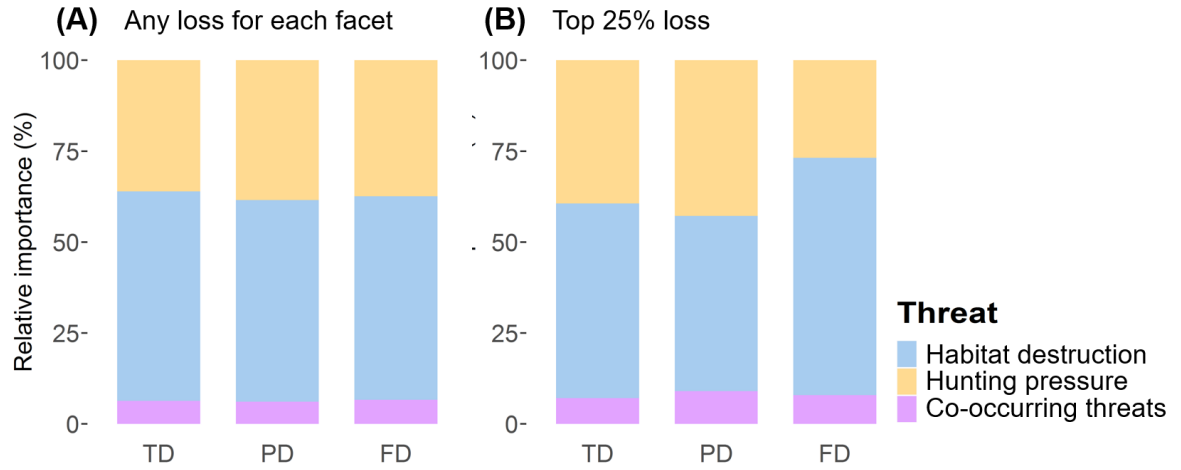


Figure SI IV-7: Relative contribution of threats to losses in taxonomic, phylogenetic, and functional distinctiveness between 1985 and 2015 focused on the areas with ≥ 5 species (where FD could be calculated). These results are shown for comparison to those for the entire Chaco shown in Figure IV-4.



Chapter V:
Synthesis

1 Summary and conclusions

Assessing how and where specific anthropogenic threats affect biodiversity is fundamental to better understand the extent of the current global biodiversity crisis, and to better inform ways to tackle it. Globally, the main threats to biodiversity are habitat destruction and overexploitation, and both threats are often prevalent within regions and often act simultaneously within the same areas. However, a lack of robust approaches to quantify the species-specific spatial impact of different threats at high spatial resolutions have limited our understanding of where these threats act alone or in combination. Furthermore, a lack of long-term biodiversity data across most tropical regions have prevented better understanding on how biodiversity is changing due to increasing anthropogenic threats. Filling these knowledge gaps is important to identify the key areas for protecting biodiversity and for abating specific threats. In this thesis, I aimed to bridge these knowledge gaps with the overarching goal of understanding the impact of habitat destruction and overexploitation on biodiversity and how their impact change over space and time.

My thesis contributes towards this goal by developing the framework of the *geographies of threat*. This framework seeks to understand the spatially-explicit footprints of multiple threats, such as habitat destruction and hunting pressure, where these threats act individually or together, where are the areas with low threats, and how these footprints change over time. The basis for this approach is the assessment of the species-specific responses to each threat. In this thesis, I applied this framework to different hierarchical levels of biodiversity (i.e., populations and species in Chapter II, and communities in Chapter III), and to different facets of biodiversity (i.e., taxonomic, phylogenetic, and functional diversity in Chapter IV).

