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Impacts of climate change in taxonomic, phylogenetic and functional diversity in snakes in largest dry forest ecoregion, the Gran Chaco

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ABSTRACT

The impacts of anthropogenic activities have significantly contributed to recent and future climate changes worldwide. The future effects of climate change on biodiversity have been intensively studied globally over the past two decades. Currently, dry ecoregions are among the most threatened ecosystems in the world. In South America, three such seasonal dry ecoregions stand out: the Cerrado, Caatinga, and the Gran Chaco. Among these, the Chaco has experienced high deforestation rates and landscape degradation over the last decade, making it a top priority for conservation efforts. In this study, we employed ecological niche modeling to estimate the present and future distribution of snakes in the Chaco region. Our goal was to assess how snake diversity will change with projected climate changes across this geographic area. Our findings suggest that snake assemblages in the Chaco will undergo significant changes under future climatic conditions, with a clear trend toward biotic homogenization of the ecoregion and a decrease in species richness. These negative changes will likely extend to the protected areas within the Chaco, resulting in biotic homogenization and a loss of species richness.

1. Introduction

The impacts of anthropogenic activities have significantly contributed to recent and future global climate changes (Hidasi-Neto et al., 2019). The current loss of habitats driven by agriculture, along with associated anthropogenic pressures, has a negative impact on biological populations by reducing landscape connectivity and impeding the movement of individuals and genes (Bellard et al., 2012; Brook et al., 2008). Consequently, species with limited dispersal abilities or inadequate adaptations to climate change would have their persistence threatened or go extinct, while opportunistic and exotic species may thrive. Moreover, species related to open areas would be favored by those changes, taking advantage of habitat disturbance (Sales et al., 2020).

The future impacts of climate changes have been long studied in the last two decades in different regions around the globe, impacting the entire ecological community (Bellard et al., 2012; Hidasi-Neto et al., 2019; Seidl et al., 2017). The ongoing climate change also produces species-specific responses, and the co-occurrence patterns are likely to be modified, resulting in a reorganization of biological assemblages (Olden et al., 2004). This reorganization can make them more homogeneous, with a decrease in the number of specialists, restricted, and endemic species, replaced by widespread and niche generalist species (Clavel et al., 2011). In this sense, if species show low levels of dispersal or adaptations to climate changes, their persistence would be threatened, or they may go extinct, while opportunistic and exotic species may thrive, often leading to biotic homogenization of habitats (Olden et al., 2004; Thuiller et al., 2013). Biotic homogenization has significant consequences in ecosystems, affecting the resilience of communities to environmental disturbances, which could result in a reduction in overall community and ecosystem function, stability, and adaptability (Olden et al., 2004).

Therefore, biotic homogenization would not only reflect in the taxonomic diversity but also functional and phylogenetic diversity of communities (Olden et al., 2004). Species with specific functionality are more threatened than others (e.g., longer and bigger species, diet specialists, endemic species), since these functional traits are related to species' performance (Pacifici et al., 2017; Violle et al., 2014). Species with specific functionality often lack time for adaptation to environmental changes, which occur faster than species' capacity to adapt,

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leading to local or regional extinction (Bellard et al., 2012). This local extinction would be reflected in the functional distinctness and phylogenetic diversity of communities (Bellard et al., 2012; Pacifici et al., 2017; Violle et al., 2017).

To comprehensively address the profound effects of climate change on biodiversity, it is imperative that research encompasses all facets, including taxonomic, phylogenetic, and functional diversity (Brum et al., 2017; Clavel et al., 2011; Pacifici et al., 2017). Studies that only include taxonomic diversity could omit important information like phylogenetic distinct clades or functional distinctness of species (Brum et al., 2017; Clavel et al., 2011). This often leads to phylogenetic and functional hotspots not being included in conservation strategies, representing a conservation conflict for conservation strategies (Brum et al., 2017). Therefore, to ensure biodiversity persistence, researches seeking to understand the impacts on biodiversity (in this case climate change) should include and maintain taxonomic, phylogenetic, and functional diversity to ensure effective conservation planning (Brum et al., 2017). Understanding where and how those changes would happen and how the decrease of taxonomic, phylogenetic, and functional diversity would affect communities is essential for assessing biodiversity (Clavel et al., 2011; Mouillot et al., 2013; Olden et al., 2004; Violle et al., 2014).

Anthropogenic activities and their resulting consequences tend to have a disproportionate impact on certain ecosystems, notably arid ones (Hidasi-Neto et al., 2019; Kuemmerle et al., 2017). Arid ecoregions are currently considered the most threatened ecosystems of the world (Kuemmerle et al., 2017) and are expected to be more affected in future scenarios of climate change (Hidasi-Neto et al., 2019). One such ecoregion is the Gran Chaco, hereafter referred to as the Chaco, which stands out as one of the most highly threatened and extensive continuous dry forest areas in South America (Kuemmerle et al., 2017). It is anticipated that arid regions like the Chaco will undergo changes in community similarity, manifested by an increase in compositional similarity. This shift is expected due to the extinction of specialists and narrowly distributed species, coupled with the expansion of generalist and widely distributed species (Collevatti et al., 2013; Prieto-Torres et al., 2016; Siqueira and Peterson, 2003). Additionally, flat regions such as the Chaco are anticipated to experience high rates of temperature changes, primarily attributable to their lack of topographic complexity (flattened areas). Consequently, the Chaco assumes significance as an area crucial for understanding how species will respond to future climate changes (Loarie et al., 2009).

The Chaco is the largest continuous tropical dry forest globally (Grau et al., 2008), formed through the interplay of the Andean uplift, marine introgressions, and various alluvial systems (Gregory-Wodzicki, 2000; Hernández et al., 2005). Its primary characteristics include climatic seasonality and geomorphology, with the latter comprising an extensive sedimentary alluvial plain featuring soil derived from Quaternary sediments accumulation (Pennington et al., 2000; Prado, 1993). Comprising xerophytic vegetation, the Chaco hosts a mosaic of grasslands, savannas, open woodlands, and thorn forests (Prado, 1993; Willig et al., 2000). Generally, the Chaco exhibits minimal variation in elevation, with the sole topographic relief (1000–1200 m a.s.l.) occurring at its western border, shared between Argentina and Bolivia (Prado, 1993).

