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

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Abstract

Anthropogenic climate and land use changes are the main drivers of biodiversity loss, promoting a major reorganization of the biota in all ecosystems. Biodiversity loss implies not only in the loss of species, but also entails losses in other dimensions of biodiversity, such as functional diversity, phylogenetic diversity and the diversity of ecological interactions. 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 different facets of diversity (functional, phylogenetic, and interaction diversity) by combining empirical data on interaction networks between anurans and their prey, species distribution modeling and extinction simulations. We used species distribution modeling to forecast the redistribution of anurans and create a species vulnerability rank based on expected range changes, then we simulate the extinction of anurans based on this rank. Next, we computed the variation in the functional, phylogenetic, and interaction diversities resulting from projected extinctions in four different ecoregions in the Neotropics. We found that the anuran vulnerability to climate and land-use change varies according to the level of trophic specialization. We also found a mismatch in the response of functional, phylogenetic, and interaction diversity to species' extinction, whereby the effects on interaction diversity are stronger than those on phylogenetic and functional diversity. Although it is often assumed that interaction patterns are reflected by functional diversity, assessing the interaction patterns is necessary to understand how species loss may translate 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 expected to intensify such impacts even further (Jantz *et al.* 2015; Newbold *et al.* 2019). While land use changes generally reduce the habitat available for species (Foley *et al.* 2005; Newbold *et al.* 2016; Román-Palacios & Wiens 2020), climate change may reduce the climatic suitability within a species distribution through incremental changes in mean climate parameters (Coumou & Rahmstorf 2012). In addition, climate change enhances extinction risk due to the increase in the frequency and intensity of climate extremes (Coumou & Rahmstorf 2012). Therefore, the Anthropocene is expected to result in an unprecedented reorganization of the biota on Earth, as a result of local extinctions and climate-related migrations (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., Lourenço-de-Moraes *et al.* 2019; Brodie *et al.* 2021]. 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 spite of those broader analysis of biodiversity in recent years, a missing component of diversity in several studies of biodiversity loss is the diversity of ecological interactions (Valiente-Banuet *et al.* 2015; Gaüzère *et al.* 2022; Pugh & Field 2022). 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 reorganization 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 also 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 change and habitat loss may influence these multiple dimensions of biodiversity is crucial to understand the potential impacts on organism-mediated ecosystem goods and services.

Disturbances have pervasive effects on communities of vertebrates and invertebrates of all ecosystems (Sergio *et al.* 2018). However, climate change and habitat loss may have a particularly significant impact on amphibians, a sensitive group affected by changes in both aquatic and terrestrial ecosystems (Blaustein & Kiesecker 2002). Climate change may severely affect habitat quality as amphibians depend on water for reproduction, and also reshape interactions in diverse trophic levels, once anurans can act both as predators as prey (Ceron *et al.* 2022). 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 (Cushman 2006; Becker *et al.* 2007). Once it is well established that climate change might impact amphibian communities in the future (Vasconcelos *et al.* 2018), they are useful models for studying the impacts of climate change and habitat loss as a whole, providing valuable insights into the consequences of such disturbances to terrestrial and freshwater communities (Hopkins 2007).

Here, we examine how the different facets of diversity of anuran assemblages (functional, phylogenetic, and interaction diversity) would change if increasing sets of species went regionally extinct. We analyze anuran assemblages and anuran-prey networks from 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, and, (3) how extinction would alter network structure. We expected that anuran vulnerability rank to climate/land use projections would differ, once some anurans are disproportionately sensitive to land uses changes and others are more tolerant to these modifications (Newbold 2018). We also hypothesized that functional, phylogenetic, and interaction diversity might respond similarly to extinctions, since traits often carry strong phylogenetic signal and affect the incidence of ecological interactions (Naisbit *et al.* 2012). Yet, such properties should be more sensitive to species loss in assemblages with reduced functional redundancy. Finally, we predicted that the opportunistic dietary habits of anurans would provide anuran-prey networks with high structural robustness to extinctions (Ceron *et al.* 2019).

Methods

We sampled anurans and arthropods in 19 ponds distributed in 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). These ecoregions differ mainly in rainfall, with Cerrado and Chaco being considered a seasonally dry tropical forest, meaning that rainfall is less than c. 1800mm per year, with a period of at least 5–6 months receiving less than 100mm (Pennington *et al.* 2009). Thus, in order to perform the following analyzes, 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 R package *CoordinateCleaner* for data cleaning (Zizka *et al.* 2019). In addition, all records underwent a thorough visual inspection and quality check, according to available literature (Haddad *et al.* 2013; Ávila *et al.* 2021) and our own experience with anurans.