Understanding the geographies of threat for such varied aspects of biodiversity required advancing and combining existing approaches in new ways. In Chapter II, I advanced the single-species and single-time core/sink modelling approach developed by Naves et al. (2003) to a multitemporal one by combining it with time-calibrated models, allowing me to consistently reconstruct threat footprints over time. In Chapter III, I adapted this approach to assess the geographies of threat for multiple species for the first time. I did this by replacing the habitat suitability models that depicts hunting pressure – which requires large, spatially unbiased datasets only available for a few species – with the newly

developed hunting pressure model by Benítez-López et al. (2019), which can depict the species-specific hunting footprints. In Chapter IV, I measured the changes over time in the taxonomic, phylogenetic, and functional facets of the mammalian diversity. To be able to attribute changes in each facet to a specific threat or threat combination, I employed the concept of species' distinctiveness for each specific facet (Violle et al. 2017). Overall, advancing the framework of the geographies of threat for different biodiversity hierarchies, and biodiversity facets allowed me to answer each of the thesis' main research questions.

Research Question 1: *Where do habitat destruction and hunting pressure affect mammalian diversity, and how do the spatial footprints of these threats change over time?*

In Chapter II, I found that habitat destruction and hunting pressure on jaguar expanded by 20% and 27%, respectively, over three decades in the Gran Chaco. Similarly, in Chapter III, I found that these two threats expanded by an average of 9.6% and 8.4% for the 48 larger mammal species, respectively. The cumulative footprint of habitat destruction and hunting pressure for the mammalian community expanded across about 38% and 31% of the entire Gran Chaco, respectively. Finally, in Chapter IV, I found that habitat destruction and hunting pressure expanded across 50% and 32% of the entire Gran Chaco for all facets of biodiversity, respectively. Together, these results point to a general expansion of the footprints of habitat destruction and hunting pressure over three decades across the ranges of larger mammals, including that of the top predator, and affecting all biodiversity facets across substantial areas of the Gran Chaco. Hunting pressure often acted alone in more remote areas, and was often subsequently joined by habitat destruction, suggesting that threats may often – but not always – act in ‘stages’ in deforestation frontiers. Jointly considering the footprints of hunting pressure and habitat destruction revealed much larger total areas under threat than when considering threats in isolation. Furthermore, for multiple species, the cumulative footprint of each threat was larger than the area deforested over the last three decades.

As threats expanded, the remaining core areas – high-quality habitats with low threats – shrank over three decades for all hierarchical levels and facets of biodiversity assessed. The jaguar core areas shrank by 38% (Chapter II), while all larger mammals suffered a similar average core area shrinkage of 38%, although there was a wide variation among species ($\pm 62.2\%$ SD, Chapter III). The taxonomic, phylogenetic, and functional facets of the mammalian diversity also decreased, each across about 40% of the Gran Chaco, but

functional diversity decreased about 30% faster than the taxonomic and phylogenetic diversity. Each research chapter shows where each of the biodiversity aspects studied declined the most, highlighting the concerning defaunation process in the northern half of Paraguay. Together, these results indicated a generalised biotic impoverishment in terms of the decline of species, evolutionary history, and the ecological functions played by larger mammals across this region over recent decades. This generalised and widespread defaunation likely affects the functioning of ecosystems, and nature's contributions to people. Importantly, the approach I used permits the attribution of the decline in each biodiversity aspect to specific threats in a spatially-explicit manner, thus contributing to our understanding of the impacts of increasing impacts of human activities on biodiversity in rapidly changing regions.

Research Question 2: *What is the relative importance of habitat destruction and hunting pressure in driving mammalian diversity change?*

In Chapter II, I found that that hunting pressure currently affects an area 20% larger than that of habitat destruction for jaguar, and that hunting pressure also increased faster over time. In Chapter III, I found similar footprints of habitat destruction and hunting pressure on the range of larger mammals (covering around 49% and 45% in 2015, respectively), and that both threats increased at similar rates over time (9.6% and 8.4%, respectively), but with wide variations among species ($\pm 22.7\%$ SD and $\pm 6.7\%$ SD, respectively). Finally, in Chapter IV, I found that across all facets of the mammalian diversity, habitat destruction expanded across a 41% larger area than hunting pressure over three decades, and it was the main driver of declines. However, the relative contribution of hunting pressure increased where taxonomic and phylogenetic diversity declined the most, whereas habitat destruction became even more important where functional diversity declined the most. Taken together, these results reveal that both threats are highly important for all hierarchical levels and facets of biodiversity, but their relative importance varies among species and biodiversity facets. This highlights the importance of accounting for the species-specific impacts of both threats when assessing anthropogenic impact across deforestation frontiers.