In the Chaco, the highest absolute temperature recorded for South America has been documented (Prado, 1993). This extreme heat during summer is juxtaposed with frosty winters; across much of the Chaco, temperatures can plummet to as low as −1.1 °C in Corrientes or −7.2 °C, following an east-west pattern (Prado, 1993). Precipitation in the Chaco also exhibits an east-west gradient, ranging from over 1200 mm annually in the east to 350 mm in the west (Prado, 1993). This climatic variation manifests in distinct dry and rainy seasons, with some western areas experiencing summer rains as their sole precipitation event in the year (Prado, 1993). This characteristic divided the Chaco into two distinct regions: the Humid and Dry Chaco (Dinerstein et al., 2017). 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 characterized by xerophytic vegetation and thorny forests, extending from southwestern Bolivia through the western regions of Paraguay to northern Argentina (Prado, 1993).

Several studies have pointed out the importance of taking conservation actions in the Chaco (Kuemmerle et al., 2017; Nori et al., 2016; Romero-Muñoz et al., 2020). However, most of those works focused on mammals, birds, and amphibians, evaluating just the taxonomic or conservation facets of biodiversity (Cacciali et al., 2016; Nori et al., 2016; Romero-Muñoz et al., 2020). On the other hand, Andrade-Díaz et al. (2019) identified priority conservation areas for 12 endemic snake species in the Dry Chaco. While their study focuses specifically on the Dry Chaco region in Argentina, it highlights the potential negative effects of agricultural expansion on the distribution of snakes in this area.

Besides the Chaco, there is a notable dearth of research connecting climate change with spatiotemporal biodiversity patterns in the broader Neotropics (Brook et al., 2008). Furthermore, there is a scarcity of research aimed at comprehending the biotic homogenization of ecosystems driven by climate change. Considering the imminent threat that climate change poses to arid regions (Hidasi-Neto et al., 2019; Kuemmerle et al., 2017) and the limited knowledge regarding its impact on snakes in this ecoregion, especially when assessing the taxonomic, phylogenetic, and functional dimensions of snake biodiversity simultaneously, it becomes crucial to include these three dimensions for more effective conservation planning (Brum et al., 2017; Clavel et al., 2011). Thus, in this study, we employ taxonomic, phylogenetic, and functional data in ecological niche modeling to evaluate the potential influence of climate change on snake diversity across the geographic area of the Gran Chaco. Our specific research questions are as follows: (1) Will climate changes lead to a reduction in species diversity among snake assemblages, resulting in biotic homogenization? (2) What is the expected loss of snake species, phylogenetic clades, or functional diversity within the Gran Chaco due to anticipated climate changes? (3) How are these changes distributed spatially within the Gran Chaco and its Protected Areas (PAs)?

2. Material and methods

2.1. Occurrence data

Our data was compiled from the literature and revision of museum specimens. The studied specimens belong to the collections: Museo Nacional de Historia Natural del Paraguay (MNHNP), Instituto de Investigación Biológica del Paraguay (IIBP–H), Fundación Miguel Lillo (FML), Colección Herpetológica Universidad Nacional del Nordeste (UNNEC), Laboratorio de Genética Evolutiva/Instituto de Biología Subtropical (LGE), Coleção Zoológica da Universidade Federal Mato Grosso do Sul (ZUFMS). Additionally, we accessed pertinent literature sources (Cacciali et al., 2016; Nogueira et al., 2019). We only considered accurate localities, duplicate records, characterized by identical species, locality, and different specimens, were eliminated from our dataset, using CoordinateCleaner package (Zizka et al., 2019) in R (R Core Team, 2019). The final dataset comprised a total of 51,081 records, representing 141 snake species (refer to Table S1 for details).

2.2. Climatic data

We utilized 19 climatic variables downloaded from WorldClim at a 10-arc-minute resolution, approximately equivalent to 20 km (Fick and Hijmans, 2017). These variables encompassed aspects of precipitation and temperature for two time periods: 1950–2000 (present) and 2081–2100 (future) as defined by the IPCC in 2021. For the future scenario, we specifically focused on the non-mitigation scenario known as SSP585 (Shared Socioeconomic Pathways), chosen due to the pressing need to address climate change impacts on biodiversity within the

Chaco ecoregion (Kuemmerle et al., 2017). Historically, the Chaco has been largely overlooked in terms of conservation strategies and stands as one of the most threatened regions in South America. Over the past 15 years, deforestation rates in the Chaco have experienced a considerable increase, primarily driven by agricultural and livestock production (Andrade-Díaz et al., 2019; Baumann et al., 2017; Kuemmerle et al., 2017; Mereles and Rodas, 2014; Romero-Muñoz et al., 2021). These changes in the original landscape of the Chaco are leading to high habitat fragmentation with adverse impacts on biodiversity (de la Sancha et al., 2021; Grau et al., 2005). Consequently, we have chosen to focus our work on the worst-case scenario for the Chaco, as none of the current threats facing the region are anticipated to decrease, potentially exacerbating climate change in the Chaco (de la Sancha et al., 2021; Grau et al., 2005; Mereles and Rodas, 2014).

In our analysis, we employed three generalized circulation models (GCMs): CNRM-CM6-1, MIROC6, and MRI-ESM2-0, for projecting future climate conditions. This choice was made to account for the inherent uncertainty in predicting species' habitat suitability under various climate models (Moura et al., 2023a). To mitigate multicollinearity, we performed a Principal Component Analysis (PCA) on the bioclimatic data, following the methodology outlined by Andrade et al. (2020). We retained the first principal components that collectively captured at least 95% of the variation in the original dataset (see Supplemental Material). For projecting future climate scenarios, we utilized the PCA loading coefficients to establish linear relationships between the raw predictor variables and the principal components, creating new layers that represent future climate conditions (Moura et al., 2023a).

2.3. Ecological niche modeling

We conducted Ecological Niche Modeling (ENM) using the ENMTML package (Andrade et al., 2020) in R (R Core Team, 2019). One crucial step in ENM is defining the species' accessible area, which represents the geographical region utilized by a species over a relevant period (Andrade et al., 2020; Barve et al., 2011). We defined the species' accessible area as a buffer with a width equal to the maximum distance between pairs of occurrences for each species (Andrade et al., 2020). To generate pseudoabsences, we randomly allocated points within the accessible area of each species, maintaining a presence/absence ratio of 1:1. This ratio has been shown to produce reliable models (Andrade et al., 2020; Leroy et al., 2018; Zaniewski et al., 2002).

The choice of algorithm can significantly impact habitat suitability estimation (Diniz-Filho et al., 2009). Therefore, to address the limitations of climate uncertainty, dispersal, and model prediction, we conducted ENM using three different algorithms and subsequently created an ensemble projection for our habitat suitability model (Araújo and New, 2007). The selected algorithms were Bioclim BIO (presences) (Hijmans and Elith, 2017), Maximum Entropy (with 10,000 background points and default features based on the MaxEnt package) (Phillips, 2021), (presence and background points), and Generalized Linear Models (GLM) using quadratic and linear terms.