Species distribution models

We downloaded 19 bioclimatic variables from the WorldClim database (see http://www.worldclim.org/ for variable descriptions) at a resolution of 10 arc-min (Fick & Hijmans 2017), averaged over the 1970–2000 period. To avoid overprediction and low specificity, we cropped the environmental layers to span from latitude -90 to -30 and longitude -50 to 15 (values in decimal degrees). Duplicates were removed from grid cells (~3 km) using the R package *spThin* (Aiello-Lammens *et al.* 2015). To avoid bias related to the multicollinearity of the environmental explanatory variables, we calculated the Variance Inflation Factor (VIF) values for variables to each species. All values that were highly correlated (VIF > 5) were removed through a stepwise procedure, using *usdm* R package (Naimi 2013).

We used species distribution modeling to generate potential distributions for each anuran species. We used nine different algorithms implemented in the *biomod2* R package (Thuiller *et al.* 2016) including the following: three regression methods (GAM: general additive model (Hastie & Tibshirani 1990), GLM: general linear model (McCullagh & Nelder 1989), MARS: multivariate adaptive regression splines(Friedman 1991); three machine learning methods (GBM: generalized boosting model (Ridgeway 1999), MAXENT: Maximum Entropy (Phillips *et al.* 2006), RF: random forest (Breiman 2001), two classification methods (CTA: classification tree analysis (Breiman 1984), FDA: flexible discriminant analysis (Hastie & Tibshirani 1990), and one envelope model (SRE: Surface Range Envelop (Booth *et al.* 2014). To meet the criteria of having absence (or pseudo-absence) data for most of these models (except SRE), we generated two equal-sized sets of random pseudo-absence (PA) points, with the same size of the sets of true presences, across the model background (500 PA points in each set). The models were calibrated using 70% of randomly selected data. The other 30% of the data were used for intrinsic model evaluation.

Individual model performance was evaluated using two metrics—true skill statistic (TSS) and the area under the curve of receiver operating characteristics (ROC) implemented in the *biomod2* R package. TSS is calculated as "sensitivity + specificity -1" and ranges from -1 to +1, where +1 indicates perfect agreement, a value of 0 implies agreement expected by chance, and a value of less than 0 indicates agreement lower than expected by chance. Only those models with high predictive accuracy (TSS > 0.8) were used for the projection of anuran distribution; poorer models were discarded. We constructed ensemble maps based on the median of two runs of all the selected models in which individual accuracy had

TSS value equal to or greater than 0.8. Continuous predictions of ensemble models were transformed into a predicted bivariate map of potential presence versus absence of the species. Variable importance in the ensemble prediction was evaluated with a permutation procedure [see Thuiller *et al.* (2016) for details].

Distribution forecasts

We forecast the future redistribution of the anurans and projected their realized niches onto scenarios of climate change. Ensembles of ecological niche models were calibrated and evaluated using present-day occurrence records of species and were projected into the future up to the years 2030s (2021-2040) and 2050s (2041-2060), based on gridded cell-based information on climate at a resolution of 10 arc-min (Fick & Hijmans 2017). We obtained information on future climate from the Coupled Model Intercomparison Project 6 (CMIP6) for two 'Shared Socioeconomic Pathways' (O'Neill *et al.* 2017): the SSP2-4.5 ("optimistic") and SSP5-8.5 ("pessimistic"). Shared Socioeconomic Pathways (SSPs) are scenarios of projected socioeconomic global changes used to infer greenhouse gas emissions according to various climate policies. The scenarios SSP2-4.5 and SSP5-8.5 represent a relatively optimistic and a more pessimistic projection, respectively, in terms of international policy towards environmental sustainability and greenhouse gas emission reduction (Meinshausen *et al.* 2020). For each SSP, the IPCC makes available climate models with distinct parameter inputs produced from different methods. To encompass the uncertainty in future climate projections, we selected three of these climate models, namely BCC-CSM2-MR, CanESM5, and MIROC6 (Sales *et al.* 2021). Regions of high habitat suitability through GCMs were identified by stacking and selecting only overlapping areas among the three GCMs to build a consensus map.