Beyond the relative importance of each threat, the importance of the areas where both threats act simultaneously increased over time. Such areas of overlap increased for the jaguar by 27% over three decades (Chapter II), by 17% ($\pm 20\%$ SD) on average for larger

mammals, and cumulatively across all species such areas expanded across 43% of the Gran Chaco area (Chapter III). These findings point to the increasing synergistic effects across broad areas of the Gran Chaco, likely exacerbating biodiversity losses beyond the impact of single threats.

Research Question 3: *What are the priority areas for conservation actions to mitigate the impact of habitat destruction and hunting pressure on mammals in the Gran Chaco?*

Applying the geographies of threat approach for different aspects of biodiversity allowed me to identify key areas for proactive land protection and reactive threat management. Across chapters, I found that priority areas (important areas with low threats) for protection were often surrounded by threat hotspots. This highlights the importance of jointly implementing complementary proactive protection of priority areas, as well as reactive threat management in threats hotspots. All three chapters pointed to the irreplaceable importance of the large transboundary area between Bolivia and Paraguay in the northern Chaco. The northern Gran Chaco harbours the stronghold for the jaguar and most other larger mammals in the Gran Chaco, and maintains the highest levels of taxonomic, phylogenetic, and functional mammalian diversity. Worryingly, this area has seen a rapid expansion of hunting pressure and habitat destruction recent years, particularly in northernmost Paraguay, highlighting the urgency for protection. Other important priority areas for the protection of several biodiversity aspects are in north-eastern Argentina, along the border with Paraguay, including areas along the Pilcomayo and Bermejo rivers. Other areas in Northeastern Paraguay, and the easternmost Argentinian Chaco, in the “Baños del Iberá” area, were highlighted as key areas for the functional facet of mammalian diversity. Importantly, Chapter IV suggests that achieving the Aichi Target 11’s top 17% areas for each of the three facets of the mammalian diversity would require the conservation of 23% of the Gran Chaco.

The areas I identified for reactive threat management show where hunting pressure or habitat destruction disproportionally affect high levels of mammal diversity. Some such areas were highlighted across all chapters. Hotspots of hunting pressure and of habitat destruction were concentrated mainly in north-western Paraguay. Other hotspots of hunting pressure are in the forested areas of the western dry Chaco in northern Argentina and southern Bolivia, as well as northernmost Paraguay, close to the border with Bolivia. Together, the priority area maps, and the threat hotspot maps produced in this thesis can

serve as templates for informing conservation planning that accounts for proactive and reactive actions to conserve the targeted biodiversity features.

2 Crosscutting insights

In this thesis, I advanced the framework of the geographies of threat by adapting it to a multitemporal context, to multiple species, and to all the facets of biodiversity. By applying this framework to these varied aspects of biodiversity, the patterns that emerged across research chapters allowed me to uncover some generalisations, as well as specific points that advance the current understanding of how and where the two main threats to biodiversity are distributed, and how these impacts change over time. More specifically, my thesis contributed four cross-cutting insights:

First, reconstructing the geographies of threat resulted in an increased understanding of where threats affect biodiversity. Previous research that mapped the impact of multiple threats to biodiversity over broad scales (Symes et al. 2018; Allan et al. 2019; Gallego-Zamorano et al. 2020) has been constrained by relying on the authors' rule-based definition of threat footprints, thus overlooking the species-specific responses to threats, and by relying on expert-derived species range maps. These constraints limit the resulting maps to very coarse resolutions or to maps with high uncertainty levels (Hurlbert & Jetz 2007; Di Marco et al. 2017). These limitations potentially mask the patterns of threats' footprints. Conversely the approach I employed accounts for the species-specific responses to each threat, and the ecological models it is based on better resemble species' actual distributions and can, therefore, produce high resolution maps (Di Marco et al. 2017).

