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LETTER

Decoupled responses of biodiversity facets driven from anuran vulnerability to climate and land-use changes

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Abstract

Biodiversity loss not only implies the loss of species but also entails losses in other dimensions of biodiversity, such as functional, phylogenetic and interaction diversity. Yet, each of those facets of biodiversity may respond differently to extinctions. Here, we examine how extinction, driven by climate and land-use changes may affect those different facets of diversity by combining empirical data on anuran–prey interaction networks, species distribution modelling and extinction simulations in assemblages representing four Neotropical ecoregions. We found a mismatch in the response of functional, phylogenetic and interaction diversity to extinction. In spite of high network robustness to extinction, the effects on interaction diversity were stronger than those on phylogenetic and functional diversity, declining linearly with species loss. Although it is often assumed that interaction patterns are reflected by functional diversity, assessing species interactions may be necessary to understand how species loss translates into the loss of ecosystem functions.

KEYWORDS
Anthropocene, Eltonian dimension, functional diversity, interaction diversity, phylogenetic diversity, trophic network

INTRODUCTION

Human-induced biodiversity loss is one of the most prominent disruptions to the natural environment (Turvey & Crees, 2019). Biodiversity changes in the Anthropocene are caused mainly by the increasing amount of the land surface used for human activities (i.e. land-use changes), but climate change is expected to intensify such impacts even further (Jantz et al., 2015; Newbold et al., 2019). Land-use changes generally reduce the habitat available for species (Newbold et al., 2016; Román-Palacios & Wiens, 2020) and may prevent species from reaching suitable environments by creating barriers for dispersal (Becker et al., 2007; Sales et al., 2020). Climate change may further reduce habitat availability by reducing the climatic suitability within a species distribution through incremental changes in mean climate parameters (Coumou & Rahmstorf, 2012). In addition, it enhances extinction risk due to the increase in the frequency and intensity of climate extremes (Coumou & Rahmstorf, 2012). Thus, climate change can interact with land-use change by exacerbating the impact of habitat loss, while land-use change may reduce species' ability to shift their distributions in response to climate warming (Oliver & Morecroft, 2014). Therefore, the Anthropocene is expected to result in an unprecedented reorganisation

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of the biota on Earth, as a result of local extinctions and climate-related distribution shifts (Newbold et al., 2019; Storch et al., 2021) driven by synergic pressures from land-use and climate changes (e.g. Guo et al., 2018; Sales et al., 2020).

The effects of climate change and habitat loss on biodiversity have been largely assessed through projections of changes in species distribution, and the resulting changes in species richness patterns (Jantz et al., 2015; Newbold, 2018). Recently, studies have also attempted to go beyond taxonomic losses and investigate losses in other components of biodiversity, such as the phylogenetic and functional diversity of communities (e.g. Brodie et al., 2021; Lourenço-de-Moraes et al., 2019). Functional diversity is traditionally assessed by the variety of biological traits present in a species assemblage that presumably influence their performance or ecosystem functioning (Petchey & Gaston, 2002; Villéger et al., 2008). Phylogenetic diversity, on the other hand, encompasses the evolutionary history of species in a community, often measured as the cumulative length of the branches on the evolutionary tree (Srivastava et al., 2012; Winter et al., 2013). By integrating these other facets of biodiversity, ecologists have been learning about how anthropogenic environmental changes may threaten ecosystem functions and services (Alahuhta et al., 2019). In this case, if shared evolutionary history among species is a good proxy for ecological similarity (the niche conservatism hypothesis), then these facets should respond similarly to species loss because losing phylogenetic diversity should result in the loss of functional diversity (Wiens & Graham, 2005).

In spite of those broader analyses of biodiversity in recent years, a missing component of diversity in several studies of biodiversity loss is the diversity of ecological interactions (Gaüzère et al., 2022; Valiente-Banuet et al., 2015). This Eltonian dimension (i.e. interactions between species and their effects on each other) may be crucial for understanding how biodiversity loss translates into the loss of ecological processes (Dehling & Stouffer, 2018). By promoting a reorganisation of ecological networks, biodiversity loss may alter ecosystem functioning (Schleuning et al., 2020). Earlier studies on the robustness of interaction networks focused on the consequences of random versus non-random biodiversity loss in ecological networks by evaluating the change in network structural metrics (Dunne et al., 2002; Memmott et al., 2004). Others have used a similar approach but simulating more realistic extinction scenarios (Donoso et al., 2020; Schleuning et al., 2020; Zamora-Gutierrez et al., 2021). Nevertheless, there is a lack of studies on how future climate change and land-use change will combine to alter ecological communities in their multiple biodiversity facets, including the interaction between species. Anticipating how climate and land-use changes may influence these multiple dimensions of biodiversity is crucial to understand the potential impacts on organism-mediated ecosystem goods and services.

Climate and land-use changes may have pervasive effects on vertebrates and invertebrates of all ecosystems (Sergio et al., 2018). Amphibians in particular are highly sensitive to climate and land use as they are affected by changes in both aquatic and terrestrial ecosystems (Blaustein & Kiesecker, 2002). Climate and land-use changes may severely affect habitat quality and availability as amphibians depend on water for reproduction and also reshape interactions in diverse trophic levels, once anurans can act both as predators and prey (Ceron et al., 2022). Because most anurans undergo ontogenetic niche shifts, land-use change can promote habitat split (i.e. spatial separation between remnants of terrestrial habitat and breeding sites), having a strong negative effect on anuran species with aquatic larvae, resulting in changes of population size, structure and distribution (Becker et al., 2007). In addition to that, because amphibians have limited dispersal ability (Green, 2003), habitat loss and fragmentation may limit gene flow and colonization success threatening the viability of populations (Becker et al., 2007; Cushman, 2006). Anurans are therefore useful models for studying the impacts of both threats, providing valuable insights into the consequences of such disturbances to terrestrial and freshwater communities (Hopkins, 2007).