To assess model extrapolation for current and future projections, we employed Mobility-Oriented Parity analysis. This procedure is based on the accessible area for each species (Moura et al., 2023a; Owens et al., 2013) as explained earlier. Validation techniques that incorporate geographical partitioning can significantly enhance error estimation when extrapolating (Roberts et al., 2017). In our study, we employed cross-validation to evaluate model performance. For our analysis of the current time, we performed cross-validation using the same random bootstrap partition method with 10 replicates. In each iteration, 70% of randomly selected samples were used to train the model, while the remaining 30% were used for testing (Andrade et al., 2020).

Model performance was assessed using the Jaccard similarity index. To create ensemble models for both current and future projections, we calculated a weighted average of the models based on their performance, as measured by the Jaccard similarity index. For each future scenario (year and SSP combination), we computed the average habitat suitability across the GCMs. Subsequently, the resulting ensemble projections were binarized into a presence-absence format using an average weighted binarization model.

For enhanced ENM accuracy and the reduction of overprediction often associated with presence-absence maps, we implemented an occurrence-based restriction. This constraint effectively guides our models based on both occurrence and suitability patterns. To determine which suitable patches should be included, we utilized the distance between points (Mendes et al., 2020). The distance threshold was established as the maximum nearest neighbor distance among pairs of species occurrences (Mendes et al., 2020). In total, we generated ENM models for species with a minimum of 10 records. Out of the 141 species considered, we were able to create ENM models for 125 species with more than 10 records (Supplemental Material). It's important to note that we developed ENM models for species across the entire Neotropics, which served as the background area for our analysis.

2.4. Presence-absence matrix

Using the ENM data, we constructed a presence-absence matrix for both present and future snake communities, with a spatial resolution of 10×10 km. Our analysis focused on calculating shifts in the geographic ranges of species across different temporal scenarios, spanning the entire distribution of species within our study area, the Gran Chaco. To predict changes in species ranges and assemblages, we estimated the area of polygons in square kilometers (km^2) for each species. For this study, we categorized species as either narrowly distributed, with an estimated range of less than 50 km^2, or widely distributed, with a range exceeding 50 km^2. We define this range following our knowledge of natural history of snakes in the Chaco.

2.5. Phylogenetic and functional data

To compute the phylogenetic metrics, we pruned the phylogeny developed by Tonini et al. (2016) to include only the species in our study area. This process was carried out using the 'phangorn' package (Schliep, 2011) and 'ape' (Paradis et al., 2004). For the assessment of functional diversity, we constructed a matrix of attributes (detailed in Table S8) related to body size, reproduction strategies, microhabitat use, and daily activity. Data sources for these attributes were obtained from Cabral et al. (2022) (Supplemental Material). From this attribute matrix, we created a multidimensional space in which functional diversity indices were computed through a Principal Coordinates Analysis (PCoA) using trait-based distances. We selected the dimensionality that best fit our data, which was determined to be four axes in our case (Table S9) following the methodology outlined by Mouillot et al. (2013). Subsequently, we constructed a functional dendrogram by applying the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) agglomeration method to the four primary PCoA axes. These analyses were conducted using the 'mFD' package (Magneville et al., 2022) in R (R Core Team, 2019).

2.6. Biodiversity metrics

We assessed beta-diversity for both present and future scenarios using the 'betapart' package (Baselga and Orme, 2012). Specifically, we calculated spatial beta-diversity for each grid by employing the Jaccard multiple site dissimilarity index. To mitigate the potential impact of cell sizes on the index, we implemented a subsampling procedure. This procedure involved randomly selecting four neighboring cells around each focal cell and then computing the average value of Beta-Jaccard across these interactions (Baselga and Orme, 2012). We computed phylogenetic beta-diversity across species assemblages for both present and future scenarios. Subsequently, we applied a null model to calculate the Standardized Size Effect (SES) of phylogenetic beta-diversity. This

allowed us to quantify phylogenetic diversity (PD) while correcting for species richness under both present and future climate scenarios. To calculate SES, we compared observed PD values to null expectations derived from shuffling tip labels multiple times (1000 runs). This tip shuffle model was executed using the 'phyloregion' package (Daru et al., 2020). Negative SES values indicate that species in the assemblages are more closely related than would be expected by chance (i.e., species cluster in the phylogeny), while positive values indicate that species in the assemblages are less related than expected by chance (i.e., species exhibit overdispersion in the phylogeny).

2.7. Temporal changes and biotic homogenization

We calculated the temporal changes in the spatial gradients of taxonomic and phylogenetic diversity for present and future scenarios, and the differences between present and future scenarios, using the ratio of Beta Diversity between future and present scenarios. By comparing the differences between future and present climate conditions, we aimed to identify assemblages undergoing either biotic homogenization (values < 0) or heterogenization (values > 0). This analysis provides insights into how species compositions are changing over time. Furthermore, we calculated changes in species richness and evaluated the proportion of widely and narrowly distributed species within species assemblages for both present and future scenarios. We then compared these values to identify differences between the two scenarios.

In our analysis, we also delved into the temporal changes in assemblages' functional diversity for both present and future scenarios. This exploration aimed to provide a deeper understanding of the temporal variations in taxonomic and phylogenetic diversity. To quantify functional diversity, we utilized the species functional dendrogram. From this dendrogram, we calculated the standardized effect size (SesFuncMPD) for all species within each community. This calculation involved employing null models with 1000 randomizations of tip labels. Positive SesFuncMPD values indicated higher functional diversity, while negative values indicated lower functional diversity. Furthermore, we computed three complementary indices for each community: Functional richness (FRic), which quantifies the amount of functional space occupied by the community (Villéger et al., 2008); Functional evenness (FEve), which characterizes the evenness of abundance distribution within a functional trait space (Villéger et al., 2008); Functional dispersion (FDis), representing the mean distance of individual species from the center of species within the community (Laliberte and Legendre, 2010). These analyses were conducted using the 'mFD' (Magneville et al., 2022) and 'picante' (Kembel et al., 2010) packages in R.

2.8. Biotic homogenization and protected areas

To assess the impact of biotic homogenization on future snake biodiversity, we integrated data on snakes' biodiversity under future scenarios with information on terrestrial Protected Areas (PAs) worldwide. Specifically, we focused on PAs located within the Chaco region and classified as categories I to IV. Information on PAs was sourced from the World Database on Protected Areas (WDPA), accessible at https://www.iucn.org/theme/protected-areas/our-work/world-database-protected-areas (accessed on January 16, 2021). By combining our database of biodiversity metrics with information on PAs, we aimed to gain insights into how biotic homogenization may impact assemblages within these protected areas.