My research confirmed the key findings by Symes et al. (2018) and Gallego-Zamorano et al. (2020) that the cumulative areas under both threats is larger than that of deforestation alone – which had been the focus of earlier research (e.g., Ocampo-Peñuela et al. 2016). Yet, my research goes beyond this finding and uncovered that the cumulative footprint of each threat on their own for a community can be larger than the area of deforestation alone. The footprint of hunting often penetrated further into remote, otherwise 'intact' forests, confirming previous research reporting the extensive spread of cryptic threats (Peres et al. 2006; Barlow et al. 2016; Benítez-López et al. 2019). The footprint of habitat destruction was also larger than that of deforestation alone, likely because of indirect effects of habitat destruction, such as the unsuitability of small fragments for wide-ranging species, edge

effects, and other disturbances such as fires (Barlow et al. 2016). Thereby, my research advances the understanding of the distribution and extent of habitat destruction and hunting pressure for biodiversity: both threats have comparable footprints for larger mammals in the Gran Chaco, and both have larger spatial impacts on biodiversity than previously thought.

Second, the consistent multitemporal reconstruction of the threats' footprints allowed me to uncover how the spatial interactions among threats change over time. When looking across the three research chapters, an emerging pattern was that hunting often impacted larger mammals further in remote areas and was in subsequent years joined by habitat destruction (see, for instance, Figure III-4). This suggests that in deforestation frontiers, often – but not always – hunting pressure acting alone represents a first stage in the impact of humans on wildlife, and a second stage is hunting pressure and habitat destruction acting together. This insight supports previous descriptions of the stages of defaunation, where human impacts on biodiversity first consists of direct exploitation of natural resources, and later by generalised habitat destruction (McCauley et al. 2015; Young et al. 2016).

A second insight, partly resulting from the patterns described above, is that the share of area where both threats act simultaneously increased over time. This likely means that synergistic effects are expanding fast, and increasingly becoming the norm across the Gran Chaco, potentially leading to higher rates of biodiversity loss than if a single threat was acting. This insight is consistent with the expectations that threats are more likely to interact under global change (Brook et al. 2008). Yet, both patterns were not apparent in other studies looking at the changes in these threats' footprints over time (Symes et al. 2018; Gallego-Zamorano et al. 2020). Such patterns may have been masked in these studies because, besides the use of expert-derived range maps and fixed rules to define threat footprints, they relied on less detailed reconstructions of the historical conditions (which were based only on the change in land cover and in human population density). Conversely, in my research, the historical conditions are based on highly detailed historical reconstructions of different land covers (forests, grasslands, and croplands), human population densities, road networks, and smallholder settlements. Overall, both insights advance our understanding on the change in the spatial interactions among threats over time, in that they point to a pattern of stages of threat prevalence, and to expanding synergistic effects among threats over time. Such patterns may be common across other deforestation frontiers in the tropics.

Third, assessing the change in core areas over time led to an increased understanding of the rate of defaunation in tropical deforestation frontiers due to increasing threats. The decline in core area extent across all assessed aspects of biodiversity were extensive, at 38% to 40% contraction for the jaguar, the entire community of larger mammals, and all facets of the mammalian diversity. In comparison, 177 mammal species around the world with known historical distributions lost about 40% on average of their range over the last century (Ceballos et al. 2017). Therefore, a similar average contraction in a third of the time in the Gran Chaco indicates a higher-than-average defaunation rate. The rate of defaunation in the Chaco when considering both threats is higher than when considering any single threat, highlighting the importance of simultaneous, multiple-threat assessments. Compared with the decline reported in other studies that accounted for habitat destruction and hunting pressure, the declines of larger mammals in the Gran Chaco are higher than for mammals larger than 10 kg across the global tropics (~10% decline over 23 years; Gallego-Zamorano et al. 2020), and comparable to the decline of forest-dependent birds in Indonesia (23% decline over 15 years; Symes et al. 2018).