Here, we examine how the different facets of the diversity (functional, phylogenetic and interaction diversity) of anuran assemblages would change if increasing sets of species went regionally extinct. We analyse anuran assemblages and anuran–prey networks representing different ecoregions in the Neotropical region under different scenarios of diversity loss by simulating the extinction of anurans according to vulnerability to climate and land-use changes. Specifically, we examine (1) how anuran vulnerability to climate-only and climate/land-use projections differ, (2) whether functional, phylogenetic and interaction diversity would respond in the same way to extinction (i.e. if they would show a joint decrease or distinct patterns due to extinction) and (3) how extinction would alter interaction patterns thus changing the structure of interaction networks. Because some anurans are disproportionately sensitive to land-use changes and others are more tolerant to these modifications, we expected that the anuran vulnerability rank to climate/land-use projections would differ (Newbold, 2018) when considering only climate or both climate and land-use scenarios. Regarding the responses of the facets of diversity to extinction, because morphological and life history traits often carry strong phylogenetic signals and are phylogenetically conserved in anurans (da Silva et al., 2012; Vidal-García & Scott Keogh, 2017) and, considering that anurans are assumed to be opportunistic predators with dietary patterns chiefly constrained by body size (Moroti et al., 2020), we hypothesized that functional, phylogenetic and interaction diversity should respond similarly to extinctions (Naisbit et al., 2012). Finally, because anurans are often regarded as opportunistic predators with

high dietary overlap (Ceron et al., 2019), we expected that anuran–prey networks would exhibit high structural robustness to extinctions, only presenting major structural changes after several species were lost.

MATERIALS AND METHODS

We sampled anurans and arthropods in 19 ponds distributed within four ecoregions, among which three were in the Chaco, five in the Cerrado, five in the Atlantic Forest and six in the Pantanal of Mato Grosso do Sul, central Brazil. For further details on sampling and a map of sampling locations, see Ceron et al. (2020, 2022). Thus, in order to perform the following analyses, we consider the set of species and interactions sampled in each region to be representative of these types of environments in each ecoregion.

Data collection

We collected geo-referenced occurrence data for 39 anuran species from the Global Biodiversity Information Facility (GBIF; www.gbif.org) and speciesLink (https://specieslink.net/). Records were downloaded using the function occ_search() from the R package *rgbif* (Chamberlain et al., 2021) then we used the package *CoordinateCleaner* for data cleaning (Zizka et al., 2019). We flagged and removed errors that are common to biological collections, including sea coordinates, zero coordinates and coordinate country mismatches. We also checked by temporal outliers and harmonisation of scientific names. In addition, all records underwent a thorough visual inspection and quality check, according to available literature (e.g. Haddad et al., 2013) and our own experience with anurans.

Species distribution models

We used species distribution modelling to generate potential distributions for each anuran species and project future changes in environmental suitability. Species distribution data were obtained from geo-referenced databases described above and from our own sampling in Mato Grosso do Sul state, resulting in a merged database with equal weights assigned to occurrences from both sources. We used 19 bioclimatic variables from the WorldClim database (Fick & Hijmans, 2017), and nine different algorithms implemented in the *biomod2* R package (Thuiller et al., 2016). We used three climate models to forecast the future redistribution of the anurans and projected their realized niches onto scenarios of climate change under two contrasting 'Shared Socioeconomic Pathways' (O'Neill et al., 2017): the SSP2-4.5 and SSP5-8.5, corresponding to optimistic and worst-case climate futures, respectively. To estimate the effects of habitat loss on species distributions, we used projections of changes in land use (Li et al., 2017) and created species-specific land-use masks, based on the IUCN habitat classification scheme (details in Supplementary Methods).

Simulating extinctions

To test how climate and land-use changes may individually affect species distribution we estimated range changes for two scenarios: (a) considering only the species' climatic niches and (b) considering both the climatic niche and land use (details in Supplementary Methods). Based on the estimated range loss, we created an anuran vulnerability rank, from the most to the least vulnerable (the expected 'losers' and 'winners' from climate change), according to the two scenarios mentioned above. Finally, we simulated the effect of the extinction of anurans according to their vulnerability to climate and land-use changes. In this sense, we assume that anurans that lost a greater proportion of their range are those species more likely to become extinct in local assemblages within each ecoregion.

Interaction networks

We built weighted matrices of interactions for each region, in which predator species are represented as columns and the abundance of prey categories (OTU) as rows. We calculated six network metrics commonly used to describe distinct aspects of the network structure: *Connectance*, *average species degree*, *modularity*, *weighted nestedness* (wNODF), *complementary specialization* (H2) and *functional complementarity* (details in Supplementary Methods). To assess the significance of the network patterns, we compared the observed values to those calculated for networks generated by the null models (details in Supplementary Methods). All network metrics and null models were calculated using the *bipartite* (Dormann et al., 2008) package in the R environment (R Core Team, 2021).

Interaction, functional and phylogenetic diversity

In order to calculate the *functional diversity* of each ecoregion, we used data on multiple species traits: size (snout-vent length, SVL, mm), mass (g), clutch size (number of oocytes), habitat use (fossorial terrestrial, aquatic or arboreal) and reproductive modes (number of reproductive modes, see Crump, 2015). Mass and size were obtained from sampled species from the four ecoregions (mean of adult individuals—a minimum of four individuals measured per species), and clutch size, habitat use and reproductive modes were obtained from specific literature

(Haddad et al., 2013; Oliveira et al., 2017). We computed the pairwise functional distances between all functional entities using the mixed variables coefficient of distance (i.e. a generalisation of Gower's distance), which quantifies the functional dissimilarity between all species pairs based on the suite of assessed traits (Pavoine et al., 2009). A functional distance matrix was obtained using ktab.list.df and dist.ktab functions of *ade4* R package (Dray & Dufour, 2007).

To compute *phylogenetic diversity*, we first built a community phylogenetic tree, including only the species sampled within a particular region, using sequences from Koroiva et al. (2020) (details in Supplementary Methods). Then we calculated pairwise phylogenetic distances among all pairs of anurans of each locality using the cophenetic distance (PDist) based on branch lengths (Sokal, 1973) using the cophenetic function of a *stats* R package (R Core Team, 2021).

To compute the *interaction diversity*, we used the weighted matrices of anuran–prey interactions, where each entry of the matrix represents the frequency of use of that prey category by each anuran species in a given ecoregion (Ceron et al., 2022). We calculated pairwise distances between all anurans using the Morisita–Horn distance, which takes into account the relative weights of pairwise interactions and is reported to be robust to under-sampling and unequal sampling sizes (Horn, 1966). To remove the influence of overabundant species, we transformed the data of Formicidae and Isoptera (most abundant interactions) using $\log(x+1)$ in all communities (Magurran, 2013). The interaction distance matrix was obtained using the vegdist function of *vegan* R package (Oksanen et al., 2017).