3. Results

3.1. Species richness

In the future (2081–2100), snake richness in the Chaco region is projected to decline, resulting in a loss of 28 species. This reduction in species richness is expected to occur across different regions (Fig. 1A–C). Currently, the highest species richness per area exceeds 60 species, but future projections indicate that this number will decrease to around 40 species. Local and regional snake populations in the Chaco are both anticipated to experience declines, with certain areas facing the loss of 27 species (Fig. 1C). More than 20% of species assemblages are predicted to experience a decrease in richness. Significant changes in species composition are expected throughout the entire Chaco region, with the most noticeable alterations occurring in the southern and northern parts (Fig. 2A–D). Furthermore, there is a likelihood of some species facing local extinction due to the loss of all suitable habitat within the

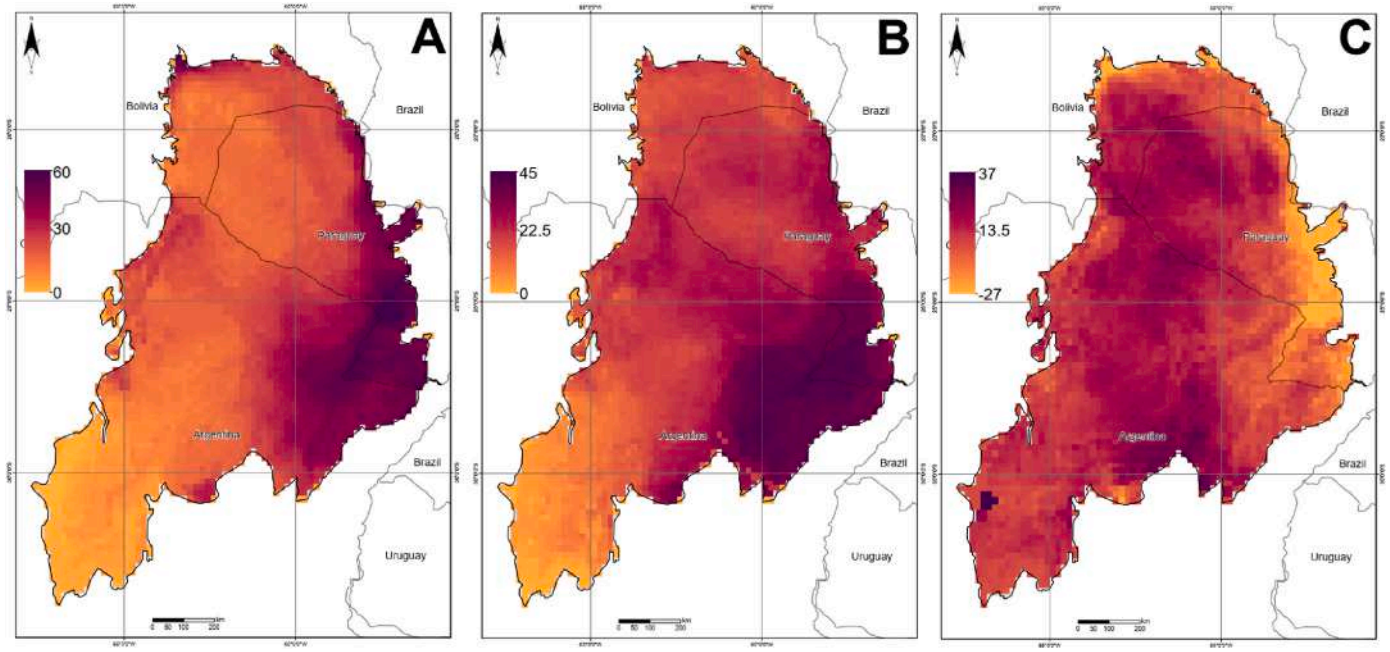

Fig. 1. Present (1950–2000) (A) and future (2081–2100) (B) species richness from the Chaco, and the projected difference in species richness between current and future (2100) (C).