Habitat loss

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, the most comprehensive effort available to characterize species habitat affiliations (https://www.iucnredlist.org/resources/habitat-classification-scheme). The major habitat types according to this scheme are forest, savanna, shrubland, grassland, wetlands (inland), rocky areas (e.g., inland cliffs, mountain peaks), caves and subterranean (non-aquatic), arid or semi-arid (desert), artificial-terrestrial (e.g., Pastureland, Plantations, Urban areas, and heavily degraded forest). We considered as habitat specialist species all those species whose occurrence was restricted to a single major land cover type (e.g., forest), regardless of the specific category of land cover. Species were, assumed to be unable to occupy major habitat types where they had not been recorded before. As these habitat types can be matched with terrestrial land use, known as the area of habitat (Brooks *et al.* 2019), we grouped the habitat data into six major land cover classes (water, forest, grassland, farmland, urban, and barren). By doing so, we were able to reconcile the information on species-habitat associations to a global model that projects changes in land-use and land-cover (LULC) [Li *et al.* 2017, described in Appendix S1 land-use and land-cover section].

Simulating extinctions

To test how climate and land use change 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. To calculate the changes in the distributions in the future scenarios we used the function BIOMOD_RangeSize of R package *biomod2* (Thuiller *et al.* 2016) to estimate the proportion and the relative number of pixels (or habitat) lost and gained under future scenarios. 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 in trophic networks 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

For each ecoregion, we built weighted matrices of interactions containing predator species 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. These metrics were calculated separately for networks representing each ecoregion. *Connectance* describes the ratio between the total number of observed links in a network and the theoretical maximum number of possible links. It can be viewed as a measure of specificity of interactions in the network, being an estimate of how interactions are constrained within the community (Jordano 1987). *Average weighted degree* is the mean of the number of prey connected to each anuran, weighted by the intensity of each edge. The weighted degree was calculated with the R package *tnet* with the parameter alpha = 0.5, treating the number and weights of interactions equally (Opsahl 2009; Opsahl *et al.* 2010).

Modularity is a network property that emerges when groups of species are densely connected and have sparser connections to other groups of interacting species. We analyzed modularity using the recently implemented "DIRTLPAwb+" algorithm, which outperforms other algorithms in detecting subsets of species interacting disproportionally among them than with other members of a bipartite weighted matrix (Beckett 2016). We set this algorithm to 100 steps to search for the highest modularity (Dormann & Strauss 2014). The modularity ranges from zero (minimum modularity) to 1 (maximum possible modularity). *Weighted nestedness*, based on the index Nestedness Metric Based on Overlap and Decreasing Fill (NODF), describes the extent to which the interaction partners of one specialist species correspond to a subset of the interaction partners of generalist species (Bascompte *et al.* 2003). Nestedness values range from 0 (non-nested network) to 100 (perfect nestedness).

Complementary specialization (H2') is derived from two-dimensional Shannon entropy and quantifies the niche partitioning among species considering partner availability (Blüthgen *et al.* 2006). Thus, it is interpreted as a measure of interaction exclusiveness. The biological assumption is that if species have preferences for specific interaction partners, these preferences would be captured as a deviation from random encounters given by partner availability (Blüthgen *et al.* 2006). Values of H_2’ range from 0 to 1 indicating the extremes of generalization and specialization, respectively. *Functional complementarity* is a measure of community-level niche complementarity, in this case, the with which anurans vary in their interaction patterns (Devoto *et al.* 2012). We used a null model (i.e., *sampling.web*) to control for variation of functional complementarity from empirical networks (i.e., relative functional complementarity).

