Animal Conservation

ORIGINAL RESEARCH

Habitat Loss and Overexploitation Subordinate Climate Change as the Main Threats to the Southern Three-Banded Armadillo in the Threatened South American Chaco

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ABSTRACT

Biodiversity in many regions is declining due to multiple extinction drivers, with habitat loss, overexploitation, and climate change often considered among the main ones. Understanding how biodiversity changes with these drivers is crucial for designing effective conservation strategies. The 1.1 million km^2 South American Chaco is one of the ecosystems facing the highest deforestation levels worldwide, but also high exploitation and changes in weather patterns due to global climatic changes. The southern three-banded armadillo (*Tolypeutes matacus)* is endemic to this biome, where it is commonly hunted. Additionally, due to its rudimentary endothermic control system, it is susceptible to climatic changes. Using ecological niche modeling (ENM) and threat index mapping, we assessed the potential impacts of climate change, habitat loss, and overexploitation on this species. Our findings suggest that, although climate change may expand the range of suitable habitats for the armadillo in the future, the current and intense threats from overexploitation and habitat degradation are likely to undermine these potential opportunities. Immediate action is required to address these pressing issues and halt the decline of the species' population. The findings underscore the necessity for integrated conservation strategies that address multiple threats simultaneously and inform policy measures. These strategies can serve as a model for other species and regions facing similar conservation challenges, ensuring the effective allocation of limited conservation resources and guiding comprehensive approaches to biodiversity preservation.

RESUMEN

La biodiversidad en muchas regiones está disminuyendo debido a múltiples factores de extinción, entre los cuales la pérdida de hábitat, la sobreexplotación y el cambio climático suelen considerarse como los principales. Comprender cómo varía la biodiversidad ante estos factores es crucial para diseñar estrategias de conservación efectivas. El Chaco Sudamericano, con una extensión

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de 1,1 millones de km^2, es uno de los ecosistemas que enfrenta los niveles más altos de deforestación a nivel mundial, además de una intensa explotación y cambios en los patrones climáticos debido al cambio climático global. El mataco bola (*Tolypeutes matacus*) es endémico de este bioma, donde es comúnmente cazado. Además, debido a su rudimentario sistema de control endotérmico, es particularmente vulnerable a los cambios climáticos. Utilizando modelos de nicho ecológico (ENM) y mapas de índices de amenaza, evaluamos los posibles impactos del cambio climático, la pérdida de hábitat y la sobreexplotación sobre esta especie. Nuestros resultados sugieren que, aunque el cambio climático podría expandir el rango de hábitats adecuados para el armadillo en el futuro, las amenazas actuales e intensas derivadas de la sobreexplotación y la degradación del hábitat probablemente socaven estas oportunidades potenciales. Se requiere una acción inmediata para abordar estos problemas urgentes y frenar el declive de la población de la especie. Los hallazgos resaltan la necesidad de estrategias de conservación integradas que aborden múltiples amenazas de manera simultánea e informen las medidas de política. Estas estrategias pueden servir como modelo para otras especies y regiones que enfrentan desafíos de conservación similares, garantizando una asignación efectiva de los recursos limitados de conservación y guiando enfoques integrales para la preservación de la biodiversidad.

1 | Introduction

Biodiversity is increasingly threatened by habitat loss, overexploitation, and climate change, which often interact and amplify their impacts (Tilman et al. 2017). As human populations expand, natural ecosystems are converted into agricultural and urban areas, leading to habitat degradation and species decline (Brooks et al. 2002; Butti et al. 2022). At the same time, hunting and wildlife trade drive many species toward extinction (Rosser and Mainka 2002), while climate change disrupts ecosystems and alters species distributions worldwide (Malhi et al. 2020; Préau et al. 2022). These threats rarely act in isolation; for example, habitat fragmentation can limit species' ability to shift their range in response to climate change, while overexploitation can reduce dispersal by increasing mortality (Bellard et al. 2012; Botkin et al. 2007). Identifying where and how these pressures overlap is crucial for conservation, particularly for some regions experiencing rapid land-use change (Bleyhl et al. 2015; Romero-Muñoz et al. 2019).

One such region is the South American Chaco, a woodland savanna that contains the largest continuous tropical and subtropical dry forest globally (Kuemmerle et al. 2017; Morrone 2017). This vast mosaic of woodlands and savannas faces one of the highest deforestation rates globally, driven by agricultural expansion that rapidly converts forests into croplands and pastures (Baumann et al. 2022; Curtis et al. 2018). In addition, many local and external actors practice hunting for multiple purposes, which contributes to defaunation Altrichter (2006); Periago et al. (2015). Previous research has assessed the spatially explicit effects of these threats over specific species (Romero-Muñoz et al. 2019) and the mammal community (Romero-Muñoz et al. 2020, 2021), alongside the impact of recent climatic changes in this region (Torres et al. 2023). However, studies that evaluate the effects of these threats while incorporating possible future climatic changes are still lacking.

