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Diversity Loss and Homogenization in Snake Communities in a Deforestation Hotspot

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ABSTRACT

Aim: Agricultural expansion into tropical forests causes massive biodiversity loss. However, existing knowledge about these losses is heavily biased towards rainforests, as well as towards birds and mammals. Focusing on the South American Chaco, a global hotspot of deforestation and defaunation, we assessed how agriculture-driven deforestation impacted snake distribution and, thereby, snake communities.

Location: Chaco ecoregion.

Methods: We compiled a rich snake occurrence dataset and used it together with satellite-based, annual land-cover maps for 1985–2020 to build time-calibrated species distribution models. This yielded temporally and spatially detailed reconstructions of snake distributions, allowing us to identify winners (increase in suitable habitat) and losers (habitat decline) of land-use change. Further, we assessed changes in geographic patterns of taxonomic, functional, and phylogenetic diversity.

Results: We could model 72 of 142 snake species occurring in the Chaco. Among these, surprisingly, we identified more winners (35) than losers (14). We caution, however, that we were unable to model many specialist species as these were data-deficient. Among functional guilds, semiarboreal and semifossorial species were among the most negatively affected, while most of the winning species were terrestrial, generalist species. Importantly, although some species gained habitat, our analyses revealed a general decline in taxonomic, functional, and phylogenetic snake diversity in the Chaco (more than 75% of all snake communities), suggesting biotic homogenisation.

Main Conclusion: Our study uncovers an erosion of snake diversity due to agricultural expansion in the Chaco, with many snakes likely being more threatened than currently appreciated. At the community level, land-use changes and habitat loss are

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driving biotic homogenisation across snake communities, with potentially major knock-on effects on ecosystem functioning and integrity as key functional snakes are lost. Overall, our study underscores the urgency for conservation planning and action in the world's tropical dry forests, many of which are changing rapidly.

1 | Introduction

Global biodiversity is in decline, primarily due to the degradation, fragmentation, and conversion of natural ecosystems caused by the expansion of industrialised agriculture (Haddad et al. 2015; Jaureguiberry et al. 2022; Semenchuk et al. 2022). The effects of land-use change are particularly severe in tropical and subtropical forests, where commodity agriculture—such as palm oil, beef, soybean, and rubber production—continues to expand (Buchadas et al. 2022; Pendrill et al. 2022). These regions harbour the majority of the world's biodiversity, making them especially vulnerable (Haddad et al. 2015; Díaz et al. 2019; Baumann et al. 2022), yet these biomes have some of the highest deforestation rates globally (Haddad et al. 2015; Ciemer et al. 2019; Buchadas et al. 2022).

Understanding the impacts of agriculture-driven deforestation on biodiversity remains particularly critical for the world's tropical dry forests, woodlands, and savannas (hereafter: tropical dry forests). These ecosystems are home to exceptional biodiversity, including numerous endemic species (Miles et al. 2006; Pennington et al. 2018; Rivas and Cerrillo 2024). They are also culturally diverse and provide a wide range of ecosystem services to local communities (Pennington et al. 2018; Oldekop et al. 2020; Rivas and Cerrillo 2024). In addition, tropical dry forests contribute critical global ecosystem services, such as moisture recycling and carbon storage (Blackie et al. 2014; Schröder et al. 2021). Despite their importance, tropical dry forests face increasing human pressure, particularly from agricultural expansion, as these regions offer favourable agroecological conditions and contain some of the last large unconverted land reserves on the planet (Lambin et al. 2013; Meyfroidt et al. 2014; Schröder et al. 2021). However, these ecosystems have historically been undervalued and neglected (Blackie et al. 2014; Schröder et al. 2021). While conservation planning would be urgently needed to safeguard biodiversity in tropical dry forests, a lack of baseline data on biodiversity patterns and the impacts of land use change on them often prevents such planning (Schröder et al. 2021; Da Ponte et al. 2022; Buchadas et al. 2023).

Most assessments of land-use change impacts on biodiversity have focused on mammals and birds (Menezes et al. 2016; Powers and Jetz 2019; Velazco et al. 2019). Snakes are a particularly neglected group. Among reptiles, snakes are the most diverse group, with more than 3500 species described (Uetz et al. 2025). Many snakes have specialised ecological roles, with specific habitat preferences (e.g., semiaquatic, arboreal, fossorial), specialised diets (e.g., feeding exclusively on soft-shelled snails or birds), specialised morphological features such as different types of fangs (Westeen et al. 2020), and certain reproductive strategies (e.g., viviparous or oviparous) (Pizzatto et al. 2007; Vonk et al. 2008; Da Silva et al. 2018). Additionally, many snake species have small geographic ranges (de Oliveira Caetano et al. 2022; Martinez et al. 2024). Consequently, snakes are highly vulnerable to habitat loss, and many are classified as endangered (Roll et al. 2017; Guedes et al. 2018; Cox et al. 2022).

Despite their relevance for conservation, considerable knowledge gaps exist regarding key aspects of the biology and ecology of snakes, translating into barriers to conservation planning (Roll et al. 2017). Among these aspects, scarce information about snake distributions is particularly problematic (Roll et al. 2017; Gumbs et al. 2020; Cox et al. 2022). Coarse, outdated, or simply nonexistent distributional data for many snake species likely means that the conservation status of many snakes is assessed overly optimistically (Guedes et al. 2018; Gumbs et al. 2020; de Oliveira Caetano et al. 2022). Missing distributional data is also a major barrier towards conservation planning to safeguard these species (Brooks et al. 2006; Roll et al. 2017). Likewise, there is virtually no information about snakes' responses to habitat transformation (Nori et al. 2023). Assessing how agricultural expansion and resulting habitat change impact snake distributions, and through this alter snake communities, is therefore important (Gibbons et al. 2000; Reed Richard Shine 2002; Andrade-Díaz et al. 2019).

The Neotropics are home to around 25% of all snake species (Guedes et al. 2018; Nogueira et al. 2019). Although there are studies evaluating the impacts of habitat loss and fragmentation from agricultural land-use change, most of these have focused on tropical rainforests or regions outside South America (Todd et al. 2017; Guerra et al. 2023; Leal-Santos et al. 2024). In the Brazilian Cerrado, deforestation due to agricultural expansion has negative impact on reptiles in general, driving a decrease in taxonomic richness (Nogueira et al. 2011; Cordier et al. 2021). Similarly, in the Brazilian Caatinga, habitat loss drives contractions in snake distributions, with many species losing much of their habitat and several species not represented in the protected area network (Guedes et al. 2014). Finally, agricultural expansion has negatively impacted the distribution of 12 endemic snakes, with deforestation having the greatest impact (Andrade-Díaz et al. 2019). Overall, these studies underscore the importance of evaluating the impacts of land-use changes on snake communities in dry forests, but many regions remain unassessed and assessments at broader, biogeographic scales are entirely missing.

