RESEARCH ARTICLE

Partitioning the effects of habitat loss, hunting and climate change on the endangered Chacoan peccary

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Abstract

Aim: Land-use change and overexploitation are major threats to biodiversity, and climate change will exert additional pressure in the 21st century. Although there are strong interactions between these threats, our understanding of the synergistic and compensatory effects on threatened species' range geography remains limited. Our aim was to disentangle the impact of habitat loss, hunting and climate change on species, using the example of the endangered Chacoan peccary (*Catagonus wagneri*).

Location: Gran Chaco ecoregion in South America.

Methods: Using a large occurrence database, we integrated a time-calibrated species distribution model with a hunting pressure model to reconstruct changes in the distribution of suitable peccary habitat between 1985 and 2015. We then used partitioning analysis to attribute the relative contribution of habitat change to land-use conversion, climate change and varying hunting pressure.

Results: Our results reveal widespread habitat deterioration, with only 11% of the habitat found in 2015 considered suitable *and* safe. Hunting pressure was the strongest single threat, yet most habitat deterioration (58%) was due to the combined, rather than individual, effects of the three drivers we assessed. Climate change would have led to a compensatory effect, increasing suitable habitat area, yet this effect was negated by the strongly negative and interacting threats of land-use change and hunting.

Main Conclusions: Our study reveals the central role of overexploitation, which is often neglected in biogeographic assessments, and suggests that addressing overexploitation has huge potential for increasing species' adaptive capacity in the face of climate and land-use change. More generally, we highlight the importance of jointly assessing extinction drivers to understand how species might fare in the 21st century. Here, we provide a simple and transferable framework to determine the separate and joint effects of three main drivers of biodiversity loss.

KEYWORDS
agricultural expansion, deforestation, EDGE species, Gran Chaco, land-use change, overexploitation, Tayassuidae, time-calibrated SDM, tropical and subtropical dry forests

1 | INTRODUCTION

We are facing an accelerating global extinction crisis, with habitat loss and overexploitation as its main drivers (IPBES, 2019; Maxwell et al., 2016). In particular, land-cover change has a massive impact on the world's ecosystems, with natural habitat around the globe still being converted, fragmented and degraded, mainly due to agricultural expansion and intensification (Johnson et al., 2017; Newbold et al., 2015). Overexploitation (i.e. unsustainable hunting or collecting of animals and plants) is a second major threat, resulting in major waves of defaunation in habitat remnants, and leading to wildlife losses, particularly of larger-bodied species (Benítez-López et al., 2017; Dirzo et al., 2014). The pressures of land-use change and overexploitation are both expected to intensify further into the 21st century as the human population and the use of resources grow (Kehoe et al., 2017; Powers & Jetz, 2019). In addition, climate change is a rapidly increasing threat (Fox et al., 2014; Kehoe et al., 2017) and is already exerting

major impacts on biodiversity in mountain areas, high-latitude ecosystems and drylands (Chen et al., 2011; Pauchard et al., 2016).

Jointly assessing multiple threats is important to effectively evaluate their cumulative impact, which can differ substantially from their individual impacts. This includes compensatory effects, where one threat lessens the impact of another, as well as additive effects, where combined threats result in larger pressures than anyone would cause individually (Brook et al., 2008). Most worryingly though are synergistic effects, where the interactive effect of threats is disproportionately larger than their sum would otherwise be. Such synergistic effects are common, for example, between land-use change and climate change (Fox et al., 2014; Paprocki et al., 2015) and between land-use change and hunting pressure (Gallego-Zamorano et al., 2020; Romero-Muñoz et al., 2020). Nevertheless, studies exploring how land-use change, hunting and climate change interact in space and time to affect biodiversity are lacking (Bogoni et al., 2022; Jaureguiberry et al., 2022).

Tropical and subtropical dry forests provide an interesting natural laboratory to assess the three-way interactions among land-use change, hunting and climate change, as all three threats are already prevalent in them (Gallego-Zamorano et al., 2020; Miles et al., 2006). Tropical dry forests occur worldwide, constituting ca. 42% of the global tropical and subtropical forest area (Miles et al., 2006) and supporting ecosystem services benefitting humans at a global scale (Balvanera et al., 2011; Portillo-Quintero et al., 2015). Tropical dry forests also harbour rich biodiversity, including many endemics (Linares-Palomino et al., 2011). Land-use change has been particularly widespread in these ecosystems (Hoekstra et al., 2005; Portillo-Quintero & Sánchez-Azofeifa, 2010). Likewise, dry forests are hotspots of defaunation, particularly of larger mammals (Stoner & Timm, 2011). Finally, due to the close relationship between water availability and vegetation, dry forests are particularly sensitive to climate change (Miles et al., 2006; Siyum, 2020).

Among the most threatened tropical dry forest regions is the South American Gran Chaco (WWF, 2015), located in northern Argentina, western Paraguay and southeastern Bolivia (Figure 1). The 1.1 million-square kilometres covered by the Chaco region harbour the second-largest remaining continuous forest in South America after the Amazon (Eva et al., 2004; Portillo-Quintero & Sánchez-Azofeifa, 2010). These forests, that harbour rich biodiversity (TNC, FVS, FDSC, & WCS, 2005), have been a global hotspot of deforestation recently (Da Ponte et al., 2022; Gasparri & Grau, 2009; Zak et al., 2008), with massive conversion of natural ecosystems into croplands and pastures, especially during the 21st century (Baumann et al., 2017; Vallejos et al., 2015). Key drivers of

agricultural expansion have included technological advances (e.g. new soybean variants and introduction of exotic pasture grasses), surging global demand for beef and soybean, changes in export policies and changes in climatic conditions favouring agriculture (Caldas et al., 2015; Zak et al., 2008). These processes had strongly negative outcomes for Chacoan biodiversity, such as a large decrease in suitable habitat for many species (Torres et al., 2014), including the Chacoan peccary (Camino et al., 2022). Available evidence indicates that these negative effects of past habitat loss will likely continue in the future, due to the presence of extinction debt (Semper-Pascual et al., 2018, 2021). In addition to land-use change, Chacoan fauna also suffers great pressure from overexploitation, particularly unsustainable hunting, which now renders the Chaco a global hotspot of defaunation (Altrichter, 2005; Periago et al., 2015). Importantly, hunting and land-use change has acted synergistically in the Chaco (Romero-Muñoz et al., 2020, 2021). Finally, climate change has also already heavily impacted the Chaco, resulting in increasing rainfall since the mid-20th century (Bucher et al., 2006; Hoyos et al., 2013), although little information exists on how this impacted on Chacoan biodiversity. More importantly though, the impacts of how the triple threat of land-use change, hunting and climate change interact—in the Chaco, as well as in other dry forests around the globe, remains largely unknown. This is problematic because we might draft conservation strategies that are not effective if we do not get the threat specified correctly (Bellard et al., 2022).