This critical scenario has severe consequences for many Chacoan species (Nori et al. 2016). One such species is the southern three-banded armadillo, *Tolypeutes matacus* (Desmarest 1804), whose populations have been suffering declines (Ferreiro et al. 2019, 2025) which have led to documented local extinctions, for example, in Catamarca Province, Argentina Noss et al. (2014); Silverio Reyes et al. (2014). This armadillo has the unique ability to roll into a ball when threatened, protecting its whole body with the external bony shield or carapace (hence its common name "mataco bola" or "quirquincho bola") (Figure 1a). However, this defense strategy makes the species an easy prey for humans, and it has become one of the most hunted mammals in the Chaco (Figure 1b) (Altrichter 2006). Also, it is susceptible to habitat degradation, having low tolerance for agricultural land-use shifts (Noss, Superina, & Abba, 2014). These two factors, in addition to its low reproductive rates (only a cub per year), are the main causes of the significant decline of their populations,

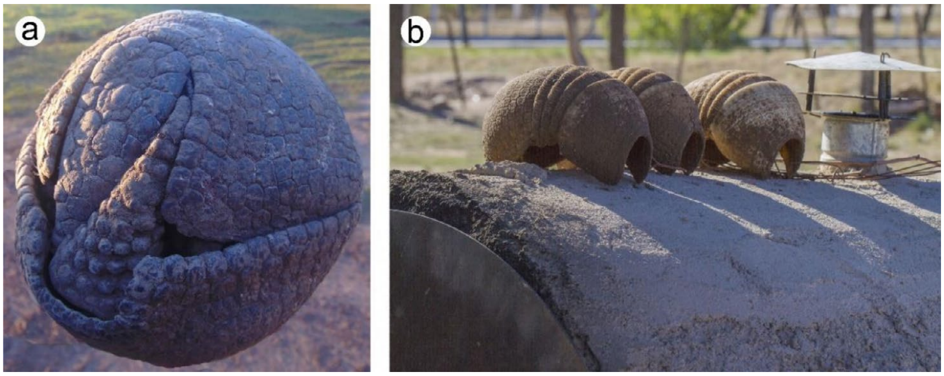

FIGURE 1 | (a) Defensive behavior of the southern three-banded armadillo (*Tolypeutes matacus*) rolling into a ball with a perfect fit between the cephalic and caudal shield (Photography: Alejandro Manuel Ferreiro). (b) Remains of *T. matacus* shells on a traditional clay oven after they were hunted and cooked by locals in San Luis Province (Argentina) (Photography: Esteban Soibelzon).

resulting in its classification as Near Threatened by the IUCN, with experts suggesting that it is close to Vulnerable (Noss, Superina, & Abba, 2014). Additionally, as a Xenarthran, this armadillo exhibits imperfect thermoregulation (McNab 1985), leading to behavioral adaptations in response to atmospheric temperature changes, such as favoring forested habitats and adopting more diurnal, shorter activity patterns under extreme temperature conditions (Attias et al. 2018). Also, phylogeographical and macroecological evidence indicates that the species has been susceptible to past climatic changes with warmer periods showing the expansion of suitable areas (Ferreiro et al. 2022, 2024). These features suggest that current climatic changes may have an impact on its geographic range, but, to date, no studies have assessed it. Overall, this species represents a suitable model to evaluate the synergetic effects of overexploitation, habitat loss, and climatic change.

Given this scenario, protected areas play a crucial role in mitigating climate change impacts and preventing further habitat loss and hunting. As key components of global conservation strategies, protected areas help maintain biodiversity by preserving intact habitats, serving as refugia, and facilitating species range shifts in response to changing climatic conditions (CBD; https://www.cbd.int/sp/targets/). However, since protected areas are geographically fixed, they may not always align with the future distribution of species as they track shifting climatic niches (Araújo et al. 2011); (Batllori et al. 2017). Expanding and strategically managing protected areas networks, particularly in regions undergoing rapid land-use change, is essential to ensure the long-term conservation of vulnerable species like *T. matacus*. Connectivity between protected areas and surrounding landscapes can enhance species persistence by providing stepping stones for movement and securing climate refugia where range shifts are not possible (Williams and Jackson 2007).

To better understand and analyze these patterns and processes, ecological niche modeling (ENM) offers a powerful tool by combining distribution data and environmental variables to infer the potential distribution for species (Peterson et al. 2011). Using models of future scenarios of climate change, ENM facilitates the inference of potential changes in range boundaries and suitable areas for species (Anderson 2013). To date, ENM has been widely used to assess the impacts of threats to biodiversity, including future climate change (Aguiar et al. 2016; Lima-Ribeiro et al. 2017), and habitat loss (Romero-Muñoz et al. 2020; Torres et al. 2023). Recent advances in remote sensing have further enhanced ENM, enabling more accurate reconstructions of land-use changes and more precise inferences about habitat destruction and its impact on species (Baumann et al. 2022; Hansen et al. 2013). Additionally, novel spatial modeling methods, such as hunting pressure models, synthesize data from local studies to quantify and map the spatial effects of hunting (Benítez-López et al. 2017, 2019). By identifying the spatial footprints of each threat, these tools provide valuable insights for assessing conservation efforts, including the effectiveness of protected areas in mitigating biodiversity loss Nori et al. (2016).

In this work, we employed ENM to assess the spatial impacts of future climate change and habitat loss, and developed hunting pressure models to evaluate the effects of overexploitation across the South American Chaco. By focusing on *Tolypeutes matacus*, an exploited, temperature-dependent mammal endemic to one of the most threatened biomes globally, we aim to answer: (1) How may the distribution range of *T. matacus* change under future climate change? (2) What are the spatial footprints of climate change, habitat loss, and overexploitation on this species, and how may the interaction of these factors enhance or constrain their effects? (3) How do these threat footprints overlap with the current network of Protected Areas?

2 | Material and Methods

2.1 | Study Area

Our research is centered on the South American Chaco, an expansive region characterized by vast plains occasionally interrupted by lower mountains in the west (Morrone 2017). The climate is semiarid, featuring significant temperature fluctuations both annually and daily. Rainfall exhibits a pronounced east–west gradient, with over 1200 mm in the east and as little as 400 mm in the southernmost part of the Dry Chaco, primarily concentrated during the summer months. The predominant vegetation comprises dry, broad-leaved, thorny forests, and shrublands, but some areas are covered by natural grasslands and seasonally flooded savannas (Grau et al. 2015; Prado and Gibbs 1993).