Agriculturally-driven deforestation has been especially rampant in the Chaco (Ciemer et al. 2019; de Sancha et al. 2021; Baumann et al. 2022). This region, extending into Argentina, Paraguay, and Bolivia, recently experienced widespread expansion of industrialised cattle ranching and cropping, particularly for soybean production. This has turned the Chaco into a global deforestation hotspot (Hansen et al. 2013; Baumann et al. 2022; Buchadas et al. 2022), with daily deforestation rates of 1000–1400 ha in the 2000s, and now over 60% of the Chaco's natural ecosystems have been converted (Mereles and Rodas 2014; WWF 2021; Baumann et al. 2022). Assessments of individual snake species and small

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study regions suggest that snakes have been notably vulnerable to these land-use changes (Nori et al. 2018; Andrade-Díaz et al. 2019). However, a Chaco-wide assessment of how land-use changes impacted the region's diverse snake communities—comprising at least 142 species—are missing (Nori et al. 2016; Andrade-Díaz et al. 2019; Torres et al. 2023).

Given the limited research on deforestation in tropical dry forests and its effects on snakes, this study focuses on the entire Chaco region to provide the first detailed assessment of agriculturally driven deforestation and its impacts on snake communities. We employ time-calibrated species distribution models and integrate a comprehensive database of snake occurrence records (Cabral et al. 2022) with a consistent land-cover time series from 1985 to 2020 to reconstruct changes in the distributions of 72 snake species due to land-use change. Specifically, we addressed the following questions:

1. How has land-use change between 1985 and 2020 changed the distribution of suitable habitat for individual snake species?
2. What has been the impact of land-use change on taxonomic, functional, and phylogenetic diversity in snake communities within the Chaco?

2 | Methods

2.1 | Study Area

The Chaco is the largest continuous tropical dry forest globally (Grau et al. 2008), extending over an extensive sedimentary alluvial plain formed by Quaternary sediments (Prado 1993; Pennington et al. 2000). The region experiences extreme summer temperatures, reaching up to 50°C, contrasted with frosty winters where temperatures can drop to below −7°C (Prado 1993). Precipitation varies markedly, ranging from over 1200 mm annually in the east to 350 mm in the west. This climatic variation results in distinct dry and rainy seasons, with western areas receiving only summer rains (Prado 1993), subdividing the Chaco into the Humid Chaco in the east and the Dry Chaco in the west (Dinerstein et al. 2017). In terms of vegetation, the Humid Chaco features a mosaic of gallery forests and flooded savannas dominated by *Copernicia alba*, spanning from eastern Bolivia to northern Argentina along the Paraguay River and parts of the Paraná River (Prado 1993). In contrast, the Dry Chaco is characterised by xerophytic vegetation and thorny forests, extending from southwestern Bolivia through the western regions of Paraguay to northern Argentina (Prado 1993).

These diverse environmental conditions contribute to the Chaco's high biodiversity, hosting over 250 species of reptiles, including at least 142 species of snakes (Williams et al. 2021; Cabral et al. 2024). Many snakes exhibit a north–south distributional pattern (Cabral et al. 2022), with species with more arboreal habits often found in the northern Chaco, while fossorial snakes are more common in the southern Chaco (Cabral et al. 2022). Several ophidians are endemic to the Chaco, with some, such as *Epicrates alvarezi*, *Philodryas erlandi*, and *Chironius maculoventris*, relatively widely distributed across the region. In contrast, others, like *Phalotris normanscotti*, *P. tricolor*, and *Phimophis vittatus*, are more range-restricted (Cacciali et al. 2016; Williams et al. 2021; Cabral et al. 2024).

The Chaco has been inhabited and used by Indigenous communities for millennia. Starting in the 19th century, Criollo settlers established themselves in the Chaco, practicing small-scale agriculture and forest-based livestock production. While these land-use changes impacted forest structure and composition, they did not lead to large-scale deforestation (Grau et al. 2005; Baumann et al. 2016). As a result, until the 1980s, natural vegetation in the Chaco remained fairly intact, with habitat change primarily occurring in the Argentinian Chaco, while the Bolivian and Paraguayan Chaco experienced minimal transformation (Baumann et al. 2022; Da Ponte et al. 2022). Marked changes began in the early 2000s, when deforestation rates escalated due to agricultural expansion, leading to widespread forest loss and fragmentation (Hansen et al. 2013; Baumann et al. 2017, 2022) (Figure 1). These processes have continued, first in Argentina, then in Paraguay, and now in Bolivia, and today less than half of the natural woodland cover remains (Hansen et al. 2013; Baumann et al. 2022) (Figure 1). The remaining natural cover in the Chaco is mostly concentrated in protected areas, especially in Bolivia and Paraguay, making these regions crucial for safeguarding the Chaco's biodiversity (Nori et al. 2016; Romero-Muñoz et al. 2021; Baumann et al. 2022). How these land-use changes have impacted the region's snake communities, however, has never been assessed at scale.

2.2 | Snake Occurrence Data

To assess the habitat suitability of snakes, we compiled a large dataset of occurrence records for all snake species known from the Chaco. We gathered these records by reviewing specimens from museum collections (Table S1). Additionally, we complemented our occurrence data with data from two studies that provided point records linked to traceable specimens (Cacciali et al. 2016; Nogueira et al. 2019; Cabral et al. 2024). Since we aimed to develop time-calibrated species distribution models (see below), we only included occurrence points with a known collection year. In total, we collected more than 13,000 records from 142 species from the Chaco. We only considered data with accurate locality data and eliminated duplicate records from our dataset using the *CoordinateCleaner* package (Zizka et al. 2019) in R (R Core Team 2019). To avoid sampling bias, we spatially filtered our presence occurrences by applying a minimum distance of 10 km between locations (Aiello-Lammens et al. 2015; Chaplin-Kramer et al. 2015), in line with the target resolution of our analysis. After the cleaning process, we retained 5820 unique records from 72 species (Figure 1).

2.3 | Environmental Predictors

We used ten environmental variables to model snake distributions at a resolution of 300 m. For land cover, we relied on a recent high-resolution (30 m) land-cover time series, derived from all available Landsat images (Baumann et al. 2017, 2022). We calculated the proportions (%) of forest, natural grasslands,