Although the use of different thresholds and the more detailed historical reconstructions of this research could partly contribute to the differences, the extraordinarily high decline rates for mammals in the Gran Chaco suggests high defaunation rates in deforestation frontiers, even when compared to the average for the tropics. Furthermore, the parallel declines across all facets of the mammalian diversity uncovered in Chapter IV provides a previously unavailable insight for the tropics. These results suggest a widespread biotic impoverishment in terms of species numbers, evolutionary history, and ecological functions across a global deforestation hotspot. Importantly, my research across chapters allows me to attribute those declines to specific threats, further contributing to understanding how specific threats are changing biodiversity. Overall, my research points to widespread and rapid defaunation rates across the Gran Chaco due to increasing habitat destruction and hunting pressure, with negative implications for preserving the tree of life and ecological functions. This worrying trend is seemingly happening across other tropical deforestation frontiers as well.

Fourth, maps of the spatial impact of habitat destruction and hunting pressure can advance conservation planning by identifying key areas for proactive and reactive management actions at high resolutions. Complementary conservation actions have been found to bring larger conservation benefits than single actions (Wilson et al. 2007). However, research incorporating multiple threats for conservation planning have often used independent

maps of biodiversity distributions and of threats' distribution (such as 'human footprints'), but without assessing the actual spatial *impact* of those threats on biodiversity (Halpern et al. 2015; Tulloch et al. 2015; Venter et al. 2016; Albouy et al. 2017). Conversely, the geographies of threat approach that I implemented across the chapters in this thesis accounts for the species-specific impacts of threats. This approach uncovered that the spatial impacts of habitat destruction and hunting pressure on biodiversity were larger than the area deforested alone. Therefore, conservation planning assessments based on independent biodiversity and threat maps might underestimate areas under actual threat and lead to misguided conservation effort. Furthermore, the approaches advanced in this thesis can be used to feed conservation planning approaches in other systems that focus on abating multiple threats for conserving biodiversity targets across different hierarchical levels and facets of biodiversity.

3 Implications for conservation practice

The results of this thesis highlight key points for conservation practice. In general, these results point to the importance of simultaneous assessments of species-specific impacts of multiple threats to devise spatially-explicit proactive habitat protection and reactive threat management strategies (Wilson et al. 2007). Second, such assessments across entire regions can provide templates for cooperative, transboundary strategies that are more likely to be effective at conserving representative areas for biodiversity than national strategies (Montesino Pouzols et al. 2014). Finally, the approaches developed across these chapters can help guide complementary proactive and reactive conservation strategies that target different hierarchies and facets of biodiversity.

More specifically, this thesis has important implications for conservation practice in the Gran Chaco. First, the rapid and widespread defaunation uncovered in this thesis highlights the urgency to act now to conserve the imperilled biodiversity in Gran Chaco. Opportunities remain to conserve the Chacoan biodiversity, but my research suggests that given the rampant advance of threats, the opportunity window is rapidly closing.

Second, the priority areas and the threat hotspots identified can serve as a template for guiding conservation and land-use planning across the Gran Chaco. The priority areas for proactive habitat protection can serve to update and complement the existing conservation plans for the Gran Chaco, which have relied on scarce and low-resolution biodiversity data

and which have not accounted for the spatial impacts of habitat destruction and hunting pressure on biodiversity (TNC et al. 2005; Nori et al. 2016; Arnold & Brown 2018). The priority areas could serve as a regional template for proactive area-based protection to complement the current protected area network that currently covers only 9% of the Gran Chaco, and to achieve the 17% protection target committed by all Chaco countries through the Convention of Biological Diversity's Aichi Target 11. An area under particularly high risk is northernmost Paraguay, which harbours high quality habitat for most larger mammals, including the jaguar, and maintains high levels for all biodiversity facets. However, threats are already causing biodiversity losses and severing the connectivity between the large protected areas in southern Bolivia and northern Paraguay.

The threat hotspots that I identified can serve to further complement priority area protection by identifying where managing threats can bring high conservation benefits. Such a specific threat management actions could particularly be implemented in the context of ensuring connectivity among priority areas. Mitigating threats will require close collaboration with local stakeholders to ensure that actions to reduce or reverse habitat destruction and hunting pressure are culturally appropriate and acceptable. Specific management actions where habitat is being destroyed may include restoration and ensuring connectivity among core area patches. Actions for reducing hunting pressure may include increasing law enforcement and improving coexistence between ranchers and wildlife thought to cause economic losses. Mitigating hunting pressure in otherwise healthy habitat could bring particularly large conservation gains, as more costly habitat restoration would not be necessary.