Here, we explored the individual and joint effects of land-use change, hunting and climate change on the distribution of suitable habitat for the Chacoan peccary (*Catagonus wagneri*), a species of
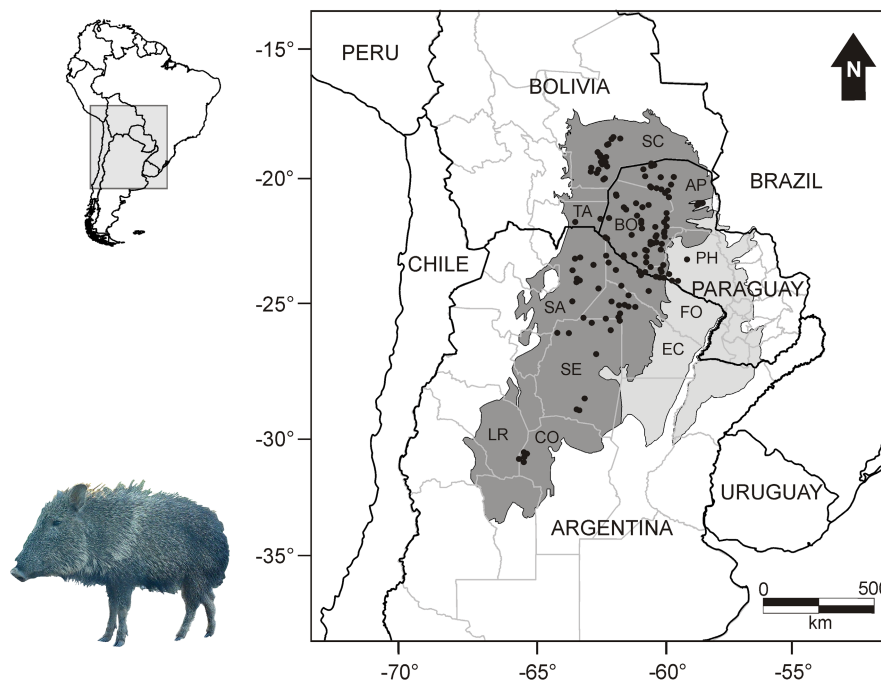
FIGURE 1 Location of the Gran Chaco in South America. Dry and Humid Chaco ecoregions (as defined by Dinerstein et al., 2017) are in dark and light grey, respectively. Black points are occurrence localities used in our model (after filtering; see Methods). Acronyms refer to Departments/Provinces with known occurrences (Paraguay: AP, Alto Paraguay; BO, Boquerón; PH, Presidente Hayes; Bolivia: SC, Santa Cruz; TA, Tarija; Argentina: SA, Salta; FO, Formosa; CH, El Chaco; SE, Santiago del Estero; CO, Córdoba; LR, La Rioja).

high conservation concern in the Chaco and globally. The Chacoan peccary is a forest dweller and avoids open, agricultural areas; therefore, the conversion of forests to agriculture constitutes a major threat (Camino et al., 2022). In addition, Chacoan peccaries are a highly preferred prey of local hunters (Altrichter, 2006; Altrichter et al., 2016; Camino et al., 2018). Specifically, the objectives of this work are (1) to assess how suitable habitats for the Chacoan peccary changed from 1985 to 2015; and (2) to evaluate the individual and joint contribution of the effects of land-use change, hunting and climate change, to peccary habitat changes. We expected a priori that these factors influence habitat availability negatively, and that interactions between them are additive.

2 | MATERIALS AND METHODS

2.1 | Study area

The Gran Chaco is located in the heart of South America and comprises the Dry Chaco and the Humid Chaco ecoregions (sensu Dinerstein et al., 2017; Figure 1). The region is an extensive plain sparsely interrupted by lower mountains towards the west. Climate is semiarid, with a large amplitude in temperature, both annually and daily, and annual mean maximum temperatures of 36°C. Rainfall is concentrated in summer and shows a strong gradient from the east (>1200 mm) to the west, with minimum rainfall in the southernmost part of the Dry Chaco (400 mm). The dominant vegetation is dry, broad-leaved, thorny forests and shrublands (hereafter '*woodlands*'), with some areas covered by natural grasslands and seasonally-flooded savannas (Cabido et al., 1994; Morello & Adámoli, 1968; Prado & Gibbs, 1993).

Recently, modern, mechanized agriculture has expanded rapidly into the Chaco, particularly after 2000, turning it into a global deforestation hotspot (Hansen et al., 2013). More than 20% of all Chacoan woodlands have been replaced by croplands and pastures between 1985 and 2015 (Baumann et al., 2017). Remaining forests are largely inhabited by forest-dependent people that often practice subsistence hunting (Camino et al., 2018; Levers et al., 2021; Saldivar-Bellassai et al., 2021; Tamburini & Cáceres, 2017).

2.2 | The Chacoan peccary

The Chacoan peccary is the largest endemic mammal of the Chaco (Nori et al., 2016) and inhabits a large share of the region, from western Paraguay and southeastern Bolivia to central Argentina (Altrichter et al., 2016; Camino & Torres, 2019). Unlike other peccary species, the Chacoan peccary lives only on the plains, below 500 m a.s.l. (Camino & Torres, 2019). Groups are typically small (4.5 individuals in average), and solitary individuals are not rare (Camino et al., 2022). The Chacoan peccary is an omnivorous species, with a marked preference for cacti (Altrichter et al., 2015). As a result of the multiple threats acting on the species, the Chacoan peccary is the

rarest and most threatened of all extant peccary species and is currently categorized as Endangered (Altrichter et al., 2015). Moreover, the species has a distinct evolutionary history and is the sole survivor of an ancient lineage (Parisi Dutra et al., 2017). Taken together, the susceptibility of the species to multiple threats, its conservation status and relevance and the fact that it is endemic to the Chaco make it an ideal study species for our purposes.

2.3 | Overview of the analytical approach

First, we developed a Species Distribution Model (SDM) that makes full use of all occurrence data in our database and projected this SDM to 1985 and 2015 based on climatic and land-use data. Second, we used a hunting pressure model (building on Romero-Muñoz et al., 2020) and projected it to the same dates. Third, we transformed the continuous SDM and hunting pressure maps to binary indicators and superimposed the resulting maps to obtain distinct combinations of habitat suitability and hunting pressure. Fourth, we identify those areas that were only affected by changes in hunting pressure. Fifth, on the remaining areas, we used change mapping and a Variation Partitioning Analysis (Peres-Neto et al., 2006) (Figure 2) to partition the individual contribution of land conversion and climate change on the habitat changes we mapped.