2.2 | Modeling Future Climatic Change Effects

We modeled climatic suitability for *T. matacus* under current and future scenarios to assess global warming impacts on its distribution. We obtained presence records from Ferreiro et al. (2022), which compiled data from field trips, specimen collections, literature e.g., Vizcaíno et al. (1995); (Soibelzon et al. 2010; Torres and Jayat 2010; Abba and Vizcaíno 2011; Feijó et al. 2015; Santos et al. 2019), and open databases (GBIF; https://doi.org/10.15468/dl.yn92aj). We sourced bioclimatic variables at 30 arc-sec resolution (~1 km^2) from CHELSA ver. 2.1 (Karger et al. 2017), representing averages from 1980 to 2010. We excluded variables combining precipitation and temperature (Bio 8, 9, 18, and 19) due to spatial discontinuities unlikely to hold biological significance (Booth 2022). We restricted presence records to 1980–2015 to align temporally with the predictors. To reduce sampling bias and overfitting, we applied spatial filtering, retaining only one record per 10 km to avoid overrepresentation of densely sampled areas. We evaluated predictor correlations (Figure S1) and retained uncorrelated, biologically meaningful variables (see Table S1 for details). We assessed multicollinearity using Pearson correlations on 50,000 random points, excluding one variable from each pair with $|r| > 0.7$ based on ecological relevance and spatial patterns. The final predictor set included: annual mean temperature (Bio 1), temperature seasonality (Bio 4), annual precipitation (Bio 12), and mean precipitation of the driest month (Bio 14). We defined the calibration area using a 150 km buffer around the minimum convex polygon of occurrences to include potential dispersal zones while excluding ecologically dissimilar regions, and sampled 10,000 background points within it. As models will be transferred to future scenarios, we performed a spatial partition of the data which allows evaluation of model transferability (See Figure S2).

We calibrated niche models using the Maximum Entropy algorithm (Phillips et al. 2017) with the cloglog output, and different combinations of regularization multiplier values (0.1, 0.25, 0.5, 1, 2, 5, 10) and feature classes (linear, quadratic, and product). We excluded combinations involving threshold or hinge features, as these features tend to overfit presence data, capturing noise and underestimating the species' broader environmental tolerance (Merow et al. 2013). Best parameter combinations were selected using the true skill statistic (TSS) metric based on a sensitivity-based threshold (sensitivity = 0.9). We selected this threshold to ensure accurate predictions by prioritizing the inclusion of most presence points (90% of them) while reducing overprediction, which is essential for identifying suitable areas critical for conservation. We also calculated area under the curve (AUC), and omission rate (OR) to evaluate model performance.

We projected the best model to current and future scenarios (2071–2100) under four shared socioeconomic pathways (SSPs: 1–2.6, 3–7.0, 5–8.5) using five global circulation models (GCMs: GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, UKESM1-0-LL). We used a 400 km buffer around the minimum convex polygon that includes occurrence data for projections to assess potential range expansions, providing a conservative area large enough to include all plausible climatically suitable habitats beyond the known range without being unrealistically large. We thresholded maps using the 0.9 sensitivity-based threshold to identify areas of species absence. We performed ensemble and uncertainty analyses across GCMs for each SSP, calculating mean suitability and standard deviation maps to represent central tendencies and spatial uncertainty (Araújo and New 2007). We evaluated extrapolation risk conditions—that is, areas with environmental values outside the calibration range—using the multivariate environmental similarity surface (MESS) metric Elith et al. (2010), as implemented in the dismo package (Hijmans et al. 2024). We conducted data preprocessing, niche modeling, and projections using the terra (Hijmans 2022) and flexSDM (Velazco et al. 2022) packages, and maps were plotted using the tmap package (Tennekes 2018).

2.3 | Modeling Habitat Loss

We modeled habitat suitability for 1985 and 2015 and then compared both spatial ranges to quantify habitat loss. Based on the assumption that habitats where occurrences were found in recent periods remained favorable in previous periods within the timespan studied, we generated an ENM using occurrence records from 1980 to 2015 and landscape predictors from 1985. We acknowledge that this approach relies on the assumption of niche conservatism and may not fully account for potential shifts in habitat preferences or landscape dynamics over time. However, given the limited availability of historical occurrence data (i.e., previous to 1995), this method provides a practical and ecologically reasonable framework for assessing long-term habitat changes. Furthermore, climate change and habitat loss were modeled independently, as these threats require different datasets, spatial resolutions, and historical coverage that cannot be fully aligned within a single temporal framework.

We used the same presence records as in the climatic models. Predictors included four landscape variables at 250 m resolution derived from MapBiomas-Chaco Project, Collection 5.0 (MapBiomas 2023). These included the proportional cover of woodlands, grasslands, pastures, and croplands (see Table S2 for the corresponding MapBiomas categories). These variables were selected to capture key habitat components relevant to *T. matacus*, considering its association with natural vegetation and potential impacts from agricultural expansion. Proportional cover was calculated within a 3 km radius (25 × 25 pixel moving window) around each cell. We also included a sand content layer from SoilGrids (Hengl et al. 2017; 0–5 cm depth), to reflect surface soil conditions critical for burrowing and foraging. This variable was assumed to remain constant across the studied periods, acknowledging the relative stability of soil texture over time.