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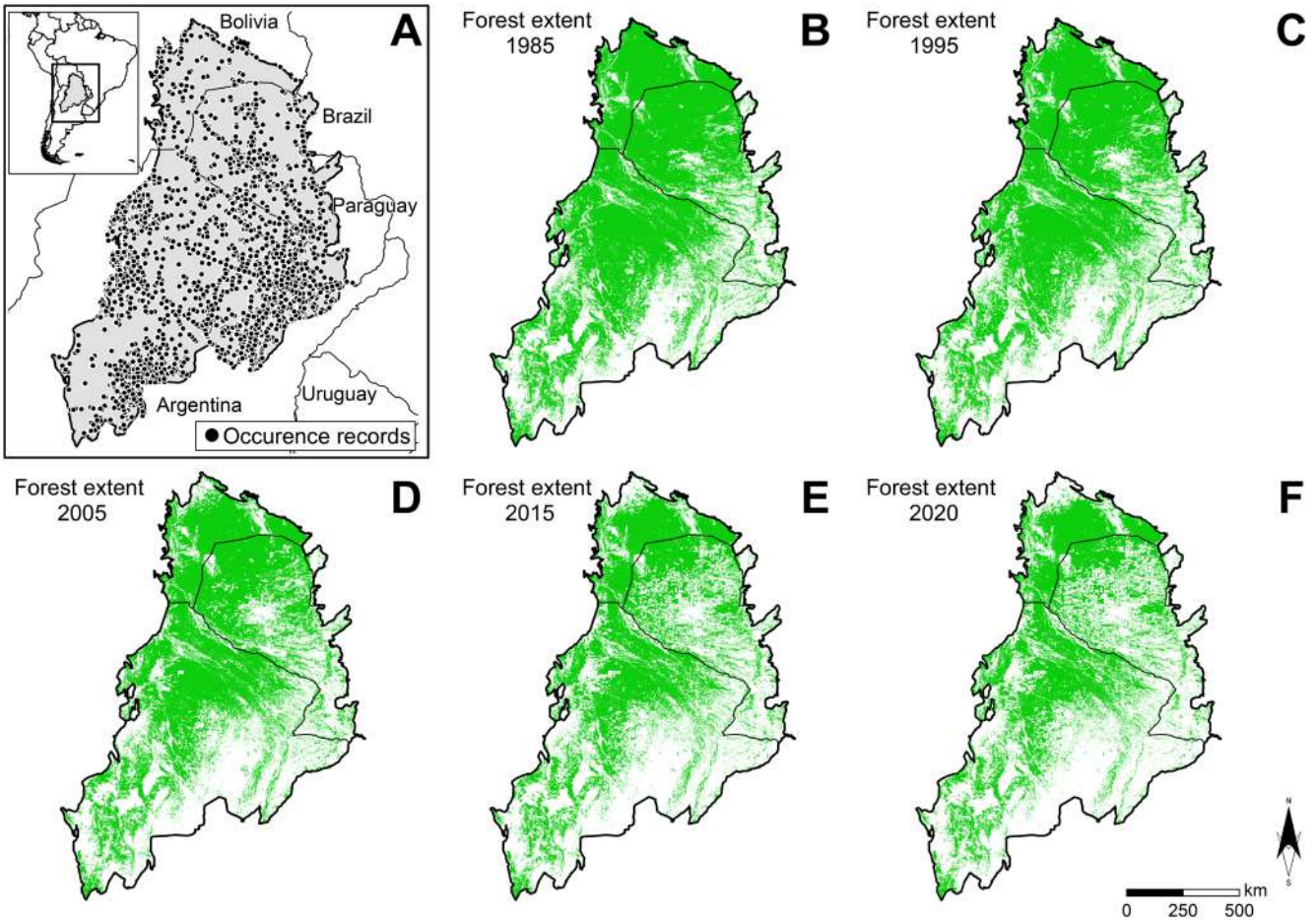

FIGURE 1 | Location of the Chaco ecoregion in South America and extent of forest cover in the Chaco at different periods. (A) Black points represent entire occurrence records used in our model, after filtering (see below). Forest cover in 1995 (B), with much of the region covered by forest, as well as in 1995 (C), 2005 (D), 2015 (F), and 2020 (E), when agricultural expansion had occurred. Note how deforestation first increased in Argentina, and later became ubiquitous in every part of the Chaco, leading to a high level of forest fragmentation.

wetlands, pastures, and cropland based on this dataset annually for 1985–2022. Additionally, we calculated the share of forest edge using Morphological Spatial Pattern Analysis (Soille and Vogt 2009; Romero-Muñoz et al. 2020), defined as the percentage of edge forest surrounding a target cell at a 300 m^2 resolution. Other environmental variables included the proportion of sandy soils, based on SoilGrids at a resolution of 250 m (Hengl et al. 2017), and the distance to the nearest water body, calculated as the Euclidean distance to the nearest water pixel. We also included mean annual temperature and precipitation seasonality, based on CHELSA climate (Karger et al. 2017); both variables were used as they provided meaningful information in previous work on snake biogeography in the Chaco (Cabral et al. 2022). We selected these variables based on their relevance to snake distribution, as indicated in the literature (Table 1). We tested the predictors for collinearity using the Pearson correlation coefficient and found no correlations exceeding |0.7| (Figure S1).

2.4 | Species Distribution Modelling

To understand the impact of land-use change, we employed time-calibrated species distribution models (Kuemmerle et al. 2012; Devenish et al. 2021). These models pair occurrence data with the environmental values corresponding to the period when each occurrence point was recorded (Romero-Muñoz et al. 2020; Devenish et al. 2021; Torres et al. 2023). Then, instead of fitting models for different periods independently, a single, temporally independent model using all available occurrence points is fitted and can then be projected onto the environmental variables for various periods (Kuemmerle et al. 2012; Devenish et al. 2021). This approach ensures that distributional changes are solely due to alterations in environmental predictors and not influenced by factors such as variations in the number of available occurrence points or differences in the spatial bias of occurrence points (Romero-Muñoz et al. 2020; Devenish et al. 2021).

To build our species distribution models, we assigned all snake records to one of five focal years or periods (10-year periods: 1985–1995, 1995–2005, 2005–2015, 2015–2020), based on the collection year information (1985, 1995, 2005, 2015, and 2020) and extracted the environmental values for these years. We use the mean value for each period to perform our species distribution models. We utilised maximum entropy modelling (Maxent), an algorithm that predicts species occurrence by comparing presence records to the overall distribution of environmental predictors within a defined study region, sampled through

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TABLE 1 | Description of predictor variables used in the species distribution models.

Variable	Description of the variable	Source	Rational habitat
% Forest	% woodland cover around target cell in buffers of 300 m	Baumann et al. (2017, 2022)	Provides resources and shelter for most of our species, but especially with arboreal habits
% Natural grasslands	% natural grasslands around target cell	Baumann et al. (2017, 2022)	Provides resources, shelter for open areas species
% Wetland	% of natural wetland around target cell	Baumann et al. (2017, 2022)	Provides resources, shelter for open areas and aquatic species
% Pastures	% implanted, intensified pastures around target cell	Baumann et al. (2017, 2022)	Associated with negative or positive impacts, species could lose or gain habitat
% Cropland	% cropland cover around target cell	Baumann et al. (2017, 2022)	Associated with negative or positive impacts, species could lose or gain habitat
% Edge forest	% of Edge Forest around target cell	Baumann et al. (2017, 2022)	Captures edge effects, which can be positive or negative for the species
% Sand	Proportion of sand particles (> 0.05/0.063 mm) in the fine earth fraction	Hengl et al. (2017)	Provides resources, shelter for fossorial species
Distance to water	Euclidean distance to the nearest water body	Baumann et al. (2017, 2022)	Access to water is critical for all species, whether as shelter, food resources or reproduction
Mean annual temperature	Annual average temperature from 1979 to 2013	Karger et al. (2017)	Captures temperature limitations (particularly hot temperatures)
Precipitation seasonality	Annual range of precipitation from 1979 to 2013	Karger et al. (2017)	Captures wetness limitations (particularly dryness)

background points (Elith et al. 2011; Merow et al. 2013; Phillips et al. 2017). Maxent is one of the most widely used species distribution modelling approaches and is particularly advantageous when few records are available for a species (Semper-Pascual et al. 2019; Romero-Muñoz et al. 2020; Devenish et al. 2021).