2.4 | Time-calibrated SDM

An important assumption in SDMs is that niches are stable through time, although this assumption is often ignored (Nogués-Bravo, 2009). This is problematic if environmental conditions vary over time, such as in the Chaco where marked land-use changes have happened recently. To overcome this, we used a 'time-calibrated' approach for model fitting (Devenish et al., 2021; Kuemmerle et al., 2012; Nogués-Bravo, 2009), whereby each occurrence point is matched with the environmental predictors from the time when the record was collected. This yields a single, unified SDM that uses all available data, which can then be projected into different time periods. The resulting maps are then comparable as differences in these maps are solely due to differences in the spatial patterns of predictors, but not in realized niches, or due to varying sampling bias in occurrence points (Romero-Muñoz et al., 2020; Semper-Pascual et al., 2019). Here, we related each occurrence record with the values of predictors in the same cell and from the same year the occurrence was recorded.

For our SDM algorithm, we chose the Mahalanobis Typicality, a presence-only algorithm derived from the Mahalanobis distance, which expresses the distance, in the multidimensional environmental space spanned by predictor variables, between each locality and the average of values at all known localities. A distance = 0 indicates a perfect match between the environmental conditions at any locality and the multidimensional average, while distance values increase to infinite as environmental conditions are increasingly different from the multidimensional average (Farber & Kadmon, 2003).
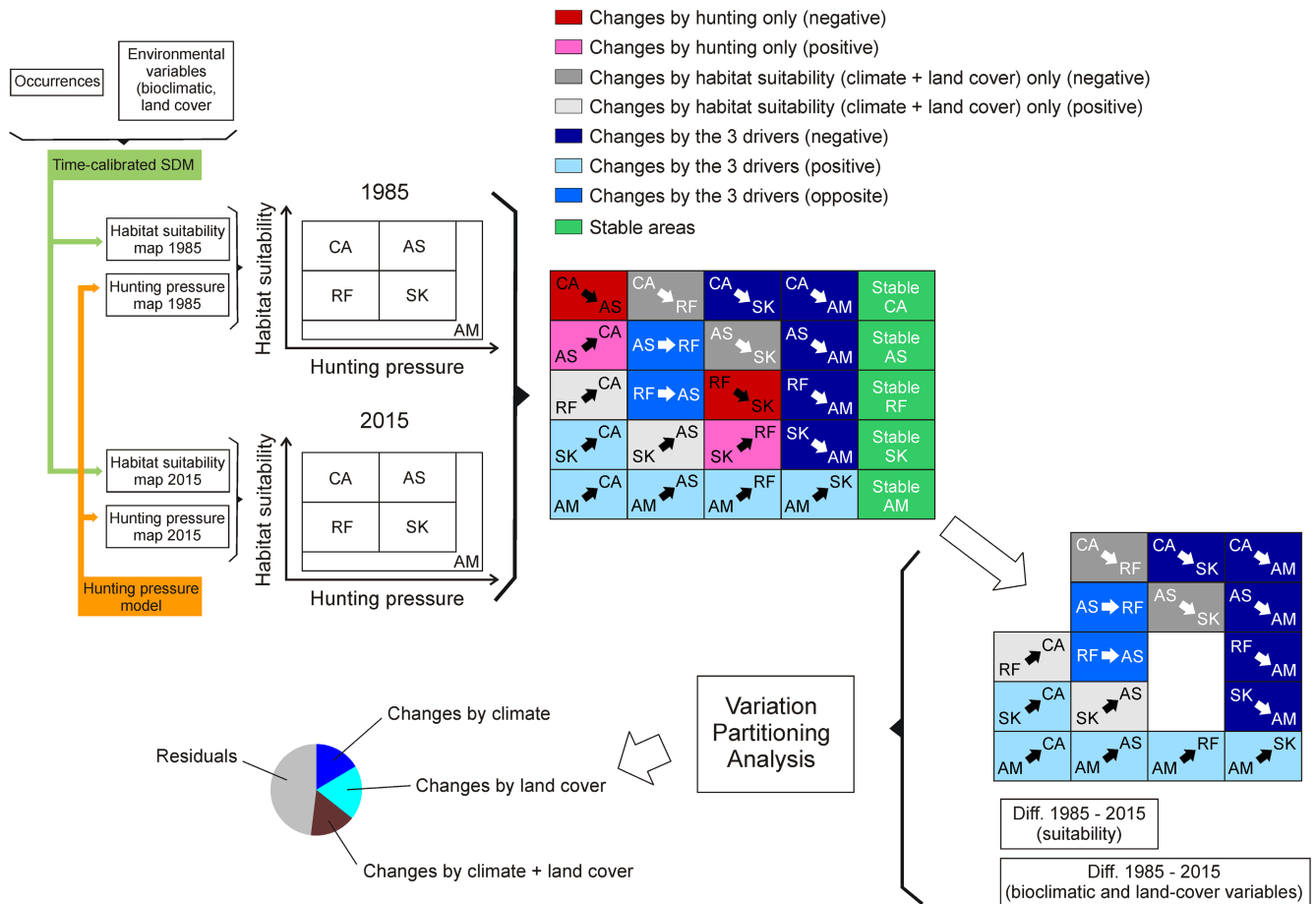
FIGURE 2 Flowchart of the main analytical steps. We first developed time-calibrated species distribution models and hunting pressure models and projected them to 1985 and 2015. Second, we superimposed the resulting maps to obtain core/sink habitat and to isolate areas undergoing changes in hunting pressure only from the rest. Third, we identified areas where habitat change was due to climate plus land-cover change vs. multiple drivers. Finally, we evaluate the separate and joint effect of climate change vs. land conversions using a Variation Partitioning Analysis. AM, Avoided matrix; AS, Attractive sink; CA, Core area; RF, Refuge; SK, Sink. Downward arrows indicate habitat degradation, upward arrows indicate habitat improvement, and horizontal arrows indicate areas with opposite effects between hunting pressure and land cover plus climate.

Mahalanobis Typicalities are derived by rescaling the Mahalanobis distances to values ranging between 0 and 1, with 1 indicating conditions identical to the multivariate mean at occurrence localities (Hernandez et al., 2008; Li & Fox, 2011). One important advantage of a Mahalanobis distance-based algorithm over other SDM algorithms is that it requires only presence data (e.g. instead of presence vs. background data) and hence is free of common problems related to the choice of background sampling. Another advantage is that Mahalanobis Typicalities are unaffected by correlation between predictors (Farber & Kadmon, 2003; Shatz et al., 2013). We used the implementation of the Mahalanobis Typicality in the Idrisi v17 Selva software (Eastman, 2012).