We assessed collinearity among variables by estimating the Pearson correlation coefficient (values shown in Figure S3). Despite finding a high correlation between woodland and grassland, we retained both variables as we considered they could enhance model predictions. Presence records were spatially thinned with a 10 km distance. We sampled 10.000 background points that were randomly allocated across the study area (defined as the Chaco biome *sensu* Morrone (2017)). To assess model performance, we implemented repeated k-fold cross-validation, partitioning the dataset into four folds with five replicates. The same modeling algorithm, parameter settings, and sensitivity-based threshold (sensitivity = 0.9) used in the climatic ENM were applied. We generated maps to visualize habitat dynamics between 1985 and 2015 by plotting areas of stable suitable habitats, habitat loss and habitat gain, based on binarized maps with the sensitivity-based threshold for each period.

2.4 | Overexploitation

We estimated overexploitation using the spatial hunting pressure model developed for the Chaco region (Romero-Muñoz et al. 2020), adapted specifically for *T. matacus*. This model combines a binomial component predicting local extirpation and a Gaussian component estimating abundance declines where populations persist (Benítez-López et al. 2019). The model was parameterized using three predictors: distance to hunter access points (settlements and roads) and human population density (derived from data spanning 1985–2015, as proxies for hunting risk), plus the species mean adult body mass (1.2 kg; Wilman et al. 2014). In our application, we used the *T. matacus*-specific parameterization from the Neotropical mammal framework re-fitted by Romero-Muñoz et al. (2020). This framework integrates species traits (e.g., body mass) and adjusts for differences across studies and geographic contexts in order to isolate the species-specific response, thereby providing estimates tailored to *T. matacus*. The resulting index ranges from 0 (no decline in abundance due to hunting) to 1 (total local extirpation) and represents hunting pressure intensity.

2.5 | Threats Intensity

To assess the spatial effect of threats affecting *T. matacus*, we integrated habitat loss and overexploitation into a single spatial framework using a weighted overlay approach (Orgiazzi et al. 2016). This approach was selected as it integrates multiple threats while accounting for their relative impacts, allowing the identification of areas under the highest cumulative pressure. Climate change projections suggested an overall expansion of suitable habitat for the species; therefore, we excluded this factor from the combined threat model to avoid overestimating its impact relative to other, more immediate threats. To generate the spatial footprints of threats, we first standardized the habitat loss and overexploitation layers to comparable scales. The habitat loss footprint was derived from an environmental change model comparing 1985 and 2015, where both lost habitat and stable unsuitable areas were reclassified as vulnerable to future degradation. A smoothing function (10 km moving window) was applied to capture edge effects and the potential spread of habitat modification, particularly due to agricultural expansion, the main driver of land-use changes in the Chaco. This approach allowed us to reflect not only past habitat loss but also areas at higher risk of future conversion due to their proximity to modified or unsuitable lands. Finally, we combined the threat layers using a weighted overlay method, assigning 60% weight to habitat loss—given its predominant role in shaping landscape transformation—and 40% weight to overexploitation, which, although more localized, still represents a significant pressure on the species due to its ease of capture.

2.6 | Representativeness in Protected Areas

To evaluate the effectiveness of the protected area network in conserving *T. matacus* across the Chaco, we estimated two representativity metrics that quantify the amount of suitable habitat within protected areas: (1) the Total Suitable Area (TSA) within protected areas (in km^2) and (2) the Proportion of Suitable Area (PSA) protected, calculated as the percentage of the total suitable habitat within the Chaco that is located within protected areas. These metrics were derived from the thresholded climatic suitability surfaces generated by our ENMs for the current conditions and three future scenarios (SSP 1–2.6, SSP 3–7.0, and SSP 5–8.5). We used the thresholded suitability surface described in the Modeling Future Climatic Change Effects subsection, where values above the threshold retained their suitability values. All climatic suitability layers were cropped and masked using the Chaco biome polygon Morrone (2017). Raster processing for metric calculation was conducted using the `terra` package, and the representativity metrics were plotted across different scenarios using the `ggplot2` package (Wickham 2016). To ensure consistency in spatial resolution, all layers were resampled using a bilinear interpolation method to match the resolution of the climatic layers (30 arc sec). All analyses described in this and the previous Methods section were conducted in R version 4.4.1 (R Core Team 2023).

3 | Results

3.1 | Climate Change Impacts

The best-performing Maxent model (LQP features, regularization multiplier 0.25) showed adequate performance (TSS = 0.298, AUC = 0.747, and Omission Rate = 0.118). Full performance metrics for all models tested are presented in Table S3. Under future climate scenarios, suitable areas for *T. matacus* are projected to expand with increasing temperatures (Figure 2). Currently, suitable habitat covers approximately 1,171,000 km^2. Projections indicate an expansion to an average of 2,007,000 km^2 under low-emission scenarios and up to 3,961,000 km^2 under high-emission scenarios (Table S4). The most notable range expansion is projected toward northern regions, with high-emission scenarios also predicting significant expansion westward and eastward. In contrast, the western limit of the distribution remains stable across time periods and scenarios, likely constrained by the geographic barrier of the Yungas Forest. Uncertainty among GCMs is highest at the distribution edges, particularly along the northern and eastern borders where the greatest expansions are predicted (Figure S4). Similarly, MESS analysis indicated that these northern and northwestern expansion areas also present non-analogous climatic conditions relative to the calibration area, warranting caution in their interpretation (Figure S5).