We performed principal coordinates analysis (PCoA) using the functional distance, phylogenetic distance and interaction distance matrix separately for each ecoregion. Entities coordinated on the first three principal axes (PC) of each PCoA were kept to build a multidimensional functional, phylogenetic and interaction space (Villéger et al., 2011). The three principal axes explained more than 50% of the variation across species for all facets of diversity and the deviation between distances and standardized distances (see Maire et al., 2015) using three axes was below 0.2 for all comparisons and decreased slowly as the number of axes increases, suggesting that three axes indeed represent most of the variation across species. To make sure that our choice of the number of dimensions was not affecting our interpretation of the results, we performed a sensitivity analysis recalculating functional, phylogenetic and interaction diversity with four, five and six axes (Figure S1). Next, we calculated the volume of each space using the convhulln function of the R package *geometry* (Habel et al., 2015). We then computed variation in the functional, phylogenetic and interaction spaces resulting from projected extinctions and compared how these trajectories differ from those obtained from random extinctions. To do this, we used the function extinction of the R package *bipartite* (Dormann et al., 2008) with 1000 replicates. We used the function funct.space.plot of *mFD* R package to visualize and plot interaction, functional and phylogenetic diversities and the function traits.faxes.cor to test for correlations between prey abundance and anuran traits to PCoA axes, to assess the contribution of specific variables to variation along each axis (Magneville et al., 2022). The R script to reproduce the analyses is available at https://doi.org/10.5281/zenodo.7314017.

RESULTS

We used species distribution models (SDMs) to calculate the proportion of species ranges projected to be lost or gained under future scenarios. The accuracy of models, expressed by TSS, ranged from 0.82 to 0.99 (Table S2). The three most frequent climatic variables with the highest importance for the distribution of anurans were precipitation of the warmest quarter (bio18), annual precipitation (bio12) and isothermality (bio3) (Table S2). Under both the optimistic and worst-case scenarios of climate and land-use change, the majority of species are predicted to experience a decrease in the proportion of climatically suitable environments by 2061 (Table 1). These losses are consistent across ecoregions with distribution reducing on average 65% in the most optimistic climate change scenario (SSP4.5), and 74% when land use is also considered (Figure 1, Table 1).

Based on the projected changes in distribution, we generated a vulnerability rank for anurans, in which species with a greater proportional reduction in the range are more vulnerable. This rank order varied between climate-only and climate/land-use projections (Table 1, Table S3) but was generally associated with the connectivity patterns of each species in the interaction networks representing different ecoregions. Species vulnerability was negatively related to the species degree (Figure S2, $F = 16.3$, df = 76, $r^2 = 0.17$, $p < 0.01$) such that highly connected species in the trophic networks tended to be less vulnerable (Figure 1).

Functional, phylogenetic and interaction diversity showed different responses to extinctions (Figure 2, Figure S3). Phylogenetic diversity changed little with extinction simulations, with a slight increase for higher levels of extinctions (Figure 2). Functional diversity was robust to low levels of extinctions, only changing after about 50% of species were extinct, when it started decreasing steeply for all ecoregions (Figure 2). There is a notable difference in the loss of diversity according to extinction projections (Figure 3), with land-use projections impacting more the functional diversity of anurans, mainly in the Atlantic Forest. Conversely, interaction diversity decreased faster and almost linearly in response to extinctions. Indicating a high sensitivity to the loss of species, especially in the Pantanal (Figure 2). Moreover,

TABLE 1 Number of species predicted to experience an increase (winners) or decrease (losers) in the proportion of their distribution range (mean of decrease/increase), and the number predicted to become extinct (zero projected occupancy) per ecoregion by 2061 under the two climate scenarios of mitigated (optimistic) and upsurge (worst-case) and according to climate-only and climate/land-use projections.

		Optimistic			Worst-case		
Ecoregion	**Projection**	**Winners**	**Losers**	**Extinct**	**Winners**	**Losers**	**Extinct**
Atlantic Forest	Climate-only	0	18 (−61%)	0	0	18 (−71%)	0
	Climate/land-use	0	18 (−75%)	0	0	17 (−79%)	1
Cerrado	Climate-only	1 (+44%)	18 (−74%)	0	1 (+80%)	18 (−83%)	0
	Climate/land-use	0	19 (−82%)	0	0	18 (−86%)	1
Chaco	Climate-only	4 (+23%)	15 (−62%)	0	3 (+44%)	16 (−65%)	0
	Climate/land-use	0	18 (−65%)	1	1 (+27%)	16 (−69%)	2
Pantanal	Climate-only	2 (+5%)	19 (−63%)	0	1 (+8%)	20 (−72%)	0
	Climate/land-use	0	20 (−74%)	1	0	17 (−74%)	4