Finally, my thesis contributes to our understanding of the impact of the increasing reliance of the global markets on agricultural commodities produced in tropical deforestation frontiers, such as the Gran Chaco. Therefore, my research also contributes to supporting conservation actions beyond place-based interventions, which could focus on interventions on supply chains or international trade agreements. For instance, it could support demands for more stringent sustainability standards in trade agreements among countries. Indeed, the published results from Chapter II have already been extensively used in Greenpeace's "Slaughtering the Gran Chaco forest" report to link beef consumption in Europe and Israel to the decline in jaguars in the Gran Chaco, and to support their demand for zero deforestation commitments by European supermarkets and stronger policies to protect biodiversity in the Gran Chaco in trade agreements (Greenpeace 2019). My research could be further used to support demands for increased sustainability standards in the

trade agreement between the EU and MERCOSUR, of which Argentina and Paraguay are members, which could have enormous implications for biodiversity in the Amazon, the Cerrado and the Gran Chaco (Kehoe et al. 2019).

4 Future research

This thesis contributes to a deeper understanding of the spatial impact of threats on biodiversity over broad scales and their changes over time. During the development of this research, complementary questions arose that are beyond the scope of this thesis.

An exciting question arising from this research is to what degree species often targeted for conservation, such as the jaguar or the Chacoan peccary, could serve as effective surrogates for the conservation of the Chacoan biodiversity. The datasets developed in this thesis could be used to explore whether high quality habitats, or areas under specific threats for these species, overlap with other species and biodiversity facets. Such research could bring new insights on the applicability of conservation surrogates for different complementary proactive and reactive conservation strategies. Additionally, if effective, the use of such surrogate species for conservation could facilitate the communication of conservation strategies in the Gran Chaco to decision-makers and the public.

A natural extension of this work is to explicitly link the impact of the threats of habitat destruction and hunting pressure to the sources and underlying drivers of these threats. Specifically, the high-resolution, spatially-explicit and multitemporal information on the impacts of these threats on biodiversity could be linked to information on the supply chain of the commodities produced in the Gran Chaco. Appendix A is an example of such research, where I linked the shrinking jaguar distribution across Latin America to the beef and soybean exports to international markets, especially in Europe and Asia. Yet the focus on the entire continent limited the analysis to very coarse jaguar and land use distributions and only national level trade data. Other studies have linked commodity trade with potential impacts on coarse-resolution expert-derived species range maps too (e.g. Moran & Kanemoto 2017; Green et al. 2019). The high-resolution multiple-threat maps for different hierarchies and facets of biodiversity developed in this thesis could be linked with subnational data on commodity supply chains tracking from the TRASE.earth database available for Argentina and Paraguay. Such connection could bring a deeper understanding of the impact of agricultural commodity trade on biodiversity at higher spatial and

temporal resolutions that not only accounts for deforestation but for the spatial impacts of habitat destruction and hunting pressure.

Another question focused on the sources of threat is asking what the role of different land-use actors across the Gran Chaco is in generating different threats to biodiversity. Answering this question could help better understanding the impacts of different actors on biodiversity. Such understanding could be useful to guide conservation planning by identifying actor-specific, socially-acceptable strategies to mitigate specific threats, thus complementing this thesis' maps for proactive and reactive conservation actions.

A future advance for the geographies of threat framework would be to implement it in a context that allows for assessing the time-delayed responses to threats. Recent research has developed methods to map time-delayed responses to deforestation (Semper-Pascual et al. 2018) and could potentially be combined with the geographies of threat approach to account for multiple threats. Such a focus could bring further insights into the interaction of threats over time and increase our understanding on future extinctions due to past anthropogenic pressures.