3.2 | Habitat Loss

Our analysis revealed a decrease in suitable habitat for *Tolypeutes matacus* between 1985 and 2015 (Figure 3), with Argentina experiencing the most significant habitat loss. Suitability maps based on land use/land cover (LULC) and soil variables indicated that suitable areas for the species were primarily concentrated in the western regions of the Chaco biome in Argentina. Additionally, some small areas in the southern portion of the biome showed an apparent gain in suitability. However, these gains may reflect either model limitations or habitat modifications that do not necessarily benefit the species. While such discrepancies highlight potential trade-offs in our modeling approach, they should be carefully considered in future analyses.

3.3 | Threats Intensity

Threat intensity maps (Figure 4) indicated that 40.75% of the suitable habitat within the Chaco biome is currently experiencing high levels (threat intensity above 0.5) of the threats analyzed in this study. Habitat loss emerged as the most intense and widespread threat, particularly along the edges of the species' range, with Argentina being the most affected country (Figure 4a). This pattern aligns with extensive land-use changes, especially in regions with high agricultural expansion. Overexploitation exhibited the highest intensity in the southern and western borders of the Argentinean Chaco, as well as in localized patches within the Paraguayan Chaco (Figure 4b). These areas are known for their accessibility to human settlements and hunting pressures. The combined threat intensity map (Figure 4c) revealed regions in Argentina with particularly high cumulative pressure. These include the southern range of the Chaco, central Argentina, and the eastern portion of the southern Chaco, where deforestation rates have been notably high in recent years (MapBiomas 2023). These results underscore the importance of considering multiple threats when assessing the conservation status of *T. matacus*, as different pressures may interact and amplify their impact on the species.

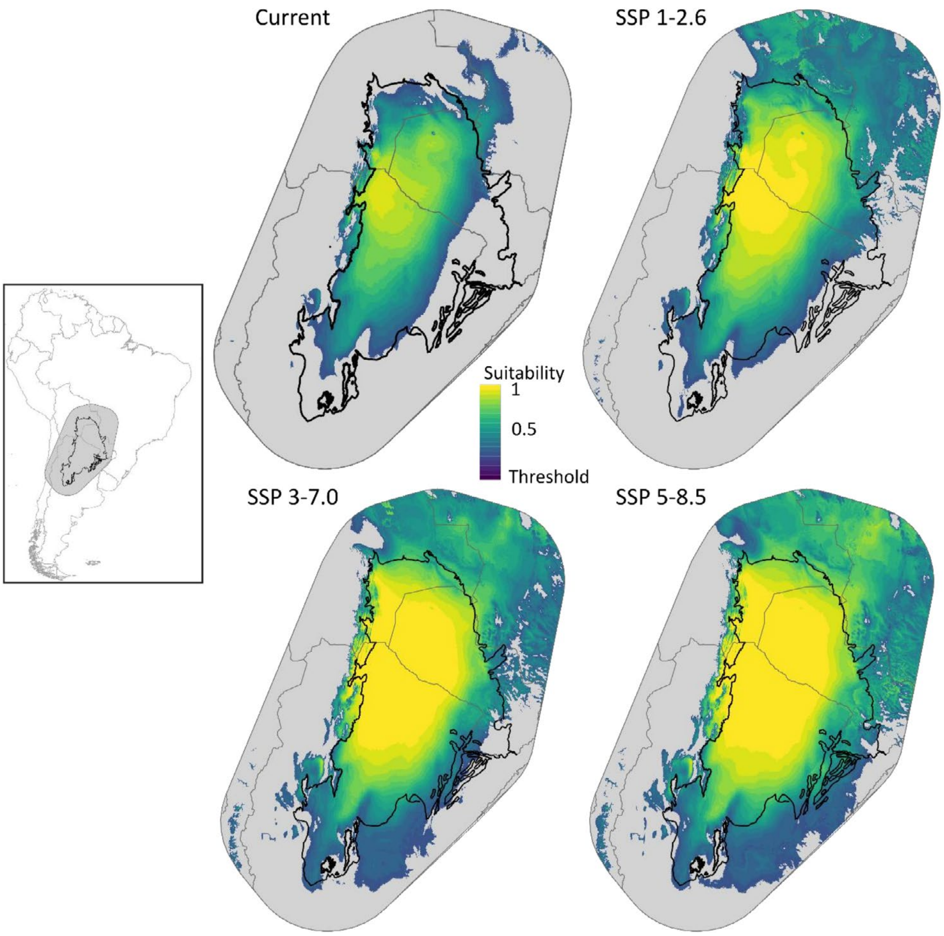

FIGURE 2 | Changes in climatic suitability for *T. matacus*, using thresholded suitability maps based on a sensitivity-based threshold (sensitivity = 0.9). The four panels represent current conditions and the average projections across global circulation models (GCMs) for three future (2071–2100) Shared Socioeconomic Pathways (SSP) scenarios. The inset map highlights in gray the area where models were projected, defined as a 450 km buffer around the minimum convex polygon enclosing the species' presence records. The Chaco biome Morrone (2017) is outlined in black.

3.4 | Representativeness in Protected Areas

Our analysis showed that out of the total suitable habitat for *T. matacus*, approximately 57,900 km^2 is currently under protection (Table 1). Future climate change scenarios suggest a potential expansion of suitable habitat within protected areas, with the total protected suitable area (TSA) reaching up to 66,000 km^2 under SSP 5–8.5, the scenario with the highest greenhouse gas emissions. However, despite this projected increase in absolute area, the proportion of suitable habitat within protected areas (PSA) is expected to decrease across all climate scenarios, from 6.8% under current conditions to 4.2%–5.4% in future projections, with lower values associated with higher emission pathways. This suggests that while more suitable habitat may become available within protected areas, its relative representation within the species' overall suitable range is expected to decline, highlighting ongoing conservation challenges.