2.4.1 | Environmental variables

Land-cover maps were available annually between 1985 and 2015 from our own prior work (Baumann et al., 2017, 2022), which resulted

in the first consistent and fully validated time series for main land-cover types in the Chaco. Specifically, our dataset distinguishes between woodlands, other types of natural vegetation (e.g. natural grasslands, savannas, etc.), croplands, pastures and other land cover (e.g. water, bare soil, salt planes, urban areas, wetlands, etc.) for the entire Chaco. For more information on the land-cover classification, we refer to Baumann et al. (2022). In this study, we focussed on three main categories, all important to the peccary: woodland (comprising natural forests and shrublands), cropland and pasture. All other classes were masked from subsequent analyses. Since we here focus on conversions between natural woodlands and agriculture, we could use the mapped changes in land cover as a direct proxy for land-use change (hereafter: land conversion). We spatially aggregated these maps to 0.5 arc-minutes (about 1 km), by calculating the percentage of each class using a 2-km radius around each grid cell. We chose a 2 km radius because it aligns well with available information on Chacoan peccary home range size (Altrichter et al., 2015; Taber et al., 1993). Those three variables (*%woodland, %cropland*

and *%pasture*) were the ones we used in the SDM (Appendix S3, Table S3.1).

All climate layers originated from the CHELSAcruts database (http://chelsa-climate.org/chelsacruts), which provides monthly averages for precipitation and temperatures for the period between 1901 and 2016 and at 0.5 arc-minutes spatial resolution (Karger et al., 2017). We used these layers to derive 19 bioclimatic variables using DIVA-GIS (Hijmans et al., 2001) for all single years between 1985 and 2015. To reduce the dimensionality of our climate variables, we conducted a PCA with the average (1985 to 2015) values of bioclimatic variables in occurrence localities and selected those variables correlating strongly ($r > 0.70$) with the first three principal components (PCs); this explained >95% of the variation. Thus, the three bioclimatic variables we selected for model fitting were (1) *mean annual temperature* (bio1; PC1), *precipitation seasonality* (bio15; PC2) and *precipitation of the warmest quarter* (bio18; PC3— Appendix S3, Table S3.1).

We evaluate the importance of each variable by comparing the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) from the full model, with the AUC values of models fitted without a respective variable. Therefore, the variable that contributes the most to the full model is the one that, when missing, causes the greatest decrease in AUC values (Phillips et al., 2006).

2.4.2 | Chacoan peccary occurrence data

We obtained occurrence points from field databases curated by the members of the IUCN SSC Peccary Specialist Group (Altrichter et al., 2016), as well as from publications and museum collections visited personally or accessed via the GBIF portal (GBIF.org, 28 April 2022; GBIF Occurrence Download https://doi.org/10.15468/dl.9tfqpp). To avoid confusion with the other peccary species inhabiting the area, we selected only records corresponding to clearly identified museum specimens or from direct sightings of individuals (e.g. via camera traps). From this database, we selected only records between 1985 and 2015, to match with the period covered by our environmental variables, except for the only recently discovered populations in southern Santiago del Estero and western Córdoba provinces, Argentina (Torres et al., 2019). As the Chacoan peccary is endemic to the Chaco, we excluded localities from outside the region ($n = 4$), which likely represent misidentified records. To reduce the potential effects of sampling bias and autocorrelation, we randomly selected occurrence records to be at least 10 km apart from each other, using the *spThin* package in R (Aiello-Lammens et al., 2015). After spatial thinning, our final set included 157 independent occurrence points.

2.4.3 | Model evaluation

To evaluate the performance of our model, we implemented a spatial-block cross-validation technique, where occurrence points

are divided into *n* spatially-segregated blocks (four blocks in our case; Kass et al., 2020). Then, the model was run using *n*-1 blocks (i.e. three blocks) of occurrences for training and leaving the remaining block for testing, with this process being repeated *n* times until all blocks were used for testing (Muscarella et al., 2014). We calculated the AUC for each testing block and averaged these values to obtain a final AUC (Muscarella et al., 2014). We additionally applied a null-model approach in each run, by comparing this value with the AUC value at the upper 95% confidence interval of a distribution of 100 null models (Bohl et al., 2019). We consider a model to perform well if its AUC based on actual data was greater than the AUC based on the distribution of null models (Kass et al., 2020). The AUC is the most widely used evaluation metric for SDM. Although interpreting it for presence-only and presence-background SDMs is sometimes challenging, it can be robustly used as a relative performance metric (i.e. to compare alternative models using the same algorithm and occurrence points, as in our case) (Peterson et al., 2011). Further explanations on model validation are provided in Appendix S2.

2.5 | Hunting pressure maps

We used the hunting pressure maps for the Chacoan peccary built in 1985 and 2015, by Romero-Muñoz et al. (2020), which followed the approach developed by Benítez-López et al. (2019). This hunting pressure model depicts the population decline across space, resulting in a hunting pressure index ranging from 0 (no decline) to 1 (total local extirpation). The model uses three predictors: two indicators of hunting risk (distance to hunters' access points and human population density) and one indicator, a species' body mass, of the intrinsic vulnerability to population decline due to hunting (Benítez-López et al., 2019). We defined the distance to hunters' access points for the Chacoan peccary as the distance to towns, roads, croplands, pastures and smallholder homesteads (Romero-Muñoz et al., 2020).

2.6 | Assessing the effect of the three threats

Once a time-calibrated SDM was fitted, we projected it to the 1985 and 2015 environmental conditions, that is, using the 1985 and 2015 climate and land-cover layers. This yields two distributional maps, which were reclassified into two classes, suitable habitats vs. avoided matrix, using the 5th percentile of the suitability value distribution at occurrence points (Pearson et al., 2004). Next, we split suitable habitats into areas of high and low suitability, using the maximum sensibility plus specificity value threshold (Liu et al., 2016). We also reclassified the hunting pressure maps into areas of high (>0.5) and low (<0.5) hunting pressure, according to the IUCN criterion A4 (50% population decline due to threats that have not ceased) used for assigning species to the category 'Endangered', in which the Chacoan peccary is categorized (IUCN, 2012).