Finally, the framework of the geographies of threat advanced in this thesis could be applied elsewhere to understand the spatial impact of multiple threats. Particularly, the methods we used permit the reconstruction of the geographies of threat across other rapidly changing regions, including where biodiversity data is scarce. Additionally, this framework could be potentially adapted to incorporate ecological models other than habitat suitability and hunting pressure models, such as spatially-explicit occupancy and abundance models, where such data is available. This thesis highlights the utmost importance of accounting for multiple threats in large-scale biodiversity assessments. Therefore, applying the geographies of threat framework across other tropical regions could bring a more complete understanding than we currently have (Newbold et al. 2016), on how and where humans are pushing biodiversity beyond its planetary boundary through multiple threats.

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Appendix A:
Beyond fangs: beef and soybean trade drive
jaguar extinction

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Increasing evidence suggests that the illegal trade of tiger (*Panthera tigris*) body parts is rapidly expanding to other large cats (Villalva and Moracho 2019), as illustrated by the recent surge in the trafficking of jaguar (*Panthera onca*) parts from across Latin America to Asia (Fraser 2018). For instance, since 2013, the fangs of hundreds of jaguars destined for China have been seized in Bolivia alone, garnering widespread attention that ultimately led to the prosecution of fang traders (Fraser 2018). However, we argue that agriculture poses a far greater threat to jaguars because its expansion is associated with widespread habitat loss and direct killing.

As the main agricultural land uses in Latin America, soy cultivation and cattle ranching now cover 400 million hectares in the region (Graesser *et al.* 2015). The vast majority of soy and a sizeable share of beef are exported (Pendrill *et al.* 2019); while most beef produced in Latin America is consumed domestically, the cities where the most beef is consumed are often located far from where ranching takes place (Pendrill *et al.* 2019). Moreover, exports of both soy and beef are increasing, particularly to Europe and Asia, to satisfy growing demand (Pendrill *et al.* 2019) (Figure A 1). Soybean cultivation has expanded by a

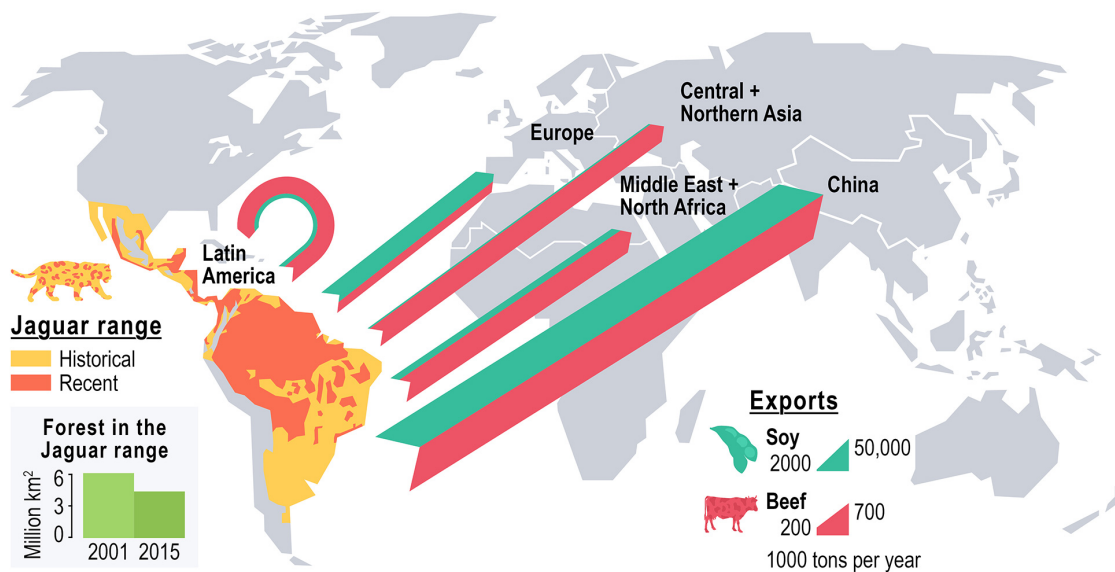


Figure A 1: Trade volume of soybeans and beef from Latin America to the main importing regions and the associated contraction of the jaguar range. Arrow thickness represents the yearly average volumes exported from Latin American countries between 2013 and 2017, expressed in thousand tons of soy and beef (data: <http://resourcetrade.earth>). Arrow thickness reflect the values as scaled in the Exports legend, where thickness range from the lowest to highest export volumes. The historical and recent jaguar ranges are shown in yellow and orange, respectively (data: Sanderson *et al.* 2002). The lower left inset shows the forest loss within the recent jaguar range in 2001 and 2015 due to commodity production (mainly beef and soybeans) (data: Curtis *et al.* 2018).