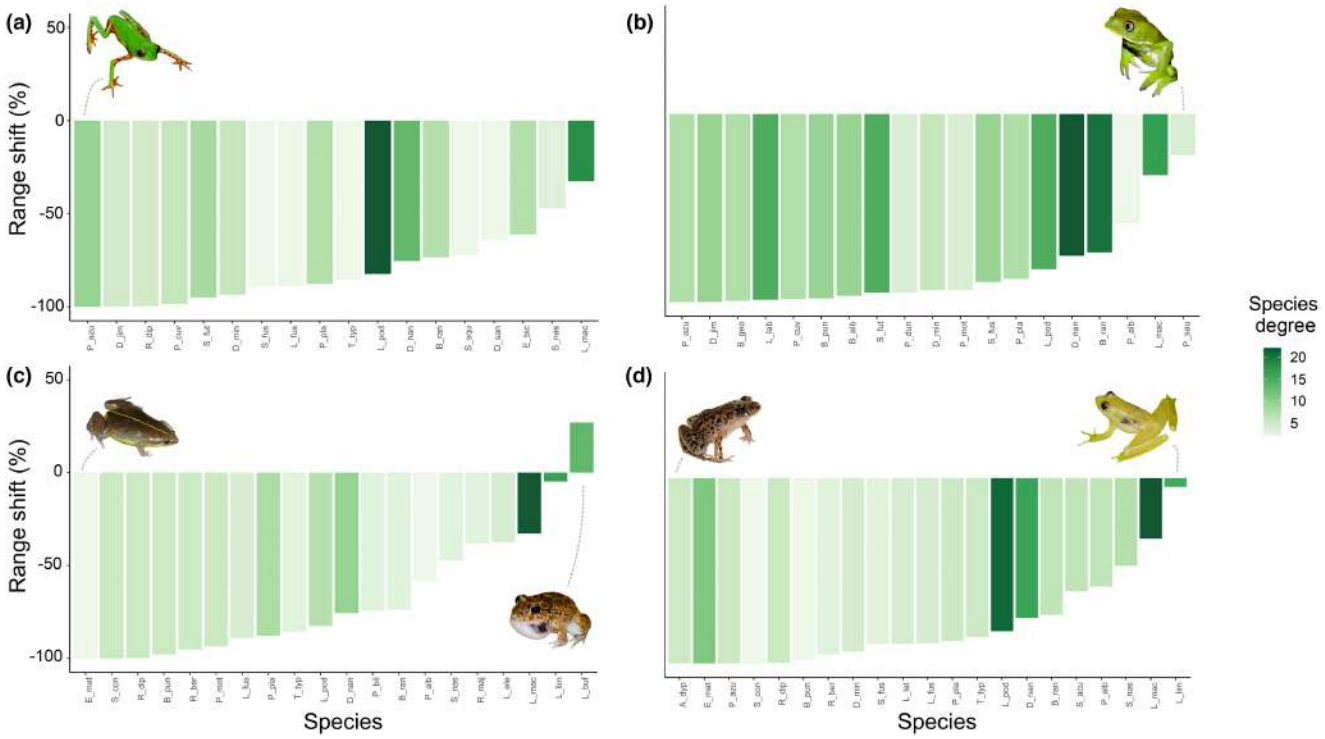

FIGURE 1 Anuran range shift in the per cent change in their distribution range (%) in each ecoregion by 2061 under the worst-case scenario: (a) Atlantic Forest, (b) Cerrado, (c) Chaco and (d) Pantanal. The colour gradient represents the number of interactions (species degree) of each species in anuran–prey networks. For species abbreviations, see Table S1.

when contrasting the effects of projected extinctions based on the vulnerability rank and random extinction sequences we found similar patterns for functional and phylogenetic diversity, but the impact on interaction diversity was generally greater than that estimated for the same levels of random extinctions (Figures S4–S6). These results were consistent when using more dimensions to compute the diversity facets, demonstrating that our choice of how many dimensions to use in the main analyses did not impact our main conclusions (Figure S1).

A more in-depth analysis of the functional space shows that functional diversity, and its reduction with extinction, were determined by different traits in different ecoregions. The volume of the functional diversity of anuran assemblages was determined by the variation of size/body mass and reproductive mode in the Atlantic Forest ($r^2_{\text{size/mass}} = 0.77$, $r^2_{\text{mode}} = 0.79$, $p<0.05$) and the Pantanal ($r^2_{\text{size/mass}} = 0.87$, $r^2_{\text{mode}} = 0.8$, $p<0.05$) (Figure 3). Functional diversity of Cerrado and Chaco were determined by the variation of reproductive modes ($r^2_{\text{Cerrado}} = 0.73$, $r^2_{\text{Chaco}} = 0.74$, $p<0.05$), together with habitat and size/clutch size, respectively ($r^2_{\text{Cerrado}} = 0.39$, $r^2_{\text{Chaco}} = 0.48$, $p<0.05$). Thus, while the reduction in functional diversity after species extinction in the Atlantic