4 | Discussion

We assessed the potential impact of future climate change, habitat loss, and overexploitation on the endemic southern three-banded armadillo (*Tolypeutes matacus*) in the South American Chaco. By modeling changes in the species' potential distribution, we found that future (2071–2100) climate change would increase the armadillo's suitable habitat, particularly in northern and eastern regions. However, despite projected future expansion, habitat loss and hunting between 1980 and 2015 have already reduced it. If these trends persist, the actual suitable area for the species will likely be smaller than predicted by climate change models alone. While *T. matacus* is currently underrepresented in the protected area network, future climate projections indicate an increase in the total suitable habitat within these areas. Nevertheless, the proportion of its habitat under protection is expected to decline, particularly under high-emission scenarios. This underscores the ongoing challenge of ensuring the long-term effectiveness of conservation efforts.

According to future ENM projections, the climatically suitable habitat for *T. matacus* is projected to expand between 2071 and 2100, increasing from 1,171,000 km^2 in current times to between 2,007,000 km^2 (low-emission scenarios) and 3,961,000 km^2 (high-emission scenarios). This projected expansion is largely concentrated in northern regions, with additional gains toward the east and south under higher emission scenarios. Although this may initially seem counterintuitive under the Thermal Tolerance Theory—which suggests that species are generally

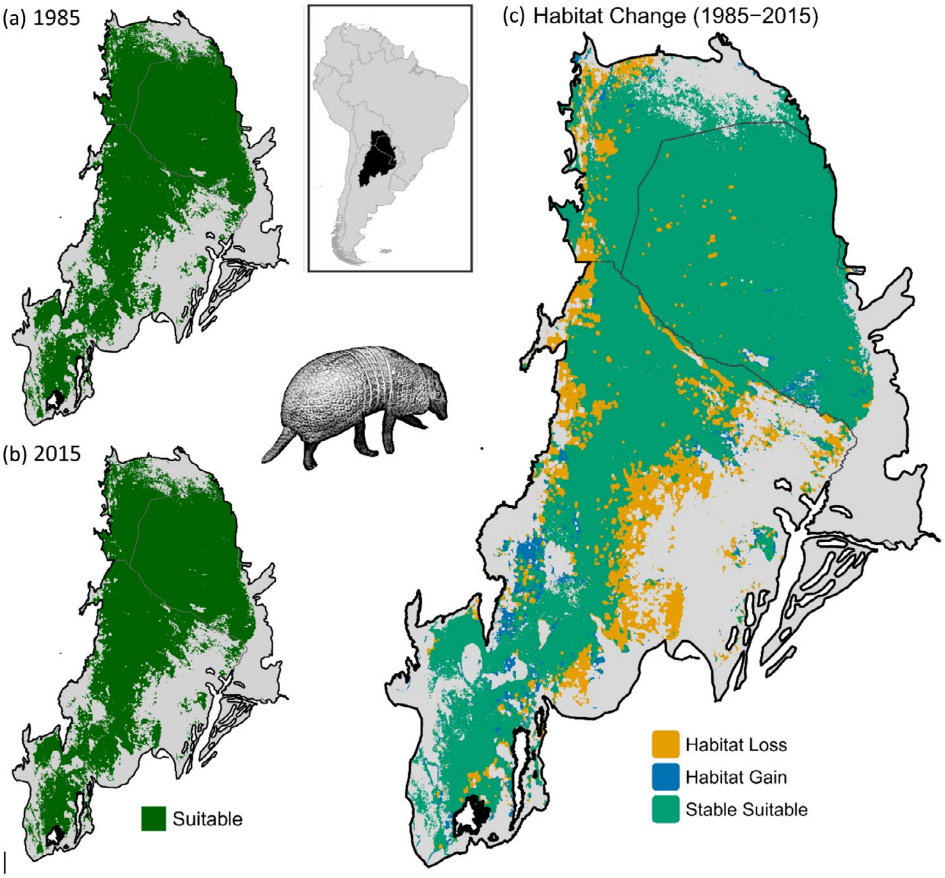

FIGURE 3 | Habitat suitability models for *T. matacus* in (a) 1985 and (b) 2015, based on land use/land cover and soil variables. (c) Spatial distribution of suitability changes, highlighting areas that were gained, remained stable, or were lost between 1985 and 2015.

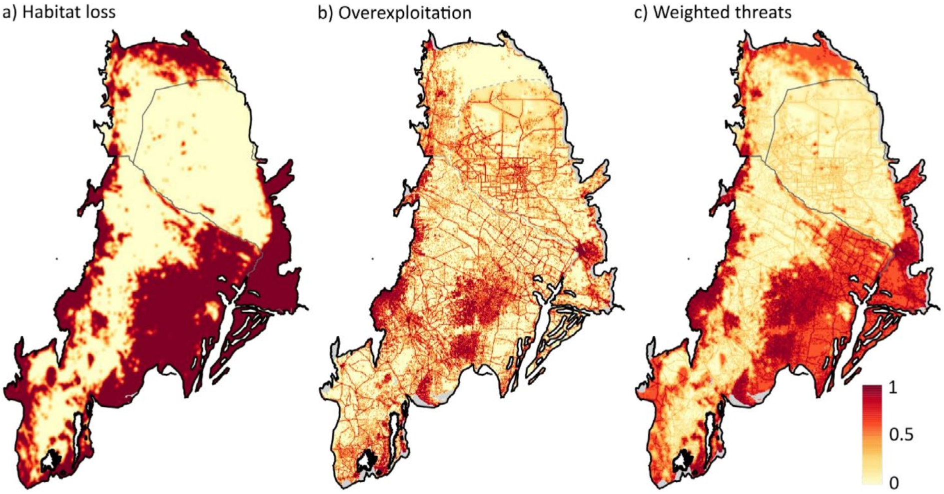

FIGURE 4 | Geographical distribution of threat intensity scores for *T. matacus*: (a) Habitat loss intensity, (b) Overexploitation intensity, and (c) Combined threat score, which integrates both threats with a higher weight assigned to habitat loss. Threat intensity values range from 0 (light yellow, low threat) to 1 (red, high threat).