Defining the area that is ecologically and geographically accessible to a species is essential for accurate species distribution modelling (Soberón 2007; Barve et al. 2011). In our analyses, we defined the accessible area as the extent of the species' distribution combined with a buffered region derived from our background points (Barve et al. 2011; de Andrade et al. 2020). To parameterise and fine-tune our models, we first created 10,000 background points for each period, distributing them proportionally according to the presence points. We then extracted the values of predictor variables using both presence and background points for each sampled period (Sieber et al. 2015). We tuned model parameters using the package *kuenm* (Cobos et al. 2019), which selects optimal parameters per species based on comparing alternative model parameterisations (Cobos et al. 2019). We cross-validated our models using four-fold cross-validation, with ten replicates, and averaged the area under the receiver operating characteristic curve (AUC) as the performance indicator, where AUC > 0.7 is considered acceptable (Dormann et al. 2013; Romero-Muñoz et al. 2020) (Table S2).

Given the spatially clustered, non-random distribution of our occurrence data, our analyses yielded a relative index of habitat suitability. We projected this habitat suitability index, ranging between 0 and 1, for each period for each species (= five habitat suitability maps per species). To separate suitable from unsuitable habitat, we binarised the continuous maps based on the 'sum of sensitivity and specificity' threshold (Liu et al. 2013). We then calculated changes in the distribution of species for each period and summarised the overall area of suitable habitat for each species.

2.5 | Snake Diversity Metrics

To analyse snake diversity across the Chaco, we established a 10-km grid (5160 cells) and overlaid it with the binary snake distribution maps to create species presence/absence matrices for each period, treating each cell as a distinct snake assemblage. As we were interested in the entire Chaco region, we chose a grid size that reflected broad-scale, macroecological

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patterns (Hurlbert and Jetz 2007), in line with prior work on snakes in the Chaco (Cabral et al. 2024). We then calculated taxonomic, phylogenetic, and functional diversity indices. For taxonomic diversity, we calculated alpha richness (i.e., # species per cell) and gamma richness (i.e., overall species diversity across communities) for each cell. We furthermore calculated beta-diversity, the variation in species composition among sites, as a result of species replacement between sites (turnover) and species loss from site to site (nestedness) for both 1985 and 2020. For all these calculations, we used the '*betapart*' package (Baselga and Orme 2012). Specifically, we calculated spatial beta-diversity for each grid by employing the Jaccard multiple-site dissimilarity index. We implemented a subsampling procedure to mitigate the potential impact of cell size on the dissimilarity index by randomly selecting four neighbouring cells around each focal cell and computing the average Beta-Jaccard value across them (Baselga and Orme 2012).

For phylogenetic diversity, we pruned the Tonini et al. (2016) snake phylogeny to include only species in our database, using the *phangorn* (Schliep 2011) and *ape* (Paradis et al. 2004) packages. For phylogenetic diversity (PD), we computed phylogenetic beta diversity across species communities for each period. We then applied a null model to calculate the Standardised Effect Size (SES) of phylogenetic beta diversity. To calculate SES, we compared the observed PD values to null expectations derived from shuffling tip labels multiple times (1000 runs). This procedure was implemented using the *betapart* package (Baselga and Orme 2012), while the tip-shuffling model was executed with the *phyloregion* package (Daru et al. 2020). We assessed biotic homogenisation by comparing phylogenetic beta diversity between 1985 and 2020, identifying communities with biotic homogenisation (values <0) or heterogenisation (values >0) (Moura et al. 2023).

For functional diversity, we constructed a trait matrix with 10 traits related to body size, reproductive strategies, microhabitat use, and activity patterns (Cabral et al. 2022) (Table S3). From this, we created a multidimensional space and computed functional diversity indices using Principal Coordinates Analysis (PCoA) on trait distances (Mouillot et al. 2013). The dimensionality that best fit our data was determined by selecting the first two axes of PCoA (Mouillot et al. 2013) (Table S4), and a functional dendrogram was built using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) on these axes. To quantify functional diversity, we calculated the standardised effect size (SesFuncMPD) using null models with 1000 randomisations, where positive values indicate higher and negative values indicate lower functional diversity. We also computed Functional richness (FRic), Functional evenness (FEve), and Functional dispersion (FDis) to assess communities' occupation, evenness, and dispersion in functional space (Villéger et al. 2008; Laliberte and Legendre 2010). These analyses were conducted in R using the *mFD* (Magneville et al. 2022) and *picante* (Kembel et al. 2010) packages.

Once our diversity metrics were calculated, we analysed changes in them across periods. Additionally, we examined the relationship between deforestation and diversity metrics by calculating deforestation percentages within each cell. We applied linear quantile regression models at the 90th percentile to examine how the upper bounds of biodiversity and functional diversity responses are related to deforestation. Uncertainty in model predictions was assessed using bootstrap resampling, yielding a 95% confidence interval around estimates.

3 | Results

Our database (i.e., 5820 occurrence points) proved sufficiently large to build time-calibrated species distribution models for 72 out of 142 snake species. Of these, 19 are endemic to the Chaco (Table S3). Our models performed overall well, with a mean AUC value of 0.80 (standard deviation 0.12). The vast majority of species had an AUC value >0.7, yet seven species fell below this threshold (see Table S2). Overall, the predicted habitat distributions from our models, representing the likely range of the snake species, were both plausible and consistent with existing knowledge (Figure 2). Habitat suitability models for all species are shown in the Supporting Information.

Many species experienced major changes in the distribution of suitable habitat (Figure 3A,B). Between 1985 and 2020, a total of 13 snake species (18% of all species) saw habitat loss (i.e., a decrease of more than 5%), 24 species (33%) had stable habitat extent (i.e., ±5%), and 35 species (49%) saw an increase in suitable habitat (i.e., an increase of more than 5%; Figure 3A). Species that were most affected included *Lygophis anomalus* (terrestrial), *Thamnophis strigatus* (semiarboreal), *Drymarchon corais* (semiarboreal), and *Apostolepis ambiniger* (fossorial), losing over 50%, 30%, 20%, and 18% of their suitable habitats, respectively. In contrast, *Lygophis flavifrenatus* (terrestrial), *Philodryas agassizzi* (terrestrial), *Bothrops ammodytoides* (terrestrial), and *Atractus reticulatus* (fossorial) benefited the most, with $>50\%$ habitat suitability increase (Figure 3A). A few endemic species were also affected by habitat loss (Figure 3A,B): *Apostolepis ambiniger* (fossorial) had the major habitat loss (see above), followed by *Phalotris tricolor* (12%) (semifossorial), *Erythrolamprus sagittifer* (10%) (terrestrial), and *E. alberthguentheri* (9%) (terrestrial) (Figure 3A,B). Four endemic species had stable habitat extent (but with a tendency towards habitat loss): *Chironius maculoventris* (semiarboreal), *Erythrolamprus poecilogyrus caesius* (terrestrial), *Phimophis vittatus* (semifossorial), and *Xenodon pulcher* (semifossorial) (Figure 3A,B).