We then overlapped our reclassified habitat suitability maps with the reclassified hunting pressure maps. For each year, this yielded a

habitat quality map (we use this term to differentiate it from the habitat suitability maps, the outcome of the SDM), with five categories: core areas (high suitability and low hunting pressure), attractive sinks (high suitability, yet also high hunting pressure), refuges (low suitability and low hunting pressure), sinks (low suitability and high hunting pressure) and avoided matrix (Figure 2; Romero-Muñoz et al., 2020, Romero-Muñoz et al., 2019). Next, we calculated a difference map between 1985 and 2015 and assessed changes between categories. We identified areas where these changes can be ascribed to changes in hunting pressure alone (i.e. where core areas changed to attractive sinks, where refuges changed to sinks, and vice versa). The remaining areas were subdivided into (1) areas where changes between categories were related to changes in habitat suitability (i.e. climate and land use) only and (2) areas where changes in categories can be ascribed to changes in both hunting pressure and habitat suitability.

To analyse to what extent the changes in habitat suitability in this second category were due to changes in climate, land conversion or both, we performed a variation partitioning analysis (Borcard et al., 1992; Peres-Neto et al., 2006). To do so, we first calculated difference maps between 1985 and 2015 for the continuous suitability maps and our climatic and land-cover predictors. We then sampled 5000 cells randomly in areas with negative and positive habitat changes each. We then carried out the variance partitioning analysis using the *varpart* function in the '*vegan*' v2.5.2 package (Oksanen et al., 2018) in R (see further details in Appendix S3). We also examined the relationships between differences in habitat suitability and predictor variables using the Pearson product–moment correlation coefficient. Finally, we determined stable core areas and evaluated to what extent these areas were covered by the current network of protected areas based on an up-to-date protected area layer from UNEP-WCMC and IUCN (2021).
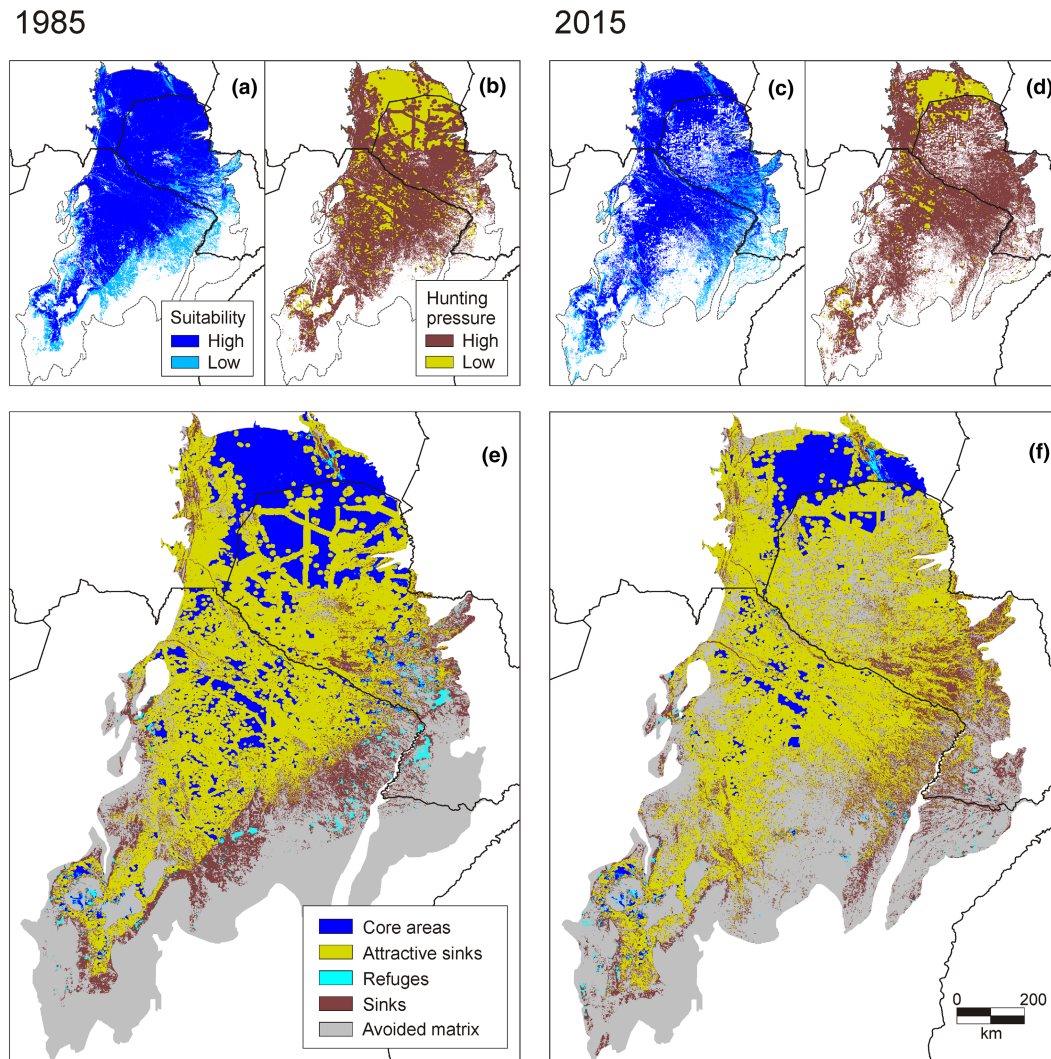
3 | RESULTS

Our time-calibrated SDM had a good fit overall, with test AUC values >95th percentile of the distribution of test AUC values from 100 null models (Figure S3.1). The mean test AUC was 0.82 (SD = 0.05). *Precipitation seasonality* (bio15) and *%woodland* were the most important variables in our model (Figure S3.2a), with suitability peaking at intermediate values in the case of *precipitation seasonality*, and at maximum values in the case of *%woodland* (Figure S3.2b). The model without *%cropland* performed slightly better than the model fitted with all variables. However, we kept this variable because we were interested in its contribution to changes in habitat suitability, given the major cropland expansion recently. Habitat suitability showed a similar response to increasing values of *%pasture* and *%cropland*, with low values even at low shares of these land-cover classes in the landscape, although Chacoan peccaries seemed to be more tolerant to pastures than to crops (Figure S3.2b). Regarding the remaining variables, habitat suitability peak at 250 mm of *precipitation in the warmest quarter* (bio18) and at a *mean annual temperature* (bio1) of 24.5°C (Figure S3.2b).

Our model projections showed a decrease of 9% in total suitable area (i.e. nonmatrix areas) from 715,833 km^2 in 1985 to 654,104 km^2 in 2015. High suitability areas also decreased by 12% between 1985 and 2015, although the share of high suitability areas remained almost unchanged (Figure 3a,c). Although suitable areas were located mainly in the Dry Chaco, we found an eastward shift (i.e. to the Humid Chaco) between 1985 and 2015 (Figure 3a,c). Our projections also showed extensive suitable habitat in the southernmost Dry Chaco, an area believed until recently to be outside the species' range (Torres et al., 2017). Our maps showed that high hunting pressure was already prevalent in 1985, with only a few relatively large patches of low hunting pressure in Bolivia and northwestern Paraguay (Figure 3b). By 2015, areas with low hunting pressure contracted further to include only the Kaa-Iya National Park and Integrated Management Area plus surrounding areas in Bolivia (Figure 3d).