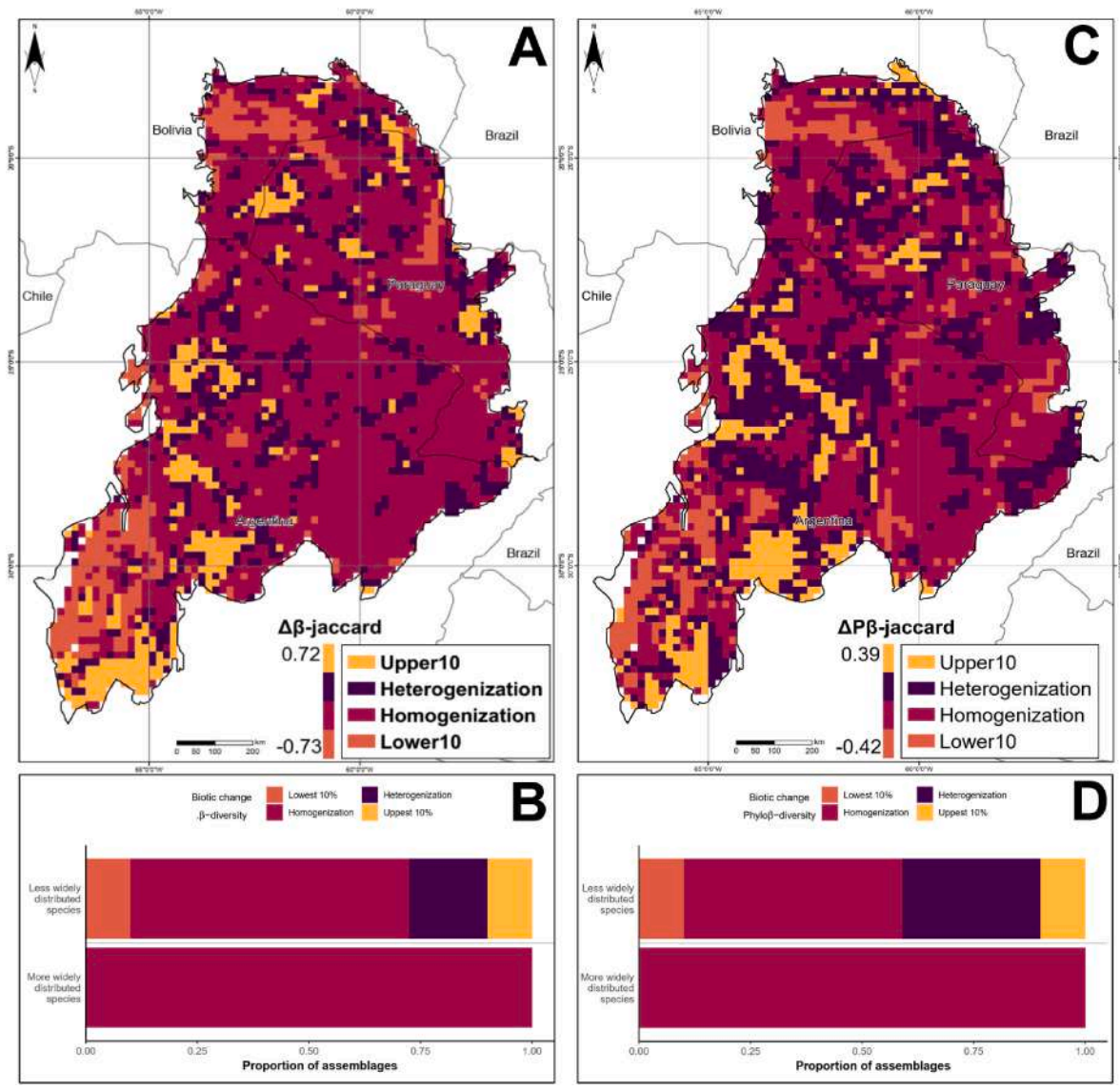

Fig. 2. Spatial pattern of expected biotic homogenization of Chaco between present and future (2100) (A–D). Taxonomic biotic homogenization Δβ-jaccard) (A) and proportion of biotic changes at assemblages' levels in β-diversity in the Chaco (B); Phylogenetic biotic homogenization ΔPβ-jaccard) (C) and proportion of biotic changes at assemblages' levels in Pβ-diversity in the Chaco (D). Biotic homogenization (values < 0), heterogenization (value > 0).

Chaco. Examples of such species include several *Chironius* spp., *Erythrolamprus aesculapii*, *E. typhlus*, *Micrurus frontalis*, and *Pseudoboa nigra* (Fig. 3A).

Among the species classified as arboreal, a significant majority, 10 out of 12 species, are expected to lose their suitable habitats within the Chaco. In contrast, for terrestrial species, 15 out of 49 are at risk of losing their entire habitats, and 10 species may experience a loss of more than 50% of their suitable habitat. Among the 10 semiarboreal species, 3 are anticipated to lose their entire habitat, while 4 face the prospect of losing at least 50% of their suitable habitat. Additionally, among the 23 semifossorial species, 6 are at risk of losing their entire habitat, and 5 could see more than 50% of their suitable habitat diminish. Finally, within the categories of 12 aquatic and 10 fossorial species, 1 species in each group is projected to lose their entire habitat, and 2 from each group may experience a reduction of at least 50% in their suitable habitat (Supplemental Material).

3.2. Biotic homogenization

Biotic taxonomic homogenization is anticipated to affect the entire snake assemblage in the Chaco (Fig. 2A and B). Conversely, we expect heterogenization to occur in roughly 30% of these assemblages, characterized by the addition of species with more restricted distributions. Widely distributed species are also poised to increase their occurrences and assume dominance in snake assemblages throughout the Chaco (Fig. 2A and B). When we consider biotic homogenization through the phylogenetic diversity metrics, it becomes apparent that approximately 60% of snake assemblages will undergo phylogenetic homogenization. This biotic homogenization is projected to span the entire Chaco region (Fig. 3C and D). Additionally, over 50% of assemblages comprising species with more restricted distributions are expected to experience biotic phylogenetic homogenization, while widely distributed species are likely to be present in 100% of the current assemblages (Fig. 2A–D).

Significantly, over 50% of snake species in the Chaco are projected to lose their suitable habitats by the year 2100, and this figure increases to more than 70% when considering their entire distribution (Fig. 3A and B). Conversely, only a small percentage of species are expected to experience a loss of less than 50% of their occurrence areas within the Chaco (Fig. 3A and B). In contrast, at least 20% of the species are predicted to retain more than 50% of their suitable areas within their entire