When comparing habitat guilds, semiarboreal and semifossorial species were the most affected, comprising 60% of the species experiencing habitat loss. This was followed by arboreal and aquatic species (30% seeing habitat loss), and fossorial species (14%; Figure 3A,B). Terrestrial species were most common in our dataset, with 20% losing suitable habitat (Figure 3A–D). However, fossorial and terrestrial species also benefited the most, with 85% and 78% of these species increasing their suitable habitat, respectively. These guilds were followed by arboreal species (66%), aquatic species (62%), semiarboreal species (37%), and semifossorial species (33%). Two arboreal species (*Philodryas trilineata* and *Philodryas varia*) had an increase in suitable habitat, but are marginally distributed in the Chaco (associated with Andean and Yungas forests). Two semiarboreal species had increasing habitat (*Epicrates alvarezi* and *Boa constrictor*), but use forest mainly as a refuge and are otherwise terrestrial.

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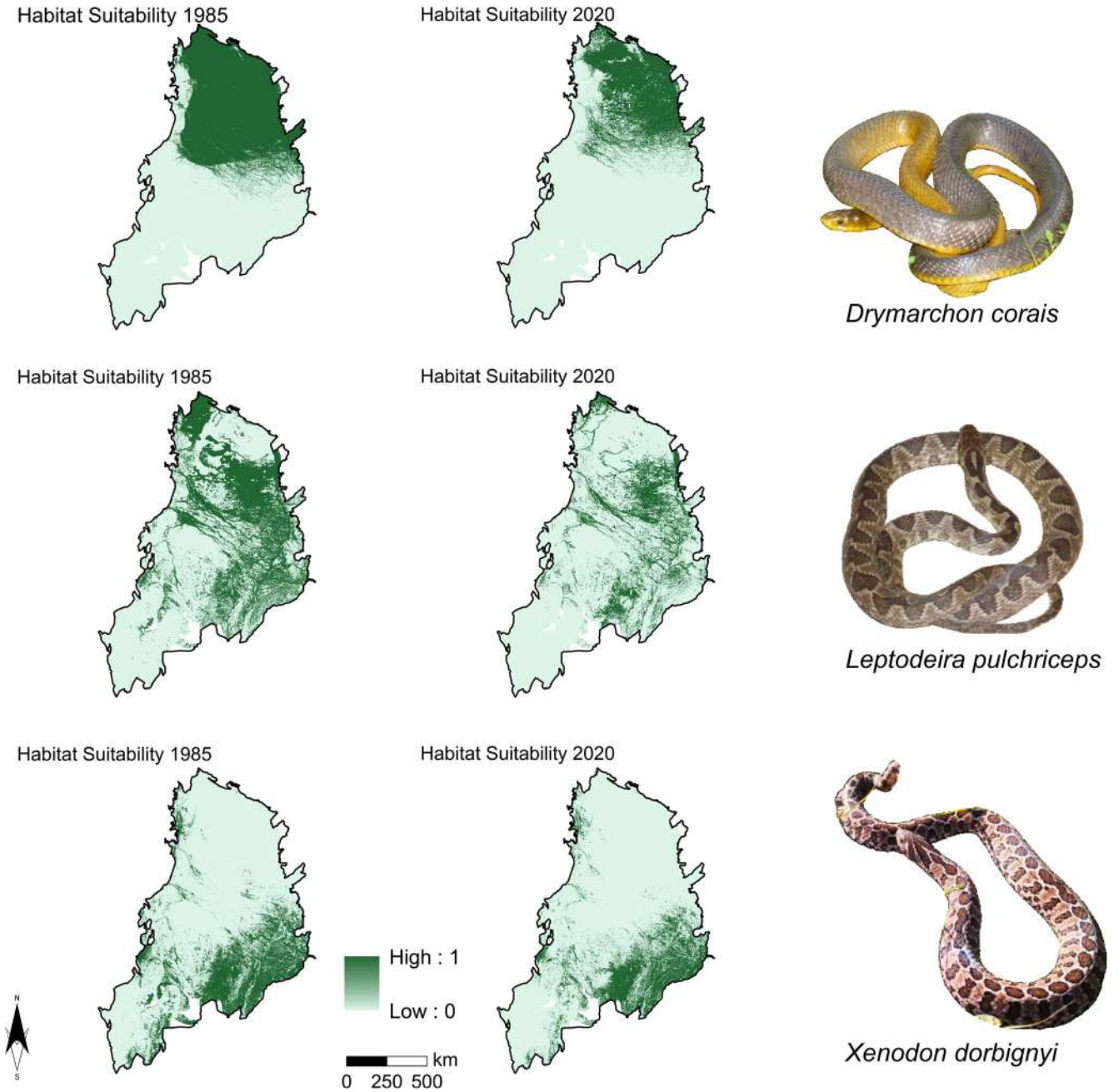

FIGURE 2 | Examples of the distributions of suitable habitat for three snake species (*Drymarchon corais*, Leptodeira pulchriceps, *Xenodon dorbignyi*) for the years 1985 (left) and 2020 (right).

Assessing how distributional changes of individual snakes impacted snake communities showed an overall decline in taxonomic diversity (Figure 4A,B,D,E). Specifically, 25% of communities experienced a loss in alpha richness (i.e., the number of species in an assemblage), with declines of up to 32 species. In terms of gamma richness (i.e., the total number of species across neighbouring communities), 39% of communities lost up to 11 species, predominantly located in the central and northern Chaco (Figure 4A,B,D,E). In terms of phylogenetic diversity (PD), 75% of communities experienced losses and were subject to biotic homogenisation. Those communities were distributed across the entire Chaco. Only a few areas in the northern and southern regions did not exhibit PD loss (i.e., maintained heterogeneity; Figure 4G,H). In terms of functional diversity, 23% of communities experienced loss, mostly concentrated in the north, central, and northeastern Chaco (Figure 4J,K). According to the models, snake communities in the Chaco tend to exhibit less heterogeneous functional compositions, even in cases where species richness is expected to increase (Figures S2–S4). The shift towards higher functional richness with stable functional evenness and dispersion suggests that communities have diversified in terms of ecological roles and trait combinations (Figures S2–S8).