To assess the significance of the network patterns, we compared the observed values of wNODF, modularity, and H_2’ to those generated by null models. We used the *vaznull* null model, which keeps the marginal totals and the connectance in the network (Dormann *et al.* 2008). To quantify the departure of the observed network values from the null expectation, we calculated null-model standardized values, *z*, for each metric, *x*, as $z = x - \bar{x}_{null}/sd(x)$(z – transformation). We considered z values higher than two indicate that the difference between the observed and null networks for that specific structural property is statistically significant. 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)). Trait data was obtained from collected specimens or the literature (Haddad *et al.* 2013; Oliveira *et al.* 2017; Ávila *et al.* 2021). We computed the pairwise functional distances between all functional entities using the mixed-variables coefficient of distance (i.e., a generalization 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, using sequences from (Koroiva *et al.* 2020), which are samples of individuals from our study localities. Additionally, five sequences from molecular samples were used from literature data (Table S1). The resulting sequences were edited and aligned using Geneious v. 9.1.2 with the MUSCLE algorithm using default parameters (Edgar 2004). The final aligned dataset used in all analyzes comprised 477 base pairs (bp) (Table S1). We used the Bayesian Information Criterion in jModelTest (Darriba *et al.* 2012) to determine that HKY+I+G was the best model of nucleotide substitution. We performed a Bayesian phylogenetic analysis of COI using BEAST v.2.6.6 (Bouckaert *et al.* 2019) for 50 million generations, sampling every 5,000 steps using a Yule Process tree prior. We checked for stationarity by visually inspecting trace plots and ensuring that all values for effective sample size were above 200 in Tracer v1.7.1 (Rambaut *et al.* 2018). The first 10% of sampled genealogies were discarded as burn-in, and the maximum clade credibility tree with median node ages was calculated with TreeAnnotator v.2.6.3 (Bouckaert *et al.* 2019). Then we calculated pairwise phylogenetic distances among all pairs of anurans of each locality using the cophenetic distance (PDist) based on branch lengths (Sneath & Sokal 1973) using cophenetic function of *stats* R package (R Core Team 2021).

To compute the *interaction diversity*, we used the weighted matrices of anuran-prey interactions containing predator species as rows and prey categories (OTU) as columns. 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 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 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 coordinates 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; Mouillot *et al.* 2014). 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) under 1,000 replicas. 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 preys and anuran traits to PCoA axes (Magneville *et al.* 2022). The R script to reproduce the analyses is available in https://github.com/karolceron/facets.

Results

We used species distribution models (SDMs) to calculate the proportion of species ranges projected to be lost under future scenarios. The accuracy of models, expressed by TSS, ranged from 0.82 to 0.99. The three most frequent climatic variables with the highest importance for the distribution of anurans were precipitation of warmest quarter (bio18), annual precipitation (bio12), and isothermality (bio3). Under both the SSP 4.5 and SSP 8.5 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 (from 79% to 100% of decrease) (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 S2), 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 weighted degree of species (Figure S1, 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).