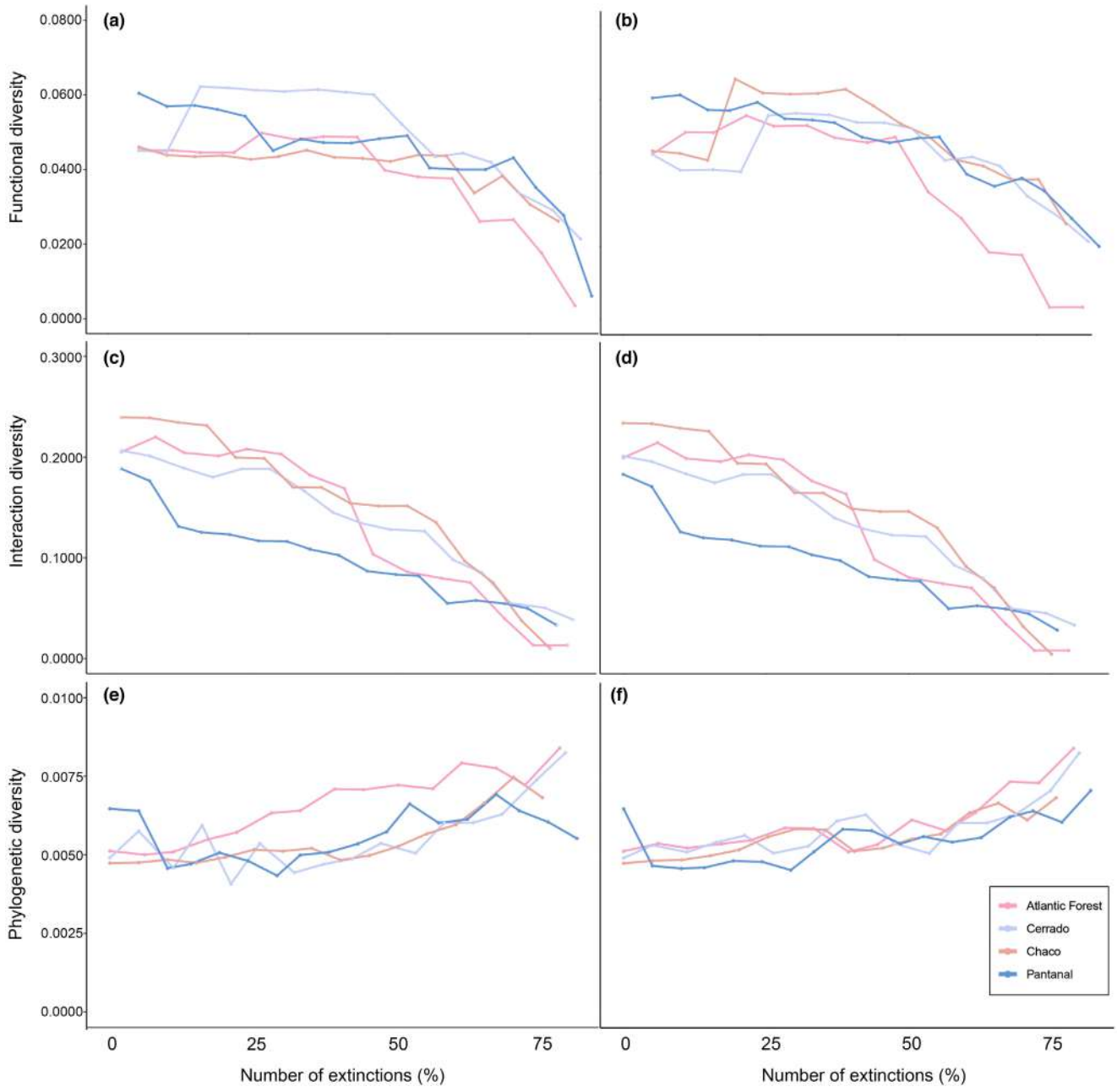

FIGURE 2 Variation in functional, phylogenetic and interaction diversity of anuran–prey networks under varying levels of species extinctions in each ecoregion. The extinction sequence was determined according to species vulnerability estimated under worst-case climate scenarios. In (a), (c), (e), the vulnerability was estimated based on range loss according to climate changes only; in (b), (d), (f), the vulnerability was estimated based on range loss according to climate and land-use changes.

Forest and Pantanal is driven mainly by the loss of large-bodied species, in the Chaco and the Cerrado reduction, is associated with reproductive traits or habitat preferences, respectively.

Interaction diversity of anuran–prey networks was determined mainly by the variation in the use of Formicidae ($r^2 = 0.40$, $p<0.05$) and Hemiptera/Odonata ($r^2 = 0.22$, $p<0.05$) in Atlantic Forest, Formicidae ($r^2 = 0.19$, $p<0.05$) and Diptera ($r^2 = 0.24$, $p<0.05$) in Chaco and Formicidae ($r^2 = 0.32$, $p<0.05$) and Araneae/Diptera ($r^2 = 0.25$, $p<0.05$) in Pantanal (Figure 4). Within the Cerrado, Hemiptera ($r^2 = 0.3$, $p<0.05$) defined the volume of interaction diversity, with no other prey group significantly correlated with the second axis ($p>0.05$). The loss in interaction diversity was greater from the start in the Pantanal, which is related to the loss of species with unique interaction patterns.

The interaction networks between anurans and their prey are structurally similar across ecoregions, showing modularity (mean 0.29) and specialisation values (mean 0.28) significantly larger than expected for randomised networks (Table S5). The main difference between

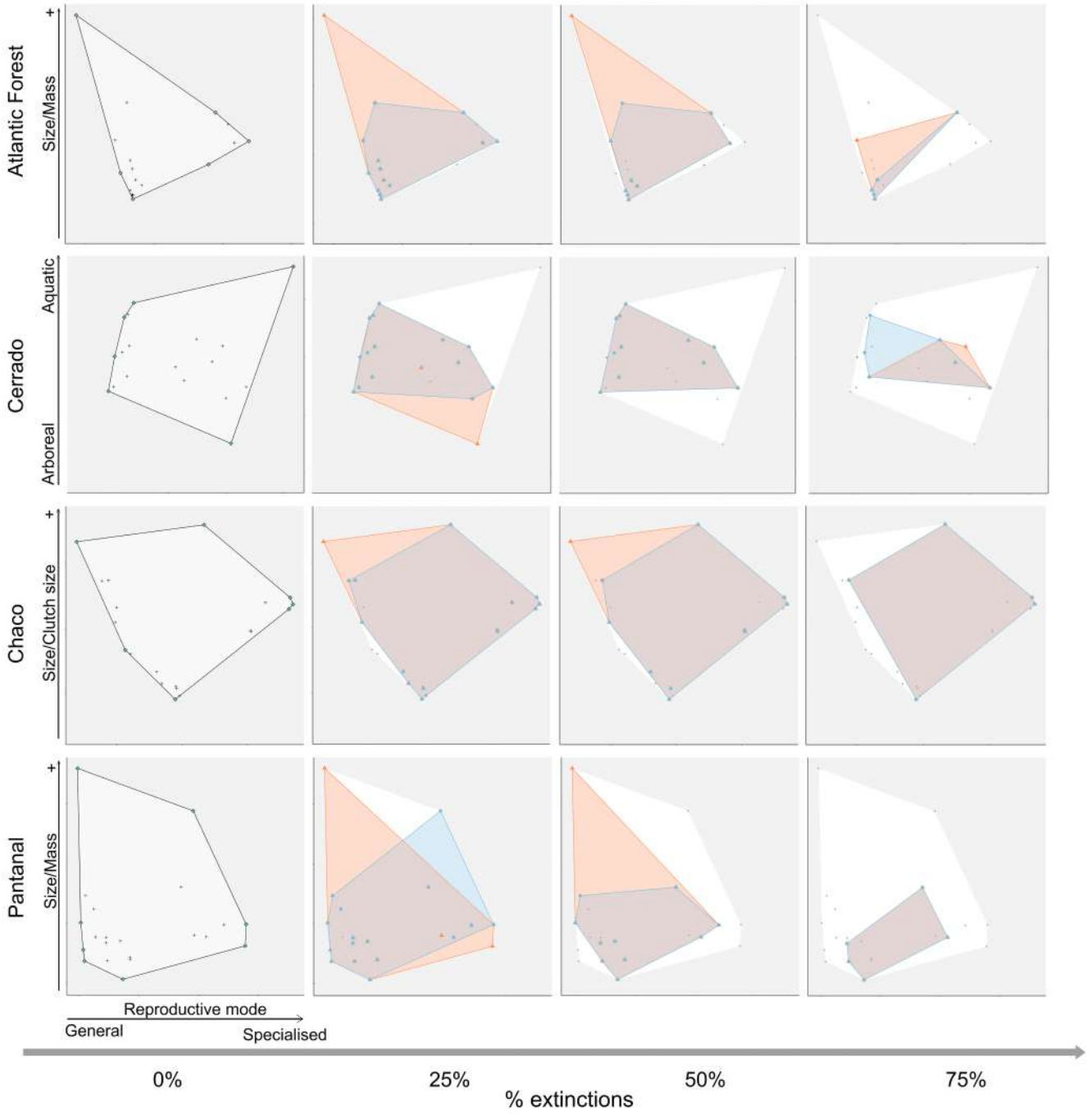

FIGURE 3 Change in the functional diversity of anuran–prey networks in response to extinctions in each ecoregion. Extinction sequence was determined according to species vulnerability estimated under the climate and land-use worst-case scenario, dots represent anuran species, the blue shape is the convex hull from climatic projection and the red shape is the convex hull from climate/land-use projection. The white polygon represents the initial space before extinction, and the purple shape is the overlap between the two projections (PC1 + PC2 > 50% of explanation).