Comparing assemblage changes to deforestation levels revealed a consistent pattern of declining taxonomic richness as

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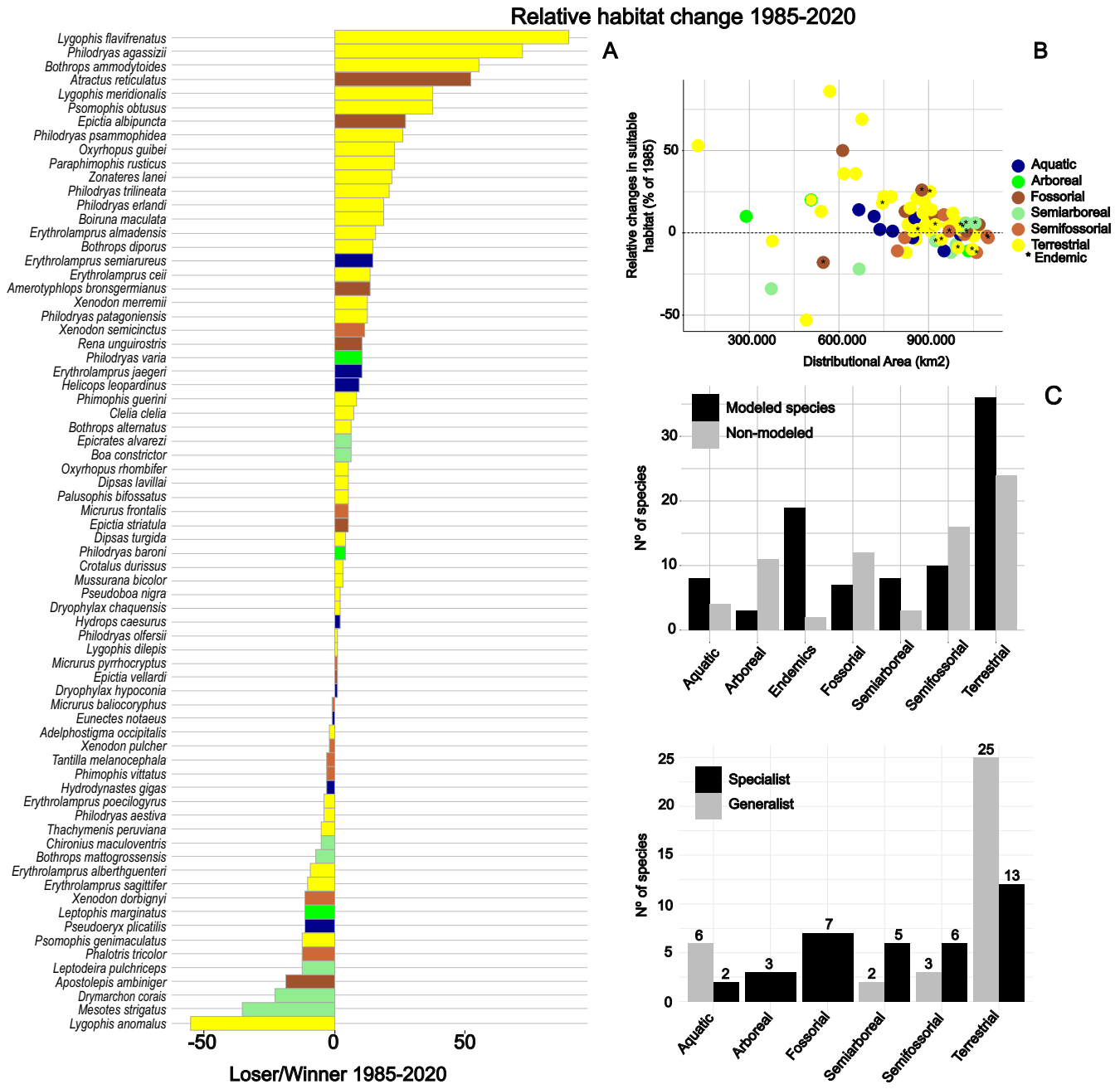

FIGURE 3 | Changes in the distribution of suitable habitat for 72 snake species in the Chaco, grouped by habitat guilds (colours). (A) Relative changes in suitable habitat between 1985 and 2020. (B) Proportional habitat changes 1985–2020 vs. habitat extent in 2020. An asterisk (*) denotes endemic species. (C) Comparison between modelled and non-modelled species per snake functional group. (D) number of specialist and generalist species per habitat type. Notice that most terrestrial species are generalists. Numbers at the top of each histogram represent the number of species.

deforestation increased (Figure 4C,F), with particularly strong declines in overall species numbers where high levels of deforestation had occurred. A similar pattern was observed for phylogenetic diversity: higher deforestation levels led to a stronger loss of phylogenetic diversity (Figure 4I). Similarly, functional richness was adversely affected by deforestation (Figure 4J). However, it is noteworthy that even in areas of low levels of deforestation, our analyses revealed substantial losses in species richness, although such regions continue to support more diverse communities compared to heavily deforested areas. Importantly, in areas without deforestation, snake communities remained stable in terms of diversity (Figure 4). Although many species saw an increase in the area of suitable habitat, deforestation led to more homogeneous snake communities. Overall, this indicates that snake communities across the Chaco are becoming increasingly similar due to land-use change.

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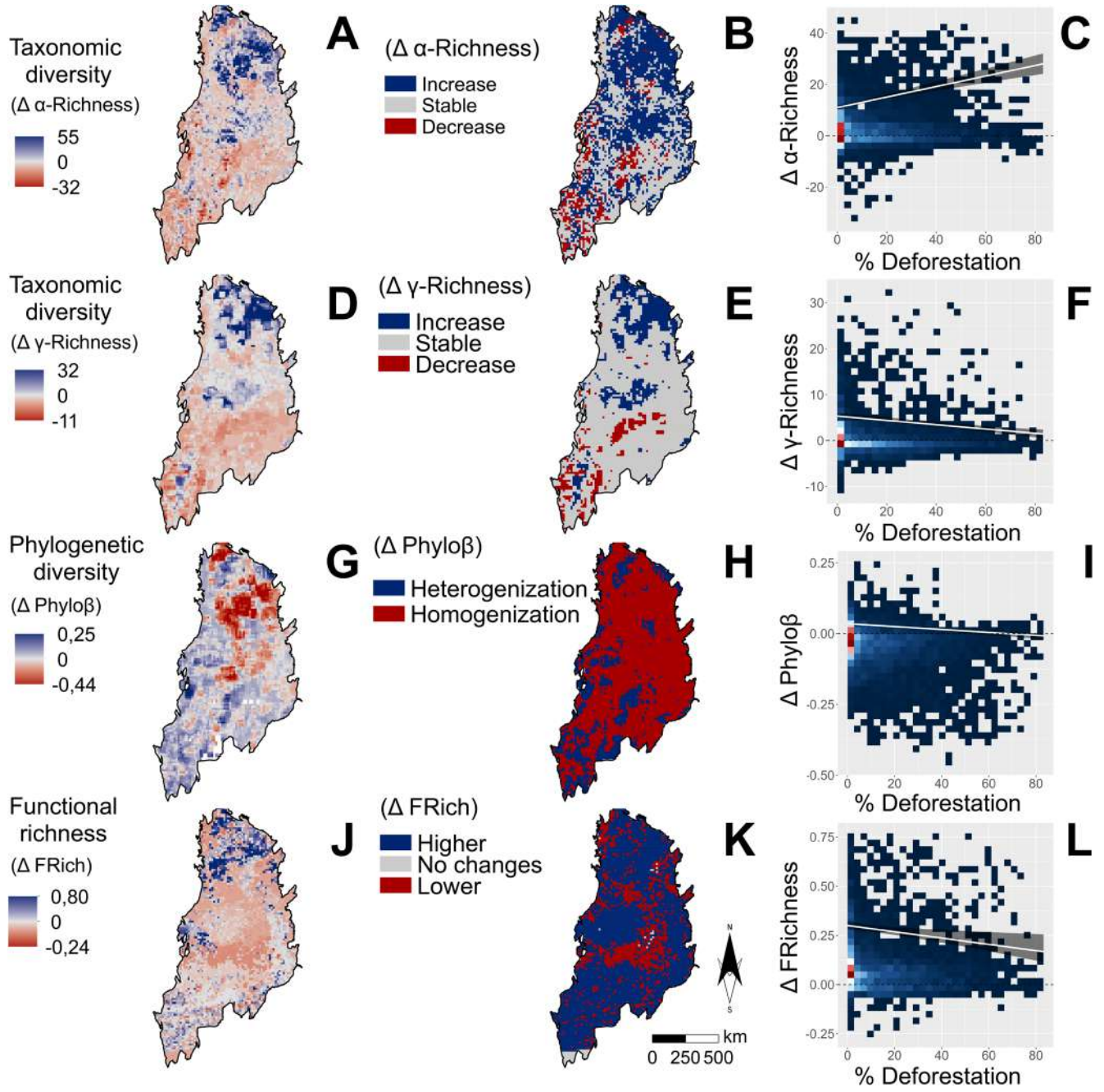