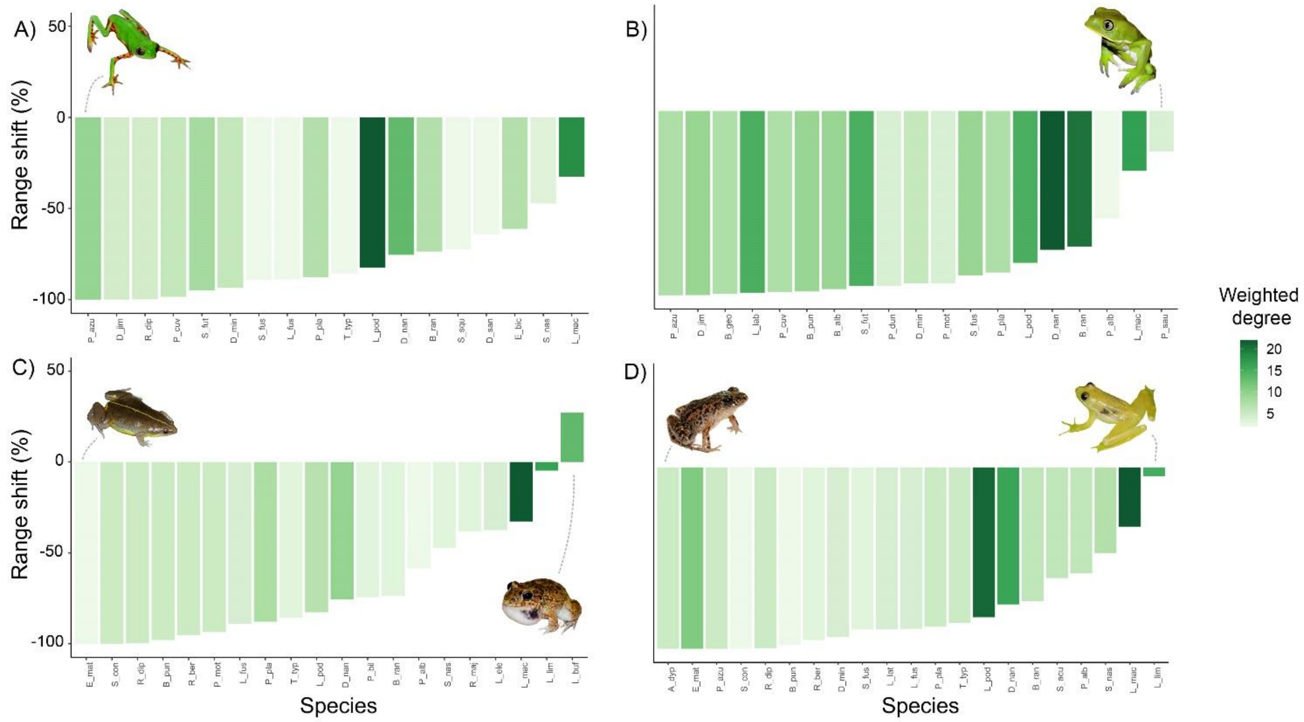

Figure 1: Anuran range shift in the percent change in their distribution range (%) in each ecoregion by 2061 under the SSP 8.5 scenario: a) Atlantic Forest, b) Cerrado, c) Chaco and d) Pantanal. Color gradient represents the number of interactions (weighted degree) of each species in anuran-prey networks. For species abbreviations see Table S1.

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 number predicted to become extinct (zero projected occupancy) per ecoregion by 2061 under the two climate scenarios of mitigated (SSP 4.5) and upsurge (SSP 8.5) and according to climate-only and climate/land-use projections.

Ecoregion	Projection	SSP 4.5			SSP 8.5		
		Winners	Losers	Extinct	Winners	Losers	Extinct
Atlantic Forest	Climate	0	18 (-61%)	0	0	18 (-71%)	0
	Land use	0	18 (-75%)	0	0	17 (-79%)	1
Cerrado	Climate	1 (+44%)	18 (-74%)	0	1 (+80%)	18 (-83%)	0
	Land use	0	19 (-82%)	0	0	18 (-86%)	1
Chaco	Climate	4 (+23%)	15 (-62%)	0	3 (+44%)	16 (-65%)	0
	Land use	0	18 (-65%)	1	1 (+27%)	16 (-69%)	2
Pantanal	Climate	2 (+5%)	19 (-63%)	0	1 (+8%)	20 (-72%)	0
	Land use	0	20 (-74%)	1	0	17 (-74%)	4

In general, there was little variation among ecoregions in functional, phylogenetic, and interaction diversity (Table 2). Interaction diversity was larger in the Chaco (0.23) and lower in the Pantanal (0.18), indicating anurans in the Chaco had lower overlap in prey use. Functional diversity was higher in Atlantic Forest and the Pantanal (0.063), indicating greater variation among anurans traits (i.e., size, mass, clutch size, habitat, and reproductive modes) compared to other regions, whereas phylogenetic diversity was higher in Pantanal (0.006).

Table 2: Overall volume of functional, phylogenetic, and interaction diversity by ecoregion

Ecoregion	Diversity		
	Interaction	Functional	Phylogenetic
Atlantic Forest	0.2000	0.0639	0.0056
Chaco	0.2344	0.0493	0.0047
Cerrado	0.2016	0.0483	0.0049
Pantanal	0.1835	0.0637	0.0065

Functional, phylogenetic, and interaction diversity showed different responses to extinctions (Figure 2, Figure S2). 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). The Cerrado ecoregion showed a higher loss of functional diversity since the beginning of the extinction sequence, both in climate and land use extinction schemes. 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 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, 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 same levels of random extinctions (Figures S3, S4, and S5).