more adaptable to cold than to heat (Araújo et al. 2013)—several factors may explain this pattern. First, historical evidence indicates that *T. matacus* has successfully adapted to past warming events, such as the transition from the Last Glacial Maximum (~20,000 years ago) to the Holocene Thermal Maximum (~6000 years ago) (Ferreiro et al. 2022). Second, building on this adaptive history, *T. matacus* may possess a broader thermal tolerance than previously assumed, allowing it to exploit new habitats under rising temperatures (Attias et al. 2018; McNab 1985). Third, future range expansions are predicted to occur in regions currently characterized by relatively higher precipitation and milder temperatures compared to the drier

TABLE 1 | Representativity of suitable habitat for *Tolypeutes matacus* within the network of protected areas under current and future climate scenarios, based on different Shared Socio-economic Pathways (SSPs). Representativity is summarized using two metrics: Total suitable habitat within protected areas (TSA, km^2) and percentage of suitable habitat under protection (PSA, %). Future projections represent multi-model averages across different Global Circulation Models (GCMs).

Scenario	TSA (km^2)	PSA (%)
Current	57,868	6.78
SSP 1–2.6	62,526	5.36
SSP 3–7.0	64,871	4.53
SSP 5–8.5	66,009	4.17

core of the Chaco, conditions that could help buffer the impacts of increasing temperatures. Similar climate-driven expansions have been observed in other mammals, particularly at higher latitudes where warming improves habitat suitability (Dawe and Boutin 2016; Paniw et al. 2021). In the Chaco, climate change between 1985 and 2015 has seemingly benefited the Chacoan peccary (*Catagonus wagneri* Rusconi, 1930), as altered rainfall patterns helped mitigate the impact of habitat degradation in dry environments (Torres et al. 2023). Altogether, these findings reinforce the notion that, as observed in other mammals, the responses of *T. matacus* to climate change are shaped not only by thermal tolerance and habitat shifts but also by species-specific ecological traits that may facilitate or constrain future range dynamics.

Despite this projected habitat expansion, the ability of *T. matacus* to colonize newly suitable areas remains uncertain. Higher uncertainty and extrapolation risk were detected in areas where the species would potentially expand. Moreover, dispersal capacity plays a key role in range shifts, and this species is considered to have low vagility, with small home ranges and limited mobility to overcome natural barriers such as watercourses or steep terrain (Attias et al. 2020; Barrientos and Cuellar 2003). Furthermore, a significant portion of the projected range expansion occurs in areas under extensive anthropogenic land use, particularly in degraded landscapes in the eastern, northern, and southern Chaco (MapBiomas 2023). Given the species' reliance on forested habitats to avoid extreme temperatures and its limited thermoregulatory capacity (Attias et al. 2018), the actual ability of the armadillo to establish populations in these newly suitable areas remains highly uncertain. Additionally, the presence of isolated habitat patches, even if climatically suitable, may not translate into occupancy due to dispersal limitations and reduced connectivity with core areas. Future research incorporating movement ecology data and fine-scale habitat assessments will be essential to determine whether these climate-driven expansions translate into actual range shifts.

Our findings indicate that habitat loss has significantly reduced suitable areas for *T. matacus* between 1985 and 2015, with Argentina experiencing the greatest declines, a pattern consistent with the widespread agricultural expansion observed in the region (Baumann et al. 2017; Fehlenberg et al. 2017). This trend is expected to continue, as global agricultural and urban expansion exerts increasing pressure on natural ecosystems and resources. Furthermore, unregulated land-use changes driven by climate change may exacerbate these impacts, particularly in agricultural sectors (Roy et al. 2022). Historical land-use analyses suggest that, if current climatic, socioeconomic, and biotechnological drivers persist, agricultural expansion will continue at the expense of Chaco forests, leading to further habitat loss in the future (Zak et al. 2008). These findings highlight the urgent need for science-based land-use policies to mitigate the negative effects of land conversion and promote long-term sustainability.

Threat intensity maps revealed that 40% of the remaining suitable habitat within the Chaco biome is currently exposed to high levels of anthropogenic threats, with habitat loss emerging as the most intense and widespread pressure, particularly in Argentina. Overexploitation was also a prominent threat, reaching peak intensity in the southern and western borders of the Argentine Chaco and in certain areas of the Paraguayan Chaco. In contrast, we detected an increase in suitability within parts of the Paraguayan Chaco, as well as in some isolated areas in the southern portion of the biome. However, these localized gains may not necessarily reflect actual improvements in habitat conditions for the species but rather model limitations or shifts in land cover that do not translate into higher habitat quality. This highlights the need for further validation through field assessments and finer scale habitat evaluations. The persistence of *T. matacus* in such a rapidly changing landscape depends on its ability to utilize these remaining suitable areas, emphasizing the urgency of implementing conservation measures to mitigate further habitat degradation. A limitation of our approach is the temporal mismatch among occurrence data, habitat loss estimates, climate projections, and exploitation risk layers. This inherent constraint of available datasets may introduce uncertainty when comparing or integrating outputs from different models. However, by modeling each threat independently within its most reliable temporal window, we aimed to maximize accuracy while still allowing qualitative comparisons across threats.