FIGURE 4 | Changes in snake communities in the Chaco between 1985 and 2020. Left: Continuous change in diversity metrics. Middle: Categorical change in the same metrics. Right: Relation between deforestation and diversity metrics. Panels A–F show changes in taxonomic richness (delta alpha richness A–C, delta gamma richness D–F), panels G–I show changes in delta phylogenetic beta diversity (biotic homogenisation: Values <0, heterogenisation: Values >0), and panels J–L show changes in delta functional richness. Panels C, F, I, and L show the relation between changes (delta) and % of deforestation in each assemblage.

4 | Discussion

Many tropical dry forests are under high and rising pressure from agricultural expansion, rendering them hotspots of deforestation and defaunation (Meyfroidt et al. 2014; Schröder et al. 2021). Biodiversity in many dry forests is weakly understood, including species' biogeography and how land-use change impacts it. This is particularly true for snakes (Guedes et al. 2014; Andrade-Díaz et al. 2019; Martinez et al. 2024). Using a comprehensive database of snake occurrences from across the entire 1.1 million km^2 Chaco, we assessed how land-use changes from 1985 to 2020 impacted snake communities. Three main insights derive from our work. First, and surprisingly, we identified more winners than losers of land-use change in the Chaco, mainly because terrestrial, generalist species were gaining in suitable habitat extent (Segura et al. 2007; Sales et al. 2020). However, many endemic and specialist species had declining habitat extent, and it is important to note that we could not model most such species due to data deficiencies (Figure 3C,D, Figure S6, see also below). Second, we show that despite some species benefiting

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from land-use change, the overall outcome of habitat change for snake communities was an erosion of diversity across facets (taxonomic, phylogenetic, and functional diversity; Figure 4, Figures S2–S4). Third, we reveal a strong trend towards biotic homogenisation of snake communities in the Chaco, with 75% of snake communities becoming more similar, with especially specialised arboreal or semiarboreal species replaced by more generalist ones (Clavel et al. 2011; Cabral et al. 2024; Figure 4 and Figures S2–S4). More broadly, our study underscores the urgent need for conservation planning and action targeted at snakes in the Chaco and likely many other tropical dry forests.

According to our distribution models, more snake species benefited from the land-use changes that have happened in the Chaco since 1985 than snake species that were negatively impacted by land-use change. At first, this is a surprising finding, but two main factors explain these results. On the one hand, while agricultural expansion into tropical dry forests leads to deforestation, it has effectively led to a savannisation of formerly heavily forested regions (Seidl et al. 2017; Sales et al. 2020). This is particularly true in the Chaco, where cattle ranching is the main proximate driver of deforestation (Baumann et al. 2017, 2022), and many grazing systems still contain some level of woody cover, such as in silvopastoral systems or woodland-based grazing systems. Generalist, terrestrial snakes thrive in such mixed, semi-open landscapes (Segura et al. 2007; Schneider-Maunoury et al. 2016), and we also find most winners to be such species (Figure 3A,B). We furthermore note that there are multiple lines of evidence suggesting that the Chaco was substantially more open historically, in recent times before the expansion of livestock grazing as well as historically, when the Chaco hosted an array of megaherbivores that interacted with vegetation (Prates and Perez 2021; Dantas and Pausas 2022).

On the other hand, the species that were losers of land-use change in the Chaco were often more specialised snakes, especially those adapted to living arboreally or semi-arboreally, as well as several small-ranged and endemic species. Overall, 13 snake species lost considerable areas of suitable habitats between 1985 and 2022, including four endemic species. Yet, unfortunately, we were only able to model about half of the 142 snake species occurring in the Chaco, due to data deficiencies (70 snakes had fewer than 15 occurrence points, or lacked information regarding the collection year; Figure 3C, Figure S5). Most species we could model were wide-ranging, common, terrestrial, and generalist species (47 of the 72 species fulfilled at least one of these criteria). This helps explain why a larger number of species appeared to benefit from habitat loss (Figure 3C, Figure S5). Conversely, many species we could not model were arboreal or semiarboreal (14) or likely small-ranged (20) – the groups that suffered the most from agricultural expansion in our work and in prior studies in the Chaco (Cabral et al. 2024) and elsewhere (Segura et al. 2007; Schneider-Maunoury et al. 2016; Rincón-Aranguri et al. 2023). It is thus reasonable to assume that the negative impacts on snakes we uncover here are a very conservative estimate. Moreover, our study shows that the lack of reliable species distribution data remains a major obstacle to adequately assessing the conservation status of snakes in the Chaco (Guedes et al. 2018; Cordier et al. 2021; Diniz-Filho et al. 2023). This reflects a well-documented knowledge gap regarding the impacts of land-use change on reptiles, particularly in under-sampled ecological groups (Cordier et al. 2021; Nori et al. 2023). Filling these data gaps is essential for developing effective conservation and management strategies to mitigate the impacts of land-use change on biodiversity—especially for reptiles, which are particularly sensitive to human activities (Cordier et al. 2021; Nori et al. 2023).