staggering 500% since the early 1980s, while livestock ranching expanded by 70% since 1990 (Graesser *et al.* 2015). Habitat destruction and degradation due to the expansion of predominantly export-oriented agriculture in Latin America are the key reasons for the disappearance of jaguars from nearly half of their historical range (de la Torre *et al.* 2018), as well as for widespread declines of associated biodiversity in the Atlantic Forest, Cerrado, Chiquitano, Gran Chaco, and Amazonia. On the basis of new maps of deforestation drivers (Curtis *et al.* 2018), we estimate that agricultural commodity production has been responsible for the destruction of 20% of forested lands (1.7 million km²) inside the jaguar's modern range since 2001 (Figure A 1) and is a primary factor driving forest fires (intentionally set to clear land for farming or ranching) within these ecoregions in 2019 (Barlow *et al.* 2019; Romero-Muñoz *et al.* 2019a).

Increased jaguar mortality is also indirectly associated with agricultural expansion, which not only allows hunters to access (and deplete prey within) formerly remote areas but also leads to increased conflicts with livestock ranchers (Romero-Muñoz *et al.* 2019b). For instance, about 180 jaguars were killed during a single year on 115 surveyed ranches (only 3% of the total ranching area) in lowland Bolivia – a hotspot for the illegal fang trade (Arispe *et al.* 2009; Inchauste 2010). The fang trade might therefore be a by-product of increasing jaguar persecution by ranchers and ranching now threatens to extend into the jaguar's remaining core habitat areas (Graesser *et al.* 2015). Indeed, Bolivia plans to triple its agricultural extent by 2025 (Romero-Muñoz *et al.* 2019a), Brazil is currently dismantling environmental policies and encouraging agricultural expansion (Fuchs *et al.* 2019), the EU and Mercosur are drafting a major trade deal that threatens to boost deforestation (Kehoe *et al.* 2019), and the ongoing US–China trade war is prompting a spike in soy exports from Latin America to China (Fuchs *et al.* 2019).

Jaguar conservation efforts have often focused on promoting human–jaguar coexistence. Although important, such initiatives – which are often local – are still rare and likely insufficient to curb the impacts of beef and soybean production on jaguars. Inclusion of the species' remaining core habitat within large protected areas is essential (Romero-Muñoz *et al.* 2019b). Likewise, measures that address the ultimate drivers of threats to jaguars are urgently needed. Supply-chain initiatives such as wildlife-friendly beef certification or other market-based mechanisms may contribute to a constellation of policies to reduce adverse impacts on jaguars, but must be accompanied by governmental regulation to avoid displacing threats to other regions (Lambin *et al.* 2018). Ultimately, reducing meat consumption inside and outside the jaguar's range will be essential to decrease habitat

destruction and associated hunting (Springmann *et al.* 2018). Meat consumption is relevant regarding both beef and soy, given that approximately three-quarters of the soy produced is used as animal feed (Graesser *et al.* 2015). Holistic approaches that consider the connections between agricultural expansion, agricultural trade, and other threats such as wildlife trafficking are needed to conserve South America's most emblematic predator.

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Eidesstattliche Erklärung

Hiermit erkläre ich, die vorliegende Dissertation selbstständig und ohne Verwendung unerlaubter Hilfe angefertigt zu haben. Die aus fremden Quellen direkt oder indirekt übernommenen Inhalte sind als solche kenntlich gemacht. Die Dissertation wird erstmalig und nur an der Humboldt-Universität zu Berlin eingereicht. Weiterhin erkläre ich, nicht bereits einen Dokortitel im Fach Geographie zu besitzen. Die dem Verfahren zu Grunde liegende Promotionsordnung ist mir bekannt.

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