After superimposing the reclassified habitat suitability and hunting pressure maps, we found large patches of attractive sinks (i.e. high habitat suitability, yet high hunting pressure) located mainly in Argentina and Paraguay, which represented the most widespread category in 1985 (i.e. 57% of the total suitable habitat; Figure 3e). Core areas (i.e. high suitability and low hunting pressure) were the second most widespread category in 1985 (22%), with large and continuous patches in Bolivia and Paraguay, and many smaller patches embedded in a matrix of attractive sinks in Argentina. In 1985, sinks (i.e. low suitability and high hunting pressure) covered 19% of total suitable habitat, mainly around attractive sinks and particularly in the Humid Chaco, while refuges (i.e. low suitability and low hunting pressure) were overall scarce (2% of the total), mainly within larger sink areas (Figure 3e). Many attractive sinks were further degraded and converted to the avoided matrix between 1985 and 2015 (Figure 4); still, attractive sinks were more widespread in 2015 than in 1985, representing 65% of the total suitable area (Figure 3f). Attractive sinks increased mainly at the expense of core areas (Figure 4). As a result, core areas in 2015 were reduced to a few continuous patches in Bolivia, plus some smaller isolated patches in Paraguay and Argentina (Figure 3f), constituting only 11% of the total suitable areas. Conversely, many sink areas improved in suitability and were upgraded to attractive sinks in 2015 (23%). Finally, refuge habitat declined significantly after 1985; by 2015, they constituted only 1% of the total suitable habitat (Figure 4).

Our analyses revealed marked differences in the importance of different drivers of habitat change. Improvement of habitat quality was exclusively related to changes in climate. By contrast, habitat deterioration was widespread and mainly related to the combined effect of all three drivers of change (accounting for 58% of total decline), although hunting pressure was the most important variable when considered in isolation (Figures 5 and S3.3). Habitat deterioration occurred mainly in the departments of Boquerón and Alto Paraguay in Paraguay, and the provinces of Salta, Santiago del Estero and El Chaco in Argentina, whereas areas that experienced habitat improvement were located mainly in Presidente Hayes in Paraguay and Santiago del Estero, El Chaco and Formosa in Argentina

FIGURE 3 Habitat maps for the Chacoan peccary. Habitat suitability for 1985 (a) and 2015 (c), hunting pressure for 1985 (b) and 2015 (d) and core/sink map, resulting from overlaying the habitat suitability and hunting pressure maps, for 1985 (e) and 2015 (f). Black lines are the borders between countries, while the grey dashed line represents the Gran Chaco limits.

(Figure S3.4). Stable, suitable habitat represented 59% (422,408 km²) of the total suitable habitat in 2015 (Figure S3.3a), most of which were attractive sinks (71%). Stable core areas (15%) were limited mainly to Bolivia, with smaller patches in northern Paraguay and northern Argentina (Figure S3.3b). The remaining stable areas were sinks (13%), whereas stable refuges in particular were scarce (1%; Figure S3.3b). Encouragingly, 65% of stable core areas were under some form of protection; by contrast, only 9% of stable attractive sinks were inside protected areas (Figure S3.5).

In those areas where hunting was not the sole driver of habitat change, the variation partitioning analysis revealed a strong and negative effect of land conversion (Figure 5), with pasture expansion being particularly important (Table S3.2), both alone and in combination with other factors (Figure S3.6). Climate change resulted in both habitat deterioration and habitat improvement (Figure 5), accounting for 48%–68% of the explained habitat changes. Climate-induced habitat deterioration occurred in areas with decreasing precipitation and temperature, while habitat improvement occurred in areas with

increasing precipitation seasonality (Table S3.2). The joint negative effects of climate and land conversion accounted for 32% of the changes in habitat suitability as explained by the partition analysis (Figure 5); this was mainly due to the co-occurrence of pasture expansion and changes in precipitation, especially in Argentina and Paraguay (Figures S3.6 and S3.7).

4 | DISCUSSION

Land-use change, overexploitation and climate change are major drivers of the ongoing extinction crisis (Leclère et al., 2020; Torres-Romero et al., 2020). Understanding how these factors impact species of conservation concern is key to help effectively safeguard species as they face intensifying threats. However, despite many studies analysing threats individually, their joint impact, including potential synergistic or compensatory effects, often remains elusive (Romero-Muñoz et al., 2020; Santos et al., 2021). A notable exception
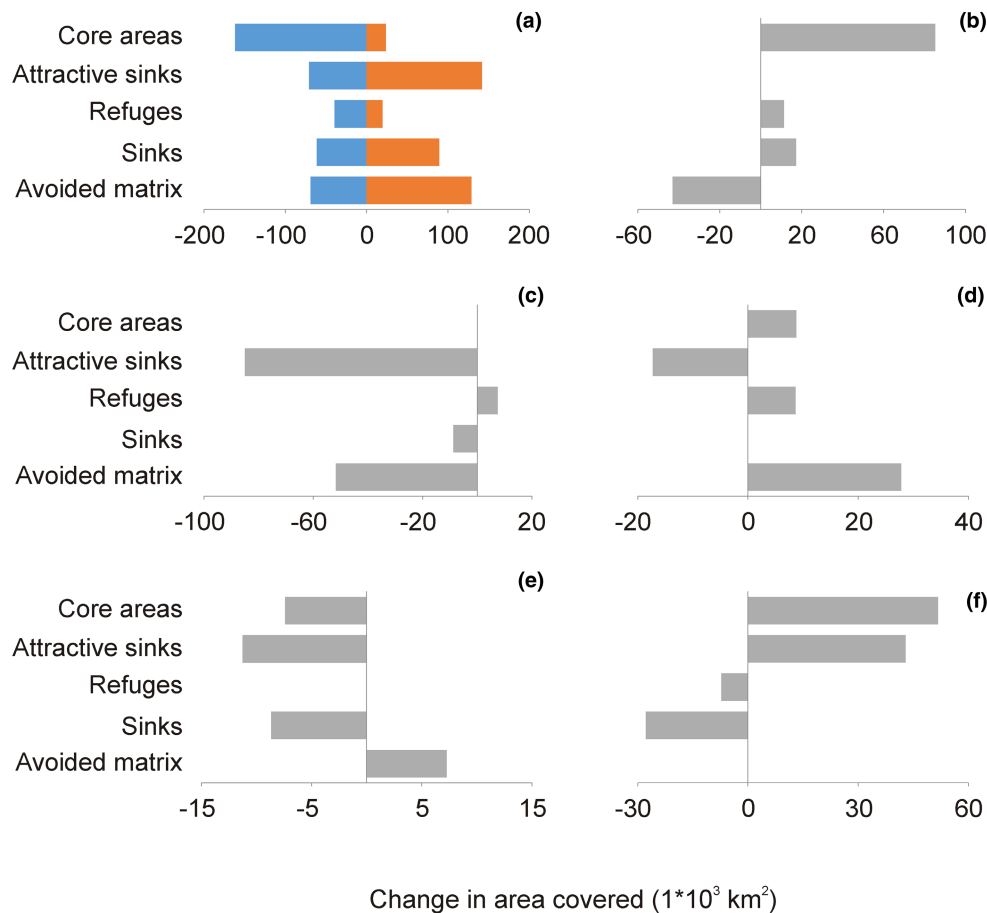
FIGURE 4 Areas of change between 1985 and 2015. Gains (orange) and losses (blue) between 1985 and 2015 (a) and contributions to net change (i.e. gains minus losses) in attractive sinks (b), core areas (c), sinks (d), refuges (e) and the avoided matrix (f). As an example, in (b) core areas were the main contributor to gains in attractive sinks between 1985 and 2015, while losses in attractive sinks during this period were due to degradation to the avoided matrix.