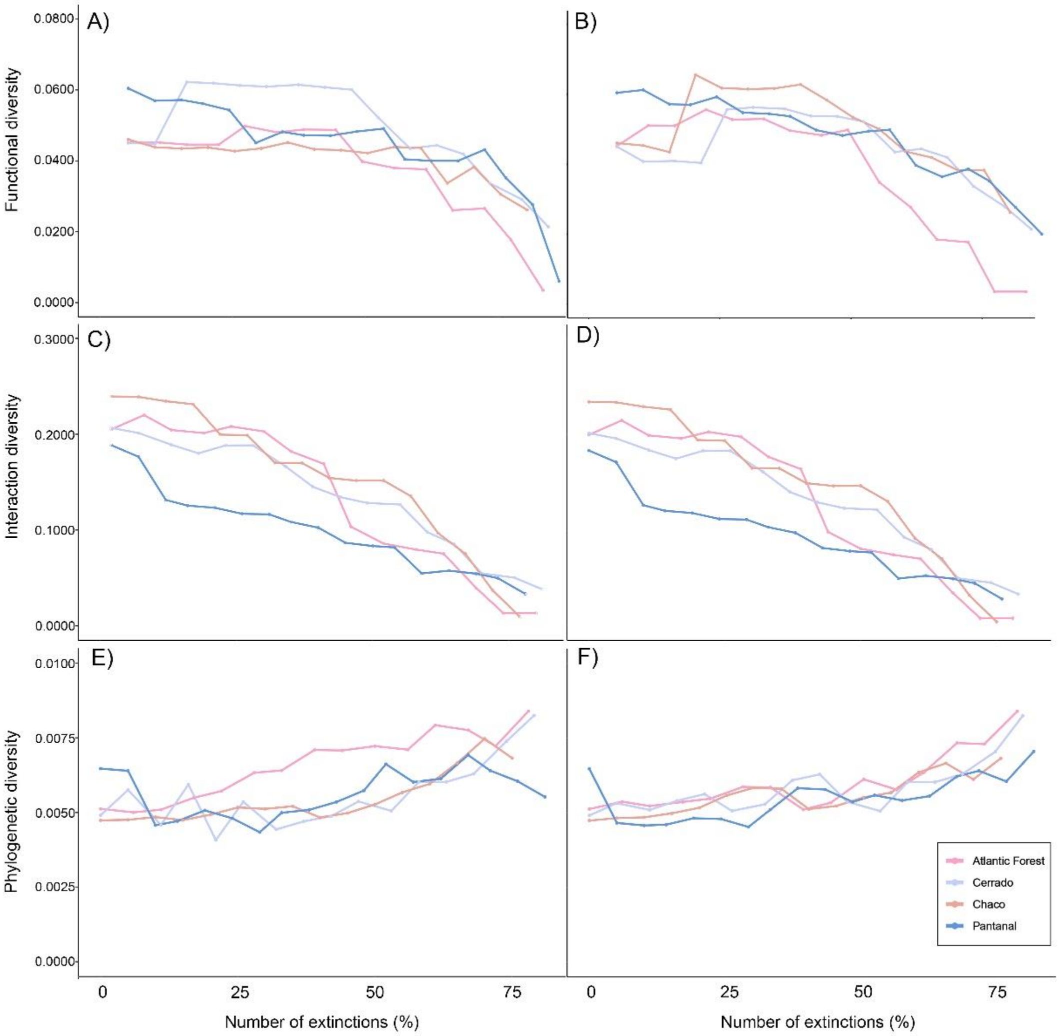

Figure 2: Variation in functional, phylogenetic and interaction diversity of anuran-prey networks under varying levels of species extinctions in each ecoregion. Extinction sequence was determined according to species vulnerability estimated under climate scenario SSP 8.5. In A, C, E) vulnerability was estimated based on range loss according to climate changes only; in B, D, F) vulnerability was estimated based on range loss according to climate and land use change.

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 ($r^2_{size/mass} = 0.77$, $r^2_{mode} = 0.79$, $p < 0.05$) and the Pantanal ($r^2_{size/mass} = 0.87$, $r^2_{mode} = 0.8$, $p < 0.05$) (Figure 3). Functional diversity of Cerrado and Chaco were determined by the variation of reproductive modes ($r^2_{Cerrado} = 0.73$, $r^2_{Chaco} = 0.74$, $p < 0.05$), together with habitat and size/clutch size, respectively ($r^2_{Cerrado} = 0.39$, $r^2_{Chaco} = 0.48$, $p < 0.05$). Thus, while the reduction in functional diversity after species extinction in the Atlantic Forest and Pantanal are 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.