The overlap of habitat degradation and hunting pressures is particularly concerning, as their combined effects can intensify population declines. For example, deforestation not only reduces available habitat but also enhances access for hunters, increasing pressure on already fragmented populations (Romero-Muñoz et al. 2020). The combined effects of these pressures could lead to localized extinctions and further range fragmentation, particularly in areas with the highest hunting intensity (Peres 2001). Notably, these threats overlap with regions that are biodiversity hotspots and priority conservation areas, which suffer from both significant habitat alteration and inadequate protection (Feijó et al. 2022). In this sense, future conservation strategies should therefore address both habitat connectivity and direct threats simultaneously. Recommended actions include strengthening and expanding protected areas, establishing ecological corridors to counteract fragmentation, and improving law enforcement to curb illegal hunting (Keane et al. 2008; Romero-Muñoz et al. 2020). Given the species' reliance on forested habitats for thermoregulation (Attias et al. 2018), targeted conservation efforts should prioritize areas with remaining native forest cover, particularly in the southernmost portion of its range, where genetic diversity is already reduced (Ferreiro et al. 2024). Furthermore, sustainable conservation strategies must incorporate local communities, as hunting is primarily driven by subsistence needs. Engaging local populations through education, incentive-based conservation programs, and participatory management approaches has proven effective in fostering compliance and promoting sustainable resource use (Challender and MacMillan 2014). Implementing such measures across both high-risk and surrounding lower threat areas will be key to ensuring the long-term persistence of *T. matacus* and preserving the ecological integrity of the Chaco biome. As habitat loss and overexploitation remain the predominant threats in the region (Nori et al. 2016), these efforts would not only benefit this species but also contribute to broader biodiversity conservation goals in the Chaco.

Currently, only 6.8% of *T. matacus*' suitable habitat is protected, underscoring the urgent need for expanded conservation efforts. This contrasts with a previous estimate of nearly 12%, (Ferreiro 2022; Ferreiro et al. 2025), which was calculated at a pixel level using ENMs combining climatic, soil, and other predictors. In our study, the 6.7% estimate reflects the area-level representativity of currently and potentially suitable habitat based on updated ENMs, different climate datasets, and modeling procedures refined during peer review. The discrepancy thus arises from differences in both the suitability metrics and methodological approaches. Our results indicate that while the total area of suitable habitat within protected areas (TSA) may increase under future climate scenarios, the proportion of suitable habitat under protection (PSA) is projected to decline to 4.2%–5.4%. Thus, while climate change might create additional areas of potential habitat, these areas will largely remain unprotected, thereby diminishing the overall effectiveness of the current protected area network. Protected areas in the Chaco have historically played a vital role in conserving biodiversity, serving as refugia for many species (Nori et al. 2016). However, their limited extent and spatial configuration currently restrict their capacity to maintain connectivity and support long-term species persistence under rapid environmental changes. Enhancing connectivity between reserves is essential to facilitate gene flow and allow species to shift their ranges in response to climate change (Di Blanco et al. 2022). In light of these findings, it is imperative to strategically expand and interconnect reserves—particularly in central and northern Argentina and southeastern Bolivia—to ensure that the protected area network can effectively safeguard suitable habitat for *T. matacus* in the future.

The conservation challenges for *T. matacus* differ from those of its congener *T. tricinctus*, a species restricted to the Caatinga and Cerrado biomes of Brazil that, despite facing similar threats such as habitat loss and hunting, exhibits distinct ecological and conservation dynamics. While *T. tricinctus* persists in human-modified landscapes under moderate hunting and habitat loss (Magalhães et al. 2022), *T. matacus* faces severe declines in Argentina due to intense deforestation and hunting pressure. Additionally, *T. tricinctus* populations are closely associated with core savanna and grassland areas in the Caatinga and Cerrado, making connectivity a key conservation priority (Feijó et al. 2023). In contrast, *T. matacus*'s future range expansion may lead to lower representation within protected areas, further complicating conservation efforts. These differences underscore the need for tailored conservation strategies addressing species-specific ecological and landscape contexts.

In summary, despite the projected expansion of climatically suitable habitat under future warming, ongoing deforestation and hunting could limit *T. matacus*'s ability to colonize these areas. The species' low dispersal capacity, combined with increasing human pressures at its range edges, creates significant barriers to natural shifts and restricts its potential to establish new populations. The overlap of these pressures suggests cumulative negative effects that could accelerate fragmentation and localized extinctions, further destabilizing the Chaco ecosystem. This highlights the urgency of addressing habitat degradation and hunting as primary threats to *T. matacus* in the South American Chaco. It underscores the need for conservation strategies that tackle habitat protection and overexploitation simultaneously, ensuring both the persistence of populations and their connectivity across the landscape. Expanding protected areas in intact habitats and fostering community involvement through participatory, incentive-based conservation will be crucial. Our findings reinforce the importance of multidimensional threat assessments for effective resource allocation and conservation planning. As the Chaco experiences rapid environmental change, integrating ecological, socio-economic, and landscape-level approaches will be key to adaptive strategies that safeguard biodiversity from complex, interconnected threats.

Author Contributions

A.M.F., A.R.-M., M.B.C., and E.S. contributed to the study conception. Data collection and analysis were performed by A.M.F., A.R.-M., E.A.I., and E.R. The first draft of the manuscript was written by A.M.F. and E.A.I. contributed substantially to revisions. All authors read and approved the final manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data used for the analysis are properly cited throughout the manuscript. Scripts used to perform the analysis are available in the GitHub repository, https://github.com/aleferreiro/Spatial_threats_Tolypeutes_matacus.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supporting Information