is the work of Oshima et al. (2021), who analyse the joint and separate effects of climate and land-cover variables on the distribution of the white-lipped peccary (*Tayassu pecari*) in Brazil; however, that work does not evaluate the effect of temporal change in these variables. We here developed a framework to evaluate the individual and combined impact of land conversion, hunting pressure and climate change and applied it to the endangered Chacoan peccary for the entire Gran Chaco, a global hotspot of deforestation and defaunation. Our methodology, based on integrating time-calibrated SDM with hunting pressure models, allowed us to partition the effects of these three threats. Our analyses ultimately yielded three major insights. First, habitat deterioration was mainly caused by the combined effects of multiple threats, highlighting the importance of considering interacting threats in conservation assessments. Second, hunting pressure was the single most detrimental driver of habitat deterioration. Spatial data on overexploitation are notoriously hard to generate and hunting pressure models, such as the one we used here, could be useful proxies to better consider overexploitation in conservation planning. Finally, in the Chaco, climate change would have had a compensatory effect via improving habitat conditions, but this positive effect was negated by the strong impacts of land

conversion due to agricultural expansion. More generally, we show the importance of jointly assessing extinction drivers to understand how species ranges and populations are affected in the 21st century, in the dry tropics and elsewhere.

Our time-calibrated SDM performed well, and the relationships between environmental variables and habitat suitability our SDM uncovered seem plausible. We found a strong association of the Chacoan peccary with woodlands and a concomitant strong negative impact of agricultural expansion into woodlands, even at low levels of habitat conversion (Figure S3.2b). This supports our understanding of this species as highly specialized, unlike the other two peccary species that inhabit a variety of close to open habitat types (Gongora et al., 2011; Keuroghlian et al., 2013). In accordance with previous findings (Altrichter & Boaglio, 2004), our models also suggest that the Chacoan peccary tolerates only low levels of anthropogenic disturbance, making the species vulnerable, consistent with its IUCN categorization as Endangered (Camino et al., 2022).

Although overexploitation is known to be a major extinction driver (Maxwell et al., 2016), its effects are often hard to quantify, especially at broader geographic extents (Peres et al., 2006). By superimposing habitat suitability with hunting pressure maps, our
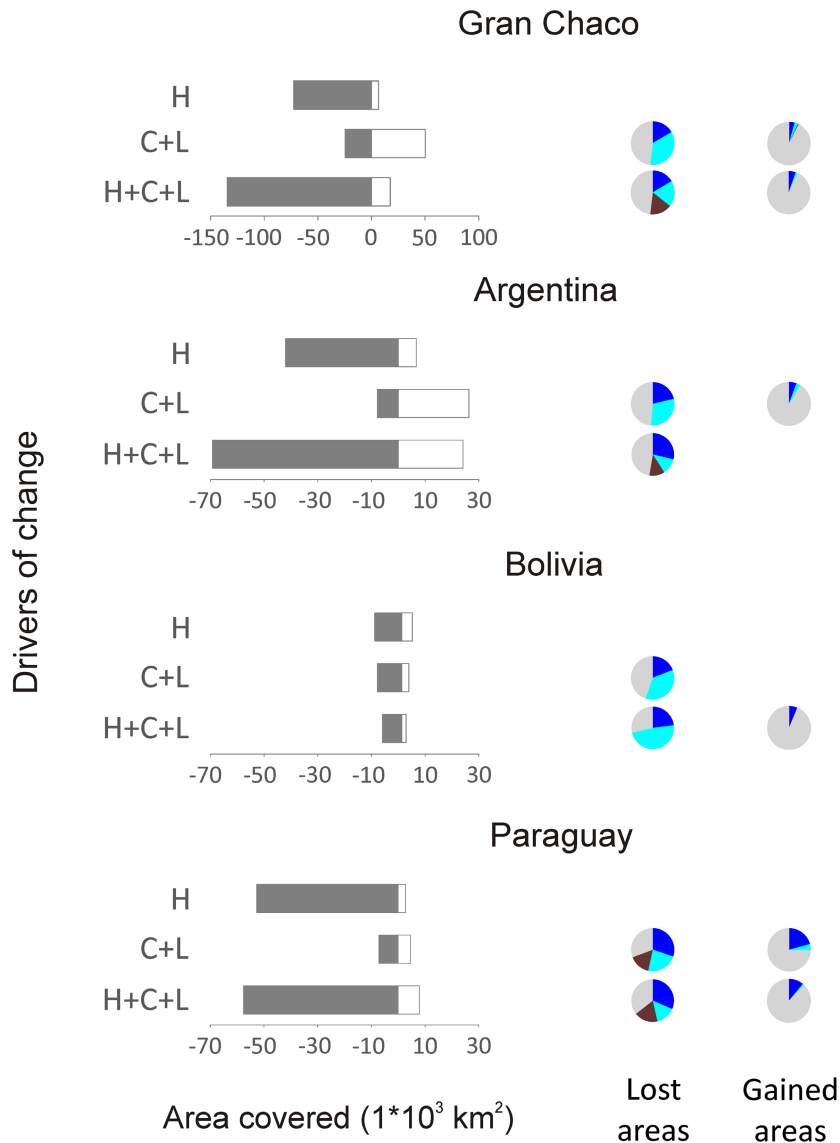
FIGURE 5 Lost and gained areas, and contribution of different threats to observed habitat changes. Barcharts show lost (grey bars) and gained (white bars) areas where changes in habitat suitability were driven by hunting pressure only (H), by climate and land use (C+L) and by the three drivers combined (H+C+L; due to their limited extent, areas with opposite effects were not considered), for the total area (Gran Chaco region) and by country. Pie charts show the separate contribution (adjusted R^2 values) of climate (blue), land-use (cyan) and climate plus land-use (brown) changes to lost (left) and gained (right) areas between 1985 and 2015, as assessed by a Variation Partitioning Analysis; residuals are shown in grey. Nonsignificant results are not shown.