networks representing different ecoregions is that in the Pantanal, anurans consume on average more prey per species and the Cerrado network has greater specialisation and lower variation in the number of interactions per species. Extinction simulations, from the most to the least vulnerable species according to the vulnerability rank, show that, even though interaction diversity drops quickly with extinction, networks present high structural robustness, with significant changes to their structure only after about 50% of species had been sequentially removed (Figure 5 and Figure S7, respectively). Overall, species removal resulted in networks that are progressively more connected, yet with greater mean specialisation for high extinction levels (Figure 5). Modularity and functional complementarity had little variation. The results were qualitatively similar for the extinctions following the vulnerability ranks based on different climate change scenarios (both optimistic and worst-case)

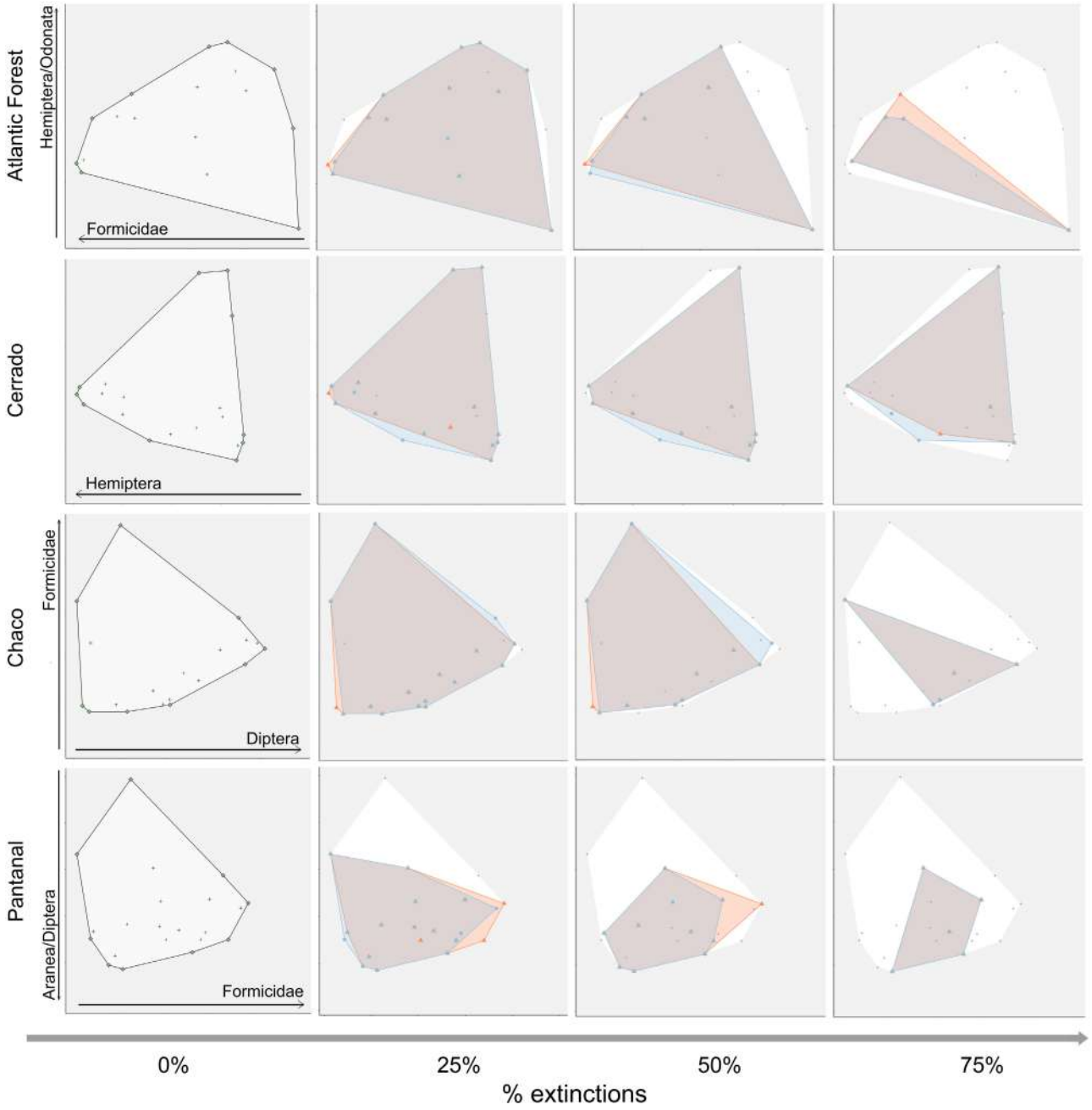

FIGURE 4 Change in the interaction diversity of anuran–prey networks in response to extinctions in each ecoregion. Extinction sequence was determined according to species vulnerability estimated under the climate and land-use worst-case scenario, dots represent anuran species, the blue shape is the convex hull from climatic projection and the red shape is the convex hull from climate/land-use projection. The white polygon represents the initial space before extinction, and the purple shape is the overlap between the two projections (PC1 + PC2 > 50% of explanation).

(Figure 5 and Figure S7, respectively). The two different extinction projections, that is climate and climate plus land use, produced meaningful differences only for the Atlantic Forest.

DISCUSSION

Changes in climate and land use are expected to reduce anuran distribution by promoting local extinctions, directly affecting functional, phylogenetic and interaction diversity in ecological communities. We found that anuran vulnerability, as measured by projected changes in geographical distribution, was generally associated with the level of trophic specialisation, signalled by the species' number of interactions in anuran–prey networks. We also found that there is a mismatch between the response of functional, phylogenetic and interaction diversity to extinction, with interaction diversity decreasing faster than phylogenetic and functional diversity, despite the overall network structure being seemingly robust to low levels of extinction.