Our second main finding was that snake diversity declined across all facets of diversity. These results are in concordance with previous studies that show a decrease in species richness due to the impact of land-use changes in the Chaco, for mammals (Romero-Muñoz et al. 2021), birds (Semper-Pascual et al. 2018), and six selected snake species (Andrade-Díaz et al. 2019). Similarly, land-use change has been shown to lead to declining species richness in other tropical dry forests (de Sancha et al. 2021; Ceron et al. 2023). We find an erosion of phylogenetic diversity, also corroborating findings for other taxa (Romero-Muñoz et al. 2021; Cabral et al. 2024). Finally, the reduction in species richness was also reflected in the decline in functional richness within snake communities, which can likely be attributed to the loss of more specialised species that are not benefitting from the savannisation described above (Pacifici et al. 2017; Menéndez-Guerrero et al. 2020; Sales et al. 2020). These losses of diversity across facets are concerning and point to an erosion of snake biodiversity as well as the potential loss of the functional roles of more specialised snakes, such as arboreal ones, in food webs (Segura et al. 2007; Alencar et al. 2017; Harrington et al. 2018). Similar patterns have been observed in other dry regions undergoing land-use expansion (Schröder et al. 2021; Buchadas et al. 2022; Rivas and Cerrillo 2024).

Our third main finding was the homogenisation of snake communities we uncovered for the Chaco. Generalist snakes tended to thrive and replace more specialised species, thus leading to less diverse communities. This pattern is typical of biotic homogenisation processes (Bellard et al. 2012; Olden et al. 2018). Worryingly, we show that these transformations happen across vast areas of the Chaco, with more than 75% of snake communities affected. The effects of biotic homogenisation are particularly evident in the decline of phylogenetic diversity. As species are lost or replaced by more generalist ones, the phylogenetic diversity across the entire region, as well as between communities, decreased, in line with predictions (Graham and Fine 2008; Winter et al. 2009; Leprieur et al. 2012). We therefore suggest the trend towards less functionally and phylogenetically diverse communities is a signal of wider negative impacts of land-use changes on ecosystem functions and stability in the Chaco and possibly other dry forests (Clavel et al. 2011; Daru et al. 2021; Hughes et al. 2022).

Beyond habitat loss, snakes in the Chaco face additional threats such as hunting, road mortality, collection for the pet trade, and climate change. These pressures likely compound the impacts of habitat loss we quantify here, undermining ecosystem functions and resilience. Addressing these threats through expanded conservation efforts, including habitat protection and sustainable land-use practices, is critical to preserving biodiversity and ecological stability in the Chaco and similar ecosystems worldwide (Borges et al. 2019; Feijó et al. 2023; Martinez et al. 2024). Addressing these threats through expanded conservation efforts, including habitat protection and more sustainable land-use practices, is critical to preserving biodiversity and ecological stability in the Chaco and other tropical dry woodlands (Naeem et al. 2012; Nori et al. 2018; Emer et al. 2019).

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Globally, the challenges observed in the Chaco resemble those in other tropical and subtropical dry forests where agriculturally driven deforestation is widespread. As we show here, snakes are a particularly vulnerable yet often overlooked taxon. In our case, of the 72 species we modelled, 24 had stable habitats (±5%), while many others face uncertain futures as land use continues to expand, especially more specialist snakes. Arboreal and semi-arboreal species, and more generally non-fossorial species, are at greater risk, lacking the ability to shelter underground and thus more vulnerable to habitat transformation (Cabral et al. 2022, 2024). Likewise, we uncover a homogenisation of snake communities that very likely is happening in other dry forests and savanna regions undergoing similar land-use change trajectories, such as the Brazilian Cerrado and Caatinga, the Bolivian Chiquitania, or the Indochina dry forests in Laos and Cambodia (Buchadas et al. 2023). Conservation planning and efforts targeted at snakes are thus urgently needed, including expanding protected areas to ensure all snake species are represented in protected area networks. Similarly, implementing more sustainable land-use practices (e.g., silvopastures rather than treeless pastures, increasing connectivity among forest remnants and private reserves) would help those habitat guilds that were among the biggest losers in our assessment (Romero-Muñoz et al. 2020; de Sancha et al. 2021; Rivas and Cerrillo 2024). More generally, addressing biodiversity declines in dry forests requires coordinated efforts to generate baseline data on species distributions and to preserve key habitats. Protecting these ecosystems is essential not only for the species they sustain but also for maintaining ecological functions that support local communities and societal well-being.

Author Contributions

Conceptualization: H.C., T.K.; Data curation: H.C.; Formal analysis: H.C., R.C.; Funding acquisition: H.C., D.J.S., T.K.; Investigation: H.C., T.K.; Methodology: H.C., A.R.-M., L.P., R.C., T.K; Project administration: H.C., D.J.S., T.K.; Resources: H.C., D.J.S., T.K.; Software: H.C.; Supervision: D.J.S., T.K.; Validation: H.C., A.R.-M., D.J.S., G.C.L., J.N., L.P., R.T., R.C., M.S.A.-D., M.B., T.K.; Visualization: H.C., A.R.-M., D.J.S., G.C.L., J.N., L.P., R.T., R.C., M.S.A.-D., M.B., T.K.; Writing – original draft: H.C., T.K.; Writing – review and editing: H.C., A.R.-M., D.J.S., G.C.L., J.N., L.P., R.T., R.C., M.S.A.-D., M.B., T.K.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Records from snakes are from the work of Cabral et al. (2024) https://doi.org/10.1016/j.jaridenv.2024.105214. Additional information supporting all results presented in this paper is available in the Supporting Information section.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70105.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Collections visited to obtain snake occurrence data. **Table S2:** Goodness of fit (measured in area under the curve value—AUC) of modelled snake species. **Table S3:** Dataset of species and traits used in our analysis of functional diversity. Measures are in millimetres and masses in grams. **Table S4:** Correlations between functional traits and principal coordinate analysis (PCoAs) axis, the name of the test performed, and the corresponding statistics and *p*-value. **Figure S1:** Pearson's correlation coefficients calculated between each explanatory variable used in our distributional models. **Figure S2:** Distribution of functional diversity changes in snake communities across scenarios, considering four different indices. Standardised effect size of mean pairwise distances in communities (SESMPD), Functional richness (FRic), Functional evenness (FEve), and Functional dispersion (FDis). **Figure S3:** Changes in functional diversity indices in each community. (A) Standardised effect size of mean pairwise distances in communities (SESMPD), (B) Functional richness (FRic), (C) Functional evenness (FEve), (D) Functional dispersion (FDis), and (E) Species richness (SppRichness). **Figure S4:** Distribution of *p*-values for Standardised effect size of mean pairwise distances in communities (SesFuncMPD) indices in 1985 and 2020 scenario communities. The dark magenta represents the overlapping values between 1985 and 2020 SESFuncMPDp. **Figure S5:** Comparison between all snake species from the Chaco base on Cabral et al. (2022, 2024), showing modelled and non-modelled species. Notice that majority of terrestrial species modelled. Tail proportion represents the relation between tail length and snout-vent length. **Figure S6:** Total number of records per habitat, notice the difference between terrestrial species and the others. **Figure S7:** Binary Maps from 1985 (left) and 2020 (right). **Figure S8:** Ensemble Maps from 1985 (left) and 2020 (right).

Biography

Hugo Cabral is interested in the taxonomy, biogeography, and macroevolution of reptiles especially snakes from the Gran Chaco. I am interested in understanding the ecological evolutionary processes that have given rise to the South American Biota. My research encompasses all snake species within the South American Gran Chaco.

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