analyses uncovered the highly detrimental effect of hunting on the Chacoan peccary in the Chaco. In fact, large areas of both high and low habitat suitability suffered from high hunting pressure, constituting more than 75% of total suitable areas both in 1985 and 2015. By contrast, areas with low hunting pressure were almost always associated with, core habitat areas, mainly inside large protected areas in Bolivia and Paraguay. This highlights the huge importance of considering hunting pressure when evaluating the current and potential distribution of threatened species, when seeking to understand the conservation status of species and when developing conservation plans (Rios et al., 2021; Sreekar et al., 2015). Similarly, our work highlights the danger of disregarding hunting pressure, as this would lead to a massive overestimation of suitable habitats and a possible misattribution of pressure to other threats, which in turn could lead to misguided or ineffective conservation interventions (Romero-Muñoz et al., 2020; Symes et al., 2018). Considering the rapid growth of attractive sinks (i.e. areas with high habitat suitability _and_ high hunting pressure) at the expense of core areas between 1985 and 2015 (Figure 4c), our study bolsters the need for improved

enforcement to combat illegal hunting (Keane et al., 2008; Romero-Muñoz et al., 2020), for promotion of sustainable wildlife use (Altrichter, 2005; Ingram et al., 2021) and for expanding protected areas and implementing corridors between them (Nori et al., 2016; Woodley et al., 2019).

Our study also provides further evidence that hunting pressure interacts with land change in synergistic ways (Gallego-Zamorano et al., 2020). For instance, agricultural expansion typically leads to the construction of roads, which grants hunters access to formerly inaccessible areas, and generally increases the interface between hunters and wildlife (Benítez-López et al., 2017, 2019; Saldivar-Bellassai et al., 2021). As we show for the Chacoan peccary, such situations are recurrent in the Chaco, where the habitat for many other mammals has been degraded or lost due to the combined effect of hunting and land conversion (Benítez-López et al., 2019; Romero-Muñoz et al., 2020). Recent research showed that agricultural expansion alone can lead to the Chacoan peccary's rapid local extinction (Camino et al., 2022). Here, we assessed the impact of three threats—land conversion, hunting and climate change—to

show that, in the last decades, most lost and degraded areas were due to the co-occurrence of all three threats (Figure 5).

Interestingly, the effects of the interaction between climate change and other threats were not always negative. Range expansion as a consequence of climate change has been documented for other large mammals, but typically only for high-latitude species for which warming leads to better habitat conditions (e.g. Dawe & Boutins, 2016). Here, we reveal that changing rainfall patterns can have a major compensatory effect in dry environments, mitigating the impact of habitat degradation. However, it remains unclear as to what extent the Chacon peccary would be able to exploit these opportunities. Species must track suitable habitat, yet the dispersal capacity can be limiting, particularly where species must traverse human-dominated areas (Ghoddousi et al., 2021; Schloss et al., 2012). This is a common situation in the Humid Chaco, where most new suitable habitat areas emerged. Importantly, our analyses do not account for dispersal limitations and thus, for the species' ability to make use of improved habitat conditions outside their current range. Future explorations using mechanistic models (e.g. individual-based population models; Fordham et al., 2021), could help to disentangle the importance of mortality during dispersal to understand whether new suitable habitat has the potential to mitigate threats in the Chacoan peccary's current range. We note recent records of the Chacoan peccary in the Humid Chaco of Paraguay (unpublished data—AG), including evidence of reproduction, showing that Chacoan peccaries may indeed be able to colonize these emerging suitable areas.

We provide a simple and robust framework to disentangle the individual and combined effects of three major threats—land conversion, hunting pressure and climate change—on the distribution of threatened species over a 30-year period. For the Chacoan peccary, we found widespread interactions among all three threats. Our approach can easily be applied to a wide range of species to assess the geographic patterns of threats they endure and to partition their impacts. Still, we caution that some limitations should be recognized. First, we acknowledge that different SDM algorithms can yield different model projections (Peterson et al., 2011) and we used only one algorithm here. Second, our hunting model shows general patterns of hunting pressure, but hunting pressure may locally vary according to variables not considered here (e.g. tenure). Lastly, our Variation Partitioning Analysis, indicated additive, though not necessarily synergistic (i.e. amplifying) impacts since threats may simply co-occur (Peres-Neto et al., 2006). More mechanistic models (e.g. population viability analyses) could help to further disentangle synergistic effects.

Land-use change, overexploitation and climate change are threatening biodiversity on a massive scale across the globe. Conservation policy-making, planning and action must urgently move beyond assessing threats in isolation, to a more holistic assessment of interactions (Brook et al., 2008; Geary et al., 2019). An important component of this is to map multiple threats in space and time (Romero-Muñoz et al., 2020; Tulloch et al., 2015). Here we provide a simple and robust framework to do so. Our results echo those of other studies highlighting the overwhelming importance of hunting and also highlight the need for, and value of, protecting large swaths of forest in areas undergoing a land-cover change in order to safeguard forest-dependent species sensitive to human pressure, such as the Chacoan peccary. This is particularly urgent in the world's tropical and subtropical dry forests and savannas, which have historically been neglected by conservation planning and policy, which are weakly protected and which are currently experiencing high levels of habitat conversion.

CONFLICT OF INTEREST STATEMENT
The authors have no conflicts of interest.

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DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.kd51c5b93 (Torres et al., 2023).

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BIOSKETCH

Ricardo Torres has a broad interest in biogeography and conservation and specifically in the conservation of South American vertebrates. He and the other authors collaborate in research aimed at the conservation of the biodiversity of the Gran Chaco region, a global hotspot of deforestation and defaunation.

Author contributions: RT and TK conceived the ideas and wrote the article, RT curated the data and performed the analyses, MB developed the land-use maps, ARM developed the hunting pressure models, RT, MA, GIB, MC, JMCK, JLC, RLC, JD, MG, AJG, LL, LM, NNN, VQ, SS, DT, JT, MV, RBW and AY provided the Chacoan peccary occurrence data, all authors reviewed and edited the article.

SUPPORTING INFORMATION

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

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