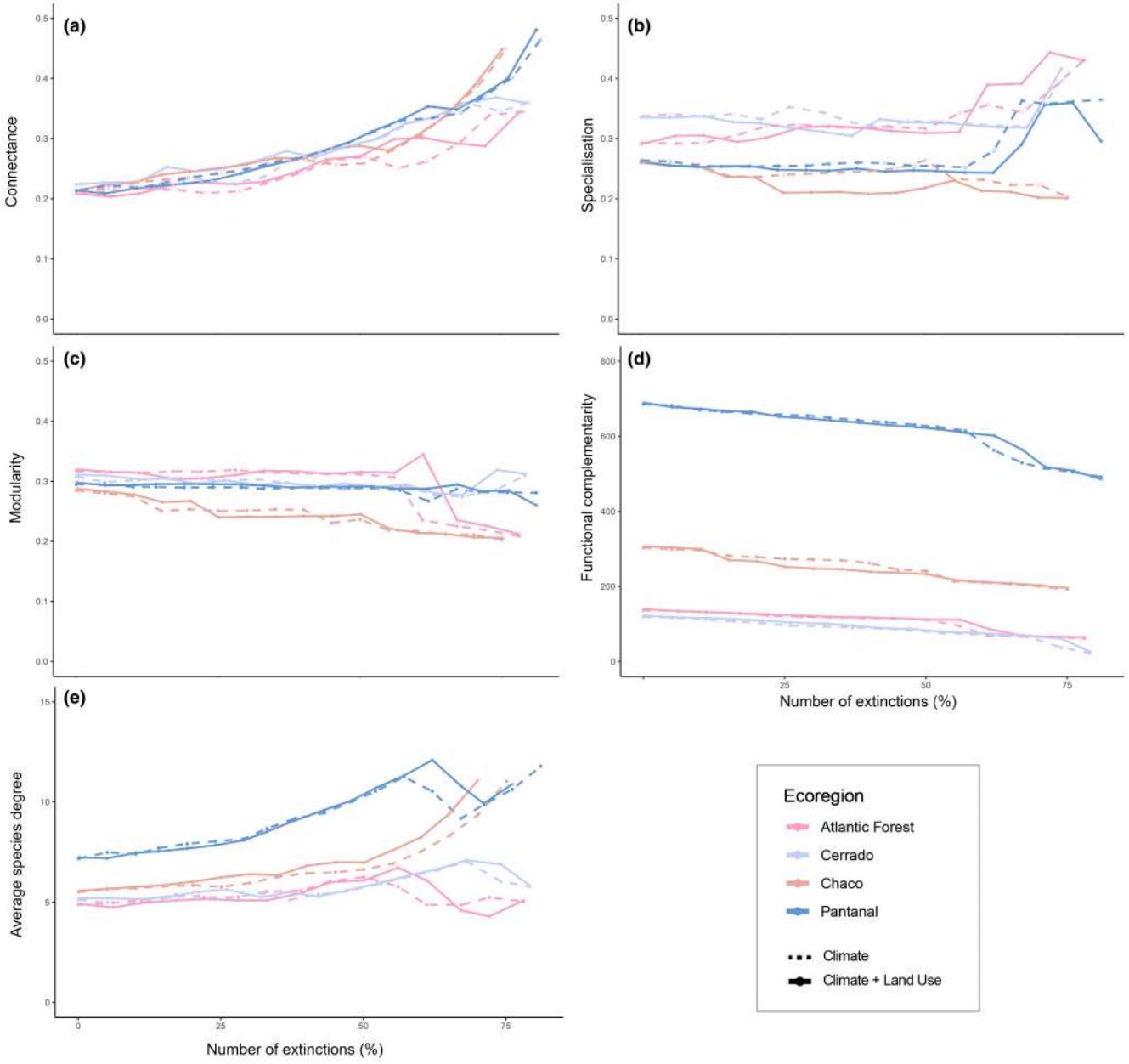

FIGURE 5 Variation in the structure of anuran–prey networks under varying levels of species extinctions in each ecoregion. The extinction sequence was determined according to species vulnerability estimated under the climate and land-use worst-case scenario.

The reduction of suitable environments driven by climate and land-use changes threatens anurans around the world (Newbold, 2018). Our study focused on amphibians from four ecoregions (Atlantic Forest, Cerrado, Chaco, and Pantanal) within the Mato Grosso do Sul state, Brazil. The knowledge of anuran diversity from this particular region is scarcely given that studies involving long-term inventories have only started at the beginning of the decade (Souza et al., 2017; Strüssmann et al., 2011). Those knowledge gaps limit our understanding of the historical changes in anuran assemblages in the study area, but the recent rise in research in this region and the advance in anuran taxonomy are contributing to a better comprehension of anuran diversity and its threats across the different ecoregions (Souza et al., 2017). A recent study on the composition of anuran assemblages in areas representing the Chaco and Cerrado found similar assemblages to those recorded in previous surveys a decade before (Santos et al., 2019), which suggests that during this period, assemblage composition has been resistant to changes. The most comprehensive work on the historical declines of amphibians focuses on the Atlantic Forest and reports that more than 100 species underwent population declines throughout the last century (Toledo et al., 2023). Because many of those declines were reported within protected areas, it is unlikely that the main driver is related to deforestation and at least some of those historical declines might be linked with

the amphibian chytrid fungus *Batrachochytrium dendrobatidis* (Bd) (Carvalho et al., 2017). Yet, our study area is located within one of the most threatened regions in the Neotropics because of the expansion of agriculture, with 27% of native vegetation lost in the past 40 years (MapBiomas, 2022). Although the sampled ponds still host relatively diverse anuran assemblages, the surrounding landscape is highly altered with the wetlands being constantly drained and vegetation replaced by pastures and cropland, mainly soybean (Gallant et al., 2007; Souza et al., 2017). One of the few studies contrasting anuran assemblages in ponds within soybean plantations and adjacent ponds outside the plantation zone found that tadpole abundance and richness were considerably lower in ponds within plantations (Cunha et al., 2021). Thus, even though communities may still be diverse locally, at the regional scale the metacommunity formed by ponds may be highly threatened. Furthermore, episodic events such as droughts and large-scale fires, which are projected to become more intense and frequent in the region (Marques et al., 2021), can drastically change anuran assemblages. Tomas et al. (2021) found that the intense wildfire that occurred in 2020 in Pantanal killed ca. 16,009,000 small vertebrates, of which 237,328 were anurans. Such massive numbers can cause extinctions at the local scale and affect long-term persistence of many species at the regional scale.