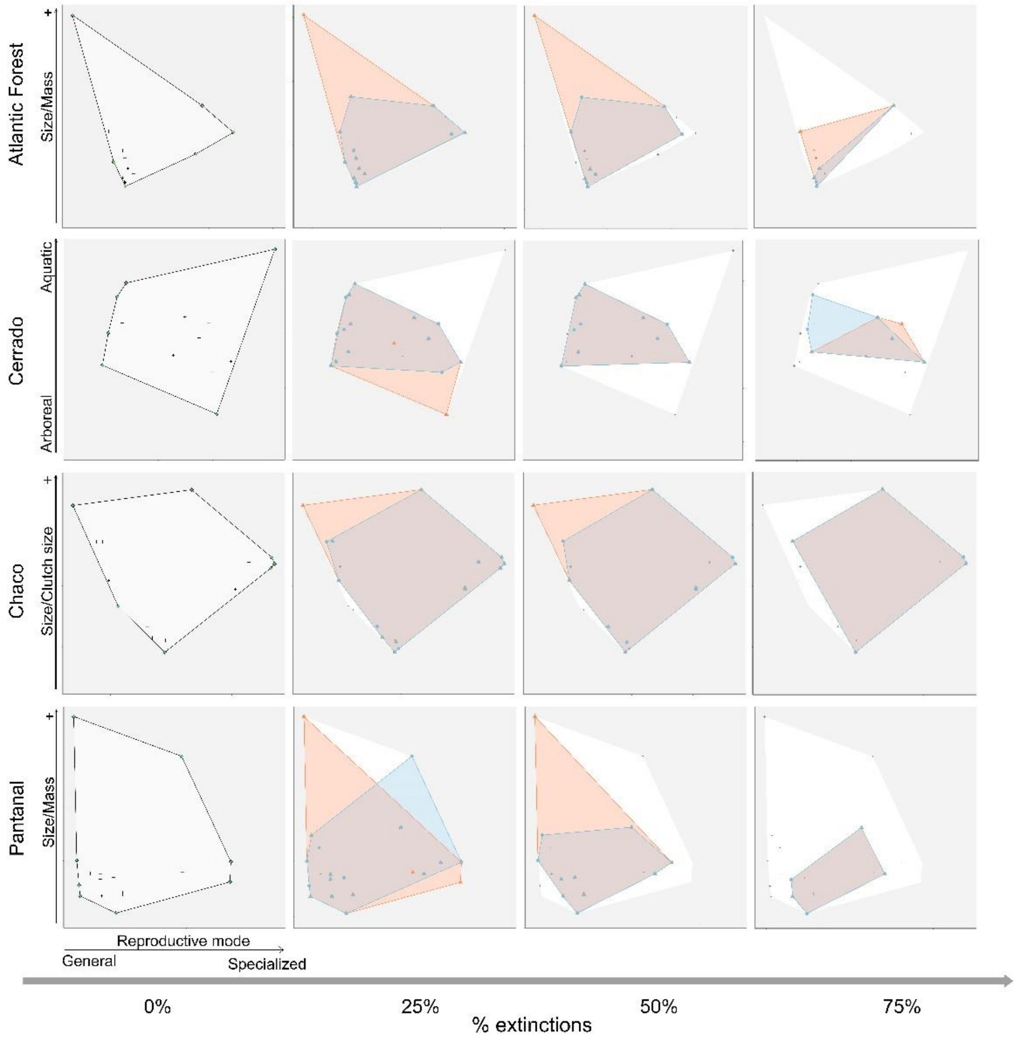

Figure 3: Change in the functional diversity of anuran-prey networks in response to extinctions in each ecoregion. Extinction sequence was determined according to species vulnerability estimated under the climate and land use scenario SSP 8.5, dots represent anuran species, blue shape the convex hull from climatic projection, red shape the convex hull from climate /land use projection. The white polygon represents the initial space before extinction and purple shape is the overlap between the two projections (PC1 + PC2 > 50% of explanation).

Interaction diversity of anurans-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.