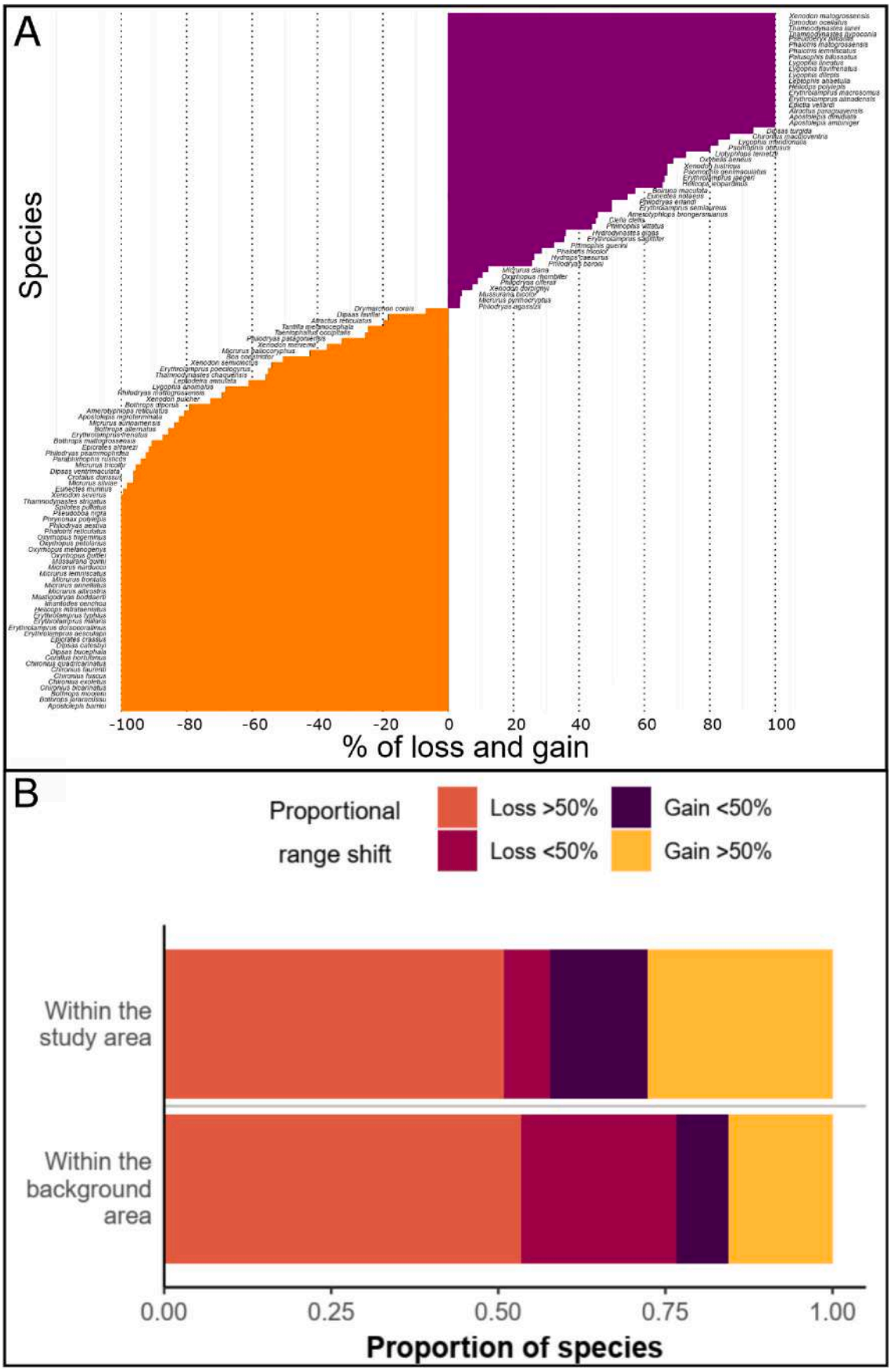

Fig. 3. Percentage of loss (negative values) and gain (positive values) of suitable habitats of snakes species in the Chaco (A). Projected changes in species range shift between the Chaco (study area) and Neotropics (Neotropics) (B). Projected changes are from present (1950–2000) to future (2081–2100).

distribution (Fig. 3A and B). Interestingly, nearly half of the species will gain suitable areas within the Chaco, and at least 25% of the species are expected to increase their suitable areas within their distribution range (Fig. 3A and B).

3.3. Functional richness

Functional richness (FRic) is expected to increase by 74% in future assemblages. However, both increases and decreases in FRic will not result in modifications to the present index value by more than 10% (Fig. 4). Changes in functional evenness (FEve) and dispersion (FDis) within assemblages are also projected to be relatively small, at approximately 2% and 3%, respectively (Table S10). It's worth noting that despite these modest changes, nearly all assemblages (93%) are likely to experience a loss of species with specific functional attributes, indicated by a decrease in their FDis, or they may not exhibit any significant change in this index, even in the presence of species replacements (Table S10).

Currently and in the future, most snake communities in the Chaco region exhibit functional diversity levels below the mean values expected in randomly assembled communities. Furthermore, in the future, this index is projected to decline even further in 74% of these communities. However, it is important to note that the observed values significantly deviate from those of null models in only 8.97% of present assemblages. This percentage increases to 10.69% in future snake communities. For a comprehensive overview of all functional diversity indexes, please refer to Table S10.

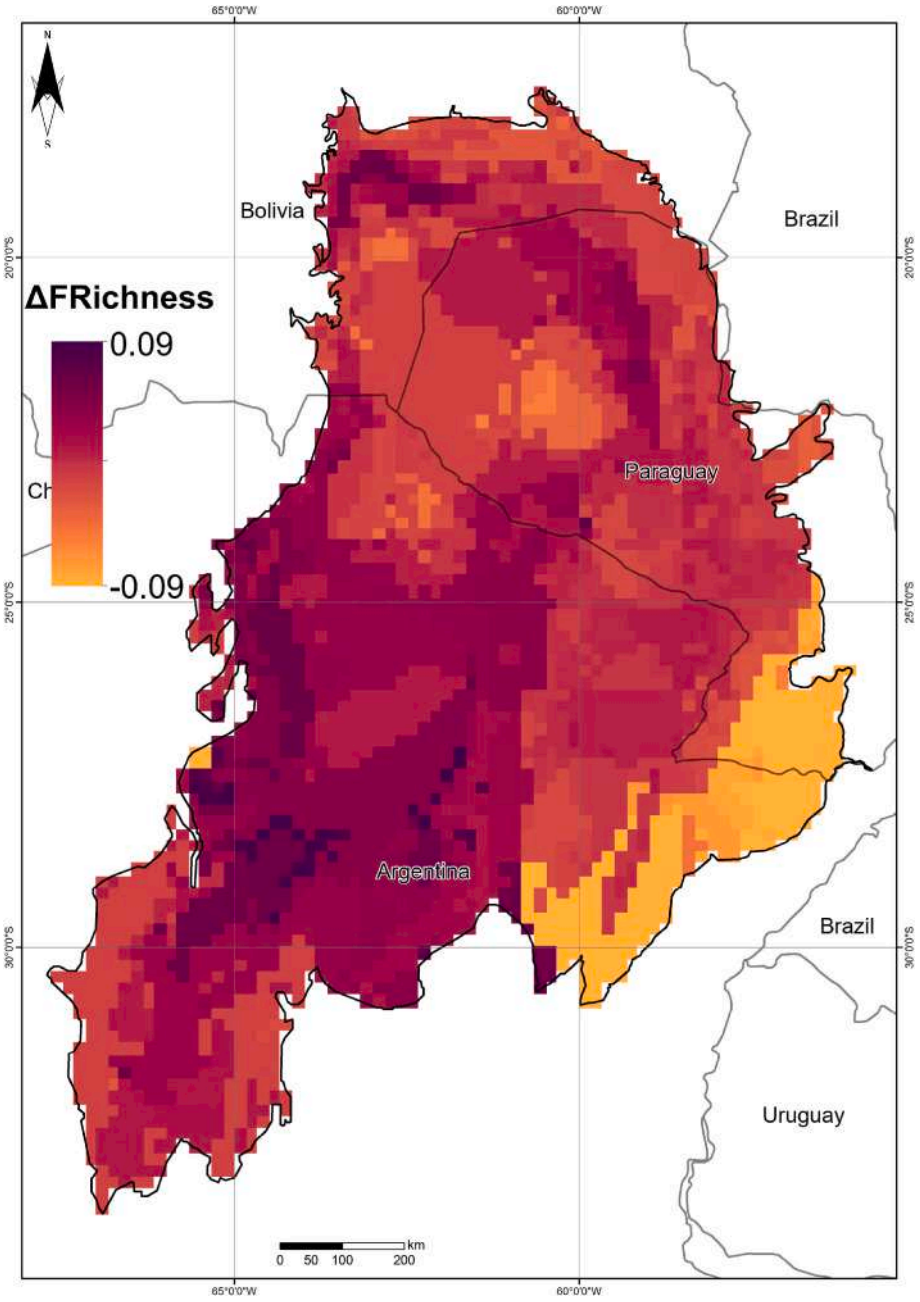

Fig. 4. Projected changes in Functional Richness between current and future Snakes communities from the Chaco. Projected changes are from present (1950–2000) to future 2081–2100).