Despite the high levels of endemism and threats to anurans from Atlantic Forest, Cerrado, Chaco and Pantanal, here we focus on species that are not threatened. Yet even for those species, we show that climate and land-use changes may result in large reductions in their potential distribution. Our projections of climate-only and climate/land-use changes show that climate change alone is projected to reduce suitable environments by more than 50% on average, while accounting for land-use changes, these losses often surpass 70% for most ecoregions. Distribution contractions have been projected for anurans in the Neotropics as a whole (Menéndez-Guerrero et al., 2020) and within certain Brazilian ecoregions such as the Atlantic Forest (Lourenço-de-Moraes et al., 2019) and the Cerrado (Alves-Ferreira et al., 2022; Vasconcelos et al., 2018). Because of their dependence on water bodies, anurans are disproportionately sensitive to climate change, which is expected to promote a shrinkage in habitat availability as precipitation patterns change and the Neotropics become drier and subject to more prolonged droughts (Nolan et al., 2018). Land-use changes will have synergetic effects with climate change by reducing habitat availability further (Newbold, 2018), besides fragmenting the landscape. Because of their limited dispersal ability, anurans may not be able to reach suitable environments as climate changes, which may confine populations in unsuitable areas. This result is in line with that found by Ramalho et al. (2021), where land-use changes intensify the effect of climate on the distribution of anurans in the Atlantic Forest and suggest that habitat protection and reforestation are key to minimise the impacts of climate change.

In addition to those well-known threats, we found that species vulnerability is related to trophic breadth which shows that extinction could be ecologically selective. The loss of ecologically distinct species may result in homogenised amphibian assemblages (Dehling & Dehling, 2021). This high vulnerability to emergent threats like climatic and land-use change allied with the fact that anurans are one of the most underrepresented groups of vertebrates in the global network of protected areas (PAs) endorse that anurans are undergoing a global conservation crisis, becoming a high-priority group for which conservation efforts must be focused (Nori et al., 2015).

Contrary to our hypothesis, the functional, phylogenetic and interaction diversities did not respond in the same way to the loss of species. Functional diversity was nearly invariant up to 50% of species extinction when it started decreasing steeply for all regions. Functional diversity was determined mainly by reproductive mode and anuran size/mass, and in less extent by clutch size, and habitat. These traits are related to the capacity of anuran to breed, grow and reach suitable environments, which is often correlated with anuran extinction risk (e.g. Anjos et al., 2020; Fontana et al., 2021). This result highlights that functional redundancy safeguards functional diversity even at moderate levels of species loss (Sura et al., 2021). Likewise, phylogenetic diversity was low and did not vary significantly with the extinctions because the vulnerability rank shows no phylogenetic-selective patterns of extinction. The low phylogenetic diversity in studied assemblages may occur because the majority of species are concentrated in a few families, such as Hylidae (harbouring 45% of species), and Leptodactylidae (harbouring 34% of species), a pattern in many Neotropical anuran assemblages (Segalla et al., 2021), which may be a result of large radiations of few lineages generated by in situ diversification after few initial immigration events (Fritz & Rahbek, 2012). The small variation in phylogenetic diversity throughout the extinction sequences demonstrated that losses are well distributed across the phylogeny and not concentrated in specifics clades, which contrasts with scenarios in which, for instance, the loss of a long ancestral branch causes a large drop in phylogenetic diversity (Faith, 2015).

Different from the other facets of diversity, interaction diversity was highly impacted by extinctions (both in climate-only and climate/land-use projections), decreasing almost linearly in response to the loss of species. Interaction diversity was mostly determined by the variation in the consumption of certain prey such as Formicidae and Hemiptera. The high contribution of Formicidae to interaction diversity in Atlantic Forest, Chaco, and Pantanal is related to the presence of ant specialists in these regions (e.g. *Elachistocleis. matogrosso*,

E. bicolor, *Rhinella bergi*, *R. major*, Ceron et al., 2020). Because extinction vulnerability was associated with a low number of interactions, such species with unique dietary patterns were lost earlier in the extinction sequence impacting interaction diversity but with little effect on network structure.

This relationship between anuran vulnerability and species degree (i.e. a number of prey connected to each anuran) explains why interaction diversity was sensitive to extinction, while networks presented high structural robustness, with networks changing their structure only after more than 50% of species had been removed. Species that are less connected in interaction networks tend to be more vulnerable to climate change because they are more sensitive to resource shortages and are less likely to switch to alternate resources (Reed & Tosh, 2019). The loss of specialists thus leads to the extirpation of unique interaction patterns, but the structural consequences and the potential cascading effects of such losses, are smaller than the loss of generalists (Dunne et al., 2002; Pires et al., 2020). The loss of generalists leads to a greater restructuring of the network, besides impacting the whole network, because the more trophic links a species has to other species in a food web, the greater its potential to affect other species (Dunne et al., 2002). Also, the elevated structural robustness of networks to extinction is related to the presence of generalists (high connectance, Dunne & Williams, 2009) and to the high level of redundancy among generalist species (Allesina et al., 2009). Yet, any extinction may affect prey dynamics, releasing prey populations or favouring the rewiring of interactions, altering the ecosystem functioning and its associated services.

Functional diversity is often viewed as a proxy for interaction diversity and is key to understand the ecosystem functioning (Song et al., 2014). Here, we show that functional diversity and interaction diversity can be decoupled and respond in different ways to species loss. In this study system, focusing exclusively on functional diversity would lead us to underestimate the effects of climate and land-use change on the ecological diversity of anurans. This is particularly important if we consider that ecological functions are not strictly associated with life history or morphological traits but are mostly dependent on species interactions. The loss of unique interactions can result in the decay of ecosystem functions, and ultimately the collapse of derived services (Schleuning et al., 2020; Valiente-Banuet et al., 2015). For example, the dynamics of biological control of pests and vector disease by anurans may be highly affected as interaction diversity reduces, even if the overall network structure is maintained up to high levels of species loss. When interaction diversity is not reflected in the functional diversity, assessing the interaction patterns is necessary to understand the unique roles of species in ecological networks and how species loss may translate into the loss of ecosystem functions.

AUTHOR CONTRIBUTIONS

Karoline Ceron and Mathias M. Pires designed the study. Karoline Ceron and Diego J. Santana collected data. Karoline Ceron wrote the manuscript and Lilian P. Sales, Diego J. Santana and Mathias M. Pires contributed to revisions.

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SUPPORTING INFORMATION

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

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