3.4. Biotic homogenization and protected areas

In total, we have identified 56 protected areas (PAs) within the Chaco region, with a concentration of PAs in the northern, central, and southeastern parts, and a smaller number in the southern region (Fig. 5A, Table S8). Among these 56 PAs, we have identified a loss of species richness at the assemblage level in 23 of them. Some PAs are expected to lose at least 2 species, while others could lose as many as 15 species (Fig. 5A). In the future, widely distributed species are projected to be present in all PAs within the Chaco (Fig. 5B), and some PAs may experience complete homogenization (Fig. 5C). Additionally, nearly all PAs in the Chaco are likely to undergo spatial-temporal changes in species composition (Fig. 5D).

4. Discussion

4.1. Temporal changes and biotic homogenization

The anticipated changes in snake assemblages within the Chaco region under future climatic scenarios, particularly by the year 2100, reveal a clear trend towards biotic homogenization. This process involves the replacement of narrowly distributed species with more widely distributed ones, leading to a decline in the number of specialists, restricted, and endemic species (Clavel et al., 2011; Menéndez-Guerrero et al., 2020). The shift in habitat suitability for species does not exhibit a distinct pattern concerning phylogenetic or functional identity, complicating predictions regarding changes in suitable areas for species (Olden et al., 2004). This observation underscores the complex interplay between climate change and ecological processes, which encompass various aspects of species' natural history, species interactions, and environmental factors.

The consequences of biotic homogenization extend beyond alterations in species composition, resulting in diminished phylogenetic diversity within and among communities (Bellard et al., 2012; Menéndez-Guerrero et al., 2020). In the Chaco, biotic homogenization contributes to less diverse species assemblages, which would impact ecosystem functions, stability, and adaptability (Bellard et al., 2012; Menéndez-Guerrero et al., 2020; Olden et al., 2004). These changes affect the entire Chaco, highlighting the pervasive nature of the ecological transformations underway.

The Chaco, characterized as a dry ecosystem with extreme temperatures, provides essential habitat for numerous species reliant on forest or vegetation cover as a refuge from harsh conditions, particularly non-fossorial species lacking underground sheltering abilities (Cabral et al., 2022). Any alterations in climatic conditions within these forested habitats could lead to the regional extinction of species unable to rapidly adapt to such changes (Bellard et al., 2012; Seidl et al., 2017). While our study does not directly address deforestation, it's crucial to recognize deforestation as a significant driver of habitat modifications and shifts in species distributions in tropical regions (Andrade-Díaz et al., 2019; Jetz et al., 2007; Romero-Muñoz et al., 2020). The heightened rates of deforestation in the Chaco exacerbate the challenges faced by its unique and vulnerable ecosystems (Baumann et al., 2017; Hansen et al., 2013). The combined pressures of climate change and deforestation pose substantial threats to species associated with forested habitats in the Chaco, risking the loss of suitable habitat and further compromising the region's biodiversity and ecological integrity.

4.2. Temporal changes in functional metrics

The findings of our study underscore the heightened vulnerability of arboreal species in the Chaco region, particularly in the northern areas, to habitat loss driven by the ongoing process of savannization (Bellard et al., 2012; Sales et al., 2020; Seidl et al., 2017). This phenomenon, linked primarily to deforestation, poses a severe threat to arboreal species, potentially pushing them towards extinction in the Chaco's future. Similar shifts towards savannization have been observed in tropical forests, highlighting the broader implications of habitat degradation for arboreal species (Bellard et al., 2012; Sales et al., 2020). The impacts of habitat changes extend beyond arboreal species to terrestrial species in the Chaco, many of which rely on forested habitats for survival. Fluctuations in temperature and other climatic factors directly affect the habitat suitability of these species, emphasizing the interconnectedness between habitat conditions and species distribution (Bellard et al., 2012; Pacifici et al., 2017; Scheffers et al., 2014).

In contrast, fossorial and semifossorial species demonstrate a degree of resilience to the impacts of climate change due to the temperature-buffering effect provided by their burrows (Pacifici et al., 2017). Their ability to dig or bury themselves helps mitigate changes in temperature and precipitation, offering a survival advantage in changing environmental conditions. Our assessments of taxonomic, phylogenetic, and functional diversity in future scenarios reflect the concept of species replacement driven by habitat requirements and vegetation changes (Baselga and Gómez, 2019; Olden et al., 2004). The observed trend towards lower functional diversity in future assemblages suggests environmental constraints will shape snake community composition, potentially challenging the persistence of species with specific ecomorphological traits in altered areas (Menéndez-Guerrero et al., 2020; Olden et al., 2004).

The marginal increase in functional richness in future snake communities is likely attributed to the introduction of widely distributed species with generalist traits or fossorial morphologies (Menéndez--Guerrero et al., 2020; Pacifici et al., 2017). Consequently, this leads to a reduction in functional dispersion within assemblages, as they become dominated by snakes with similar morphologies, further highlighting the complex interplay between habitat alterations and species diversity in the Chaco region.

Simultaneously, the marginal increase in functional richness in nearly all snake communities in the future (Fig. 4) is likely a result of the introduction of widely distributed species, many of which exhibit habitat and morphological generalist traits or typically fossorial morphologies (e.g., *Dipsas turgida*, *Boiruna maculata*, *Phalotris matogrossensis*) (Menéndez-Guerrero et al., 2020; Pacifici et al., 2017). Consequently, this leads to a reduction in functional dispersion values within these assemblages, as they are more likely to be dominated by snakes with similar general morphologies (Menéndez-Guerrero et al., 2020; Pacifici et al., 2017).

4.3. Biotic homogenization and protected areas

The adverse effects of climate change on protected areas (PAs) in the Chaco region are evident, leading to biotic homogenization and a decline in species richness within these critical habitats. This situation underscores the urgent need to prioritize conservation efforts in the Chaco and implement strategies aimed at preserving biodiversity in this vulnerable area (Nori et al., 2016; Romero-Muñoz et al., 2020). As highlighted by Kuemmerle et al. (2017), the Chaco faces significant threats and should not be overlooked in conservation agendas focusing on Neotropical dry forests.

Establishing new Protected Areas (PAs) is essential for mitigating the impacts of climate change on snake populations in the Chaco, especially in regions where PAs are currently insufficiently represented, such as the southern area. Additionally, conservation decisions must be based on comprehensive data encompassing taxonomy, functionality, and phylogenetics to ensure that conservation efforts effectively safeguard species diversity. By integrating scientific research and conservation efforts, stakeholders can develop informed strategies to address the challenges posed by climate change and protect the unique biodiversity of the Chaco region. It is crucial to act decisively to conserve these habitats and their inhabitants for the well-being of ecosystems and future generations.

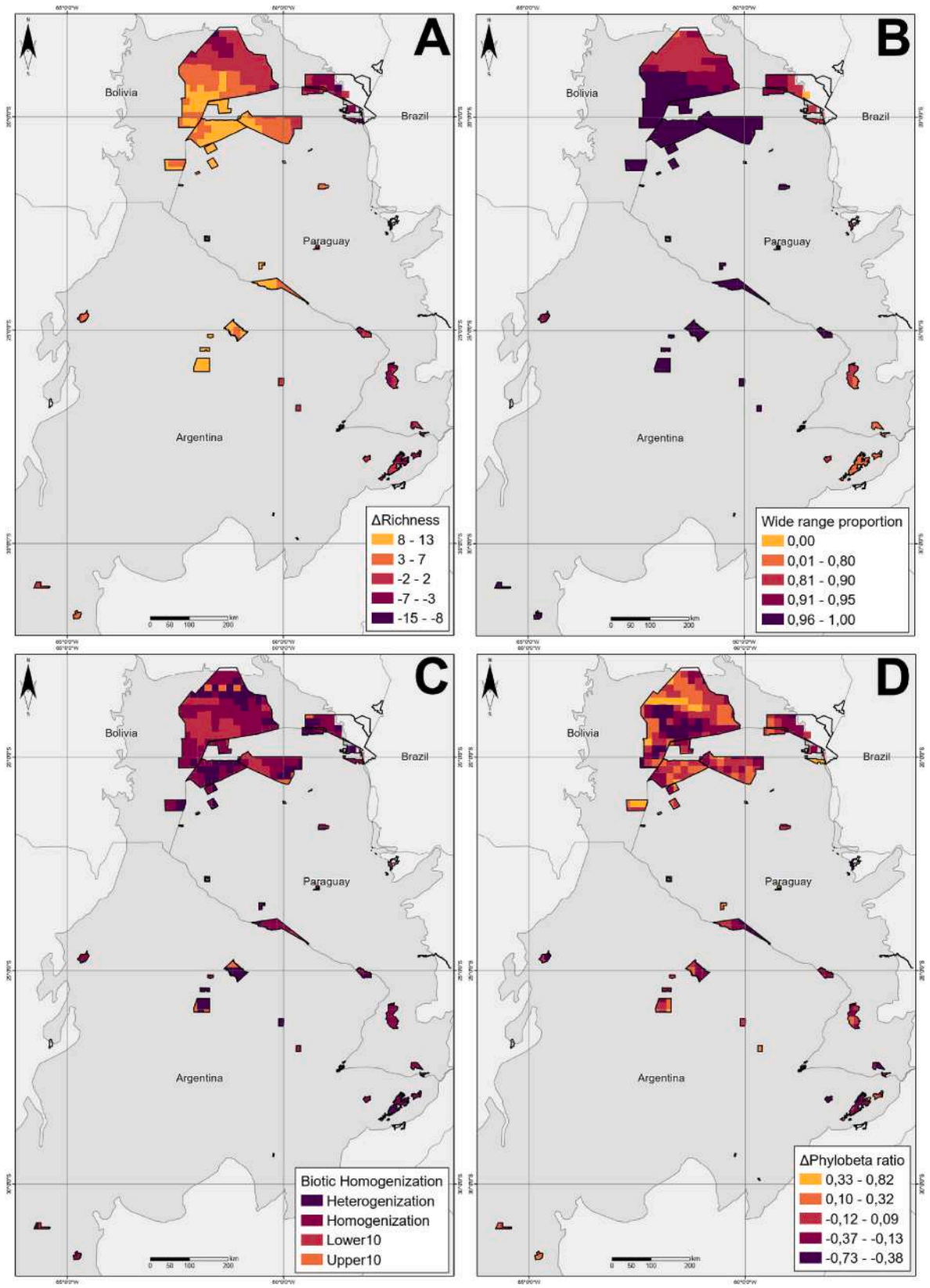

Fig. 5. Expected changes in Protected Areas in the Chaco, richness (A), proportion of widely distributed species (B), biotic homogenization (C), and spatial temporal changes in species composition (D). Projected changes are from present (1950–2000) to future (2081–2100).

5. Final conclusions

Our findings align with research conducted in other regions of South America, indicating that climate change would have a negative impact on communities, resulting in biotic homogenization across all aspects of biodiversity (taxonomy, functionality, and phylogenetics). For instance, in the Cerrado and Caatinga regions, biodiversity are vulnerable to the effects of climate change (Hidasi-Neto et al., 2019; Moura et al., 2023a; 2023b). Amphibians and birds are also susceptible to the impacts of climate change, with many areas in the Neotropics experiencing biotic homogenization (Hughes et al., 2022; Menéndez-Guerrero et al., 2020). Similar studies indicate that climate change would negatively affect amphibians and reptiles in regions adjacent to the Chaco, such as the Atlantic Forest, Cerrado, and Caatinga (Lourenço-de-Moraes et al., 2020; Maritz et al., 2016; Medina et al., 2020; Menéndez-Guerrero et al., 2020). These adverse effects would reduce the range of several species, leading to species extinction and a loss of taxonomic, functional, and phylogenetic diversity. As mentioned, numerous areas in South America are poised to suffer the consequences of climate change in the future (Medina et al., 2016; Hidasi-Neto et al., 2019; Moura et al., 2023a, 2023b). The results reveal a similar pattern for snakes in the Chaco, indicating a trend towards habitats becoming subject to biotic homogenization. Thus, the study demonstrates that snakes from the Chaco are endangered due to the adverse effects of climate change.

In conclusion, the study predicts significant changes in snake assemblages within the Chaco region in the future (2081–2100), characterized by a pronounced trend toward biotic homogenization across the ecoregion. This biotic homogenization manifests through the replacement of narrowly distributed species by widely distributed ones, resulting in the homogenization of both phylogenetic and functional diversity within local assemblages. Additionally, the loss of suitable habitat in the Chaco may lead to the local extinction of certain species. These adverse changes are not confined to snake communities alone; they extend to the protected areas (PAs) of the Chaco, where many are expected to experience biotic homogenization and a decline in species richness.

CRediT authorship contribution statement

Hugo Cabral: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Liliana Piatti:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Diego Santana:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors have declared that no competing interests exist.

Data availability

I have shared the link to my data in the Data Statement section

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2024.105214.

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