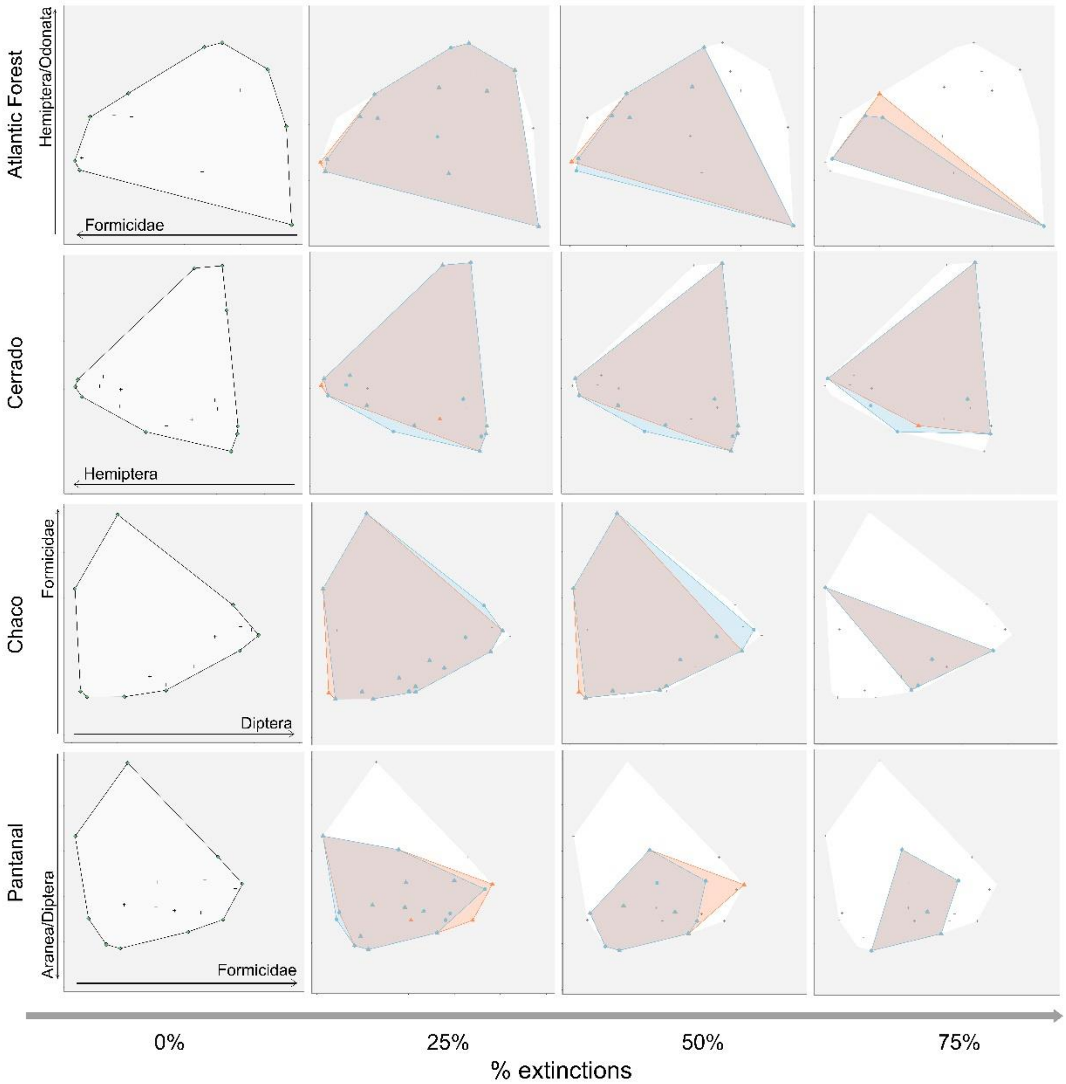

Figure 4: Change in the interaction diversity of anuran-prey networks in response to extinctions in each ecoregion. Extinction sequence was determined according to species vulnerability estimated under the climate and land use scenario SSP 8.5, dots represent anuran species, blue shape the convex hull from climatic projection, red shape the convex hull from climate /land use projection. The white polygon represents the initial space before extinction and purple shape is the overlap between the two projections (PC1 + PC2 > 50% of explanation).

The interaction networks between anurans and their prey are structurally similar across ecoregions, showing significant modularity and specialization (Table 3). The main difference between networks representing different ecoregions is that in the Pantanal, anurans consume on average more prey per species and the Cerrado network has greater specialization 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 S6, respectively). Overall, species removal resulted in networks that are progressively more connected, yet with greater mean specialization 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 SSP 4.5 and 8.5) (Figure 5 and Figure S6, respectively). The two different extinction projections, i.e., climate and climate plus land use, produced meaningful differences only for the Atlantic Forest.

Table 3: Structure of weighted anuran-prey networks by ecoregion. The variation coefficient is indicated in parenthesis. *Significant values

Ecoregion	Connectance	Nestedness	Modularity	Specialization	Relative functional complementarity	Weighted degree
Atlantic Forest	0.21	37.08	0.31*	0.29*	-0.49	3.62 (1.16)
Chaco	0.21	42.78	0.28*	0.25*	-1.82	4 (1.28)
Cerrado	0.22	20.95	0.30*	0.33*	-0.14	4.04 (0.84)
Pantanal	0.21	37.46	0.29*	0.26*	-0.21	4.28 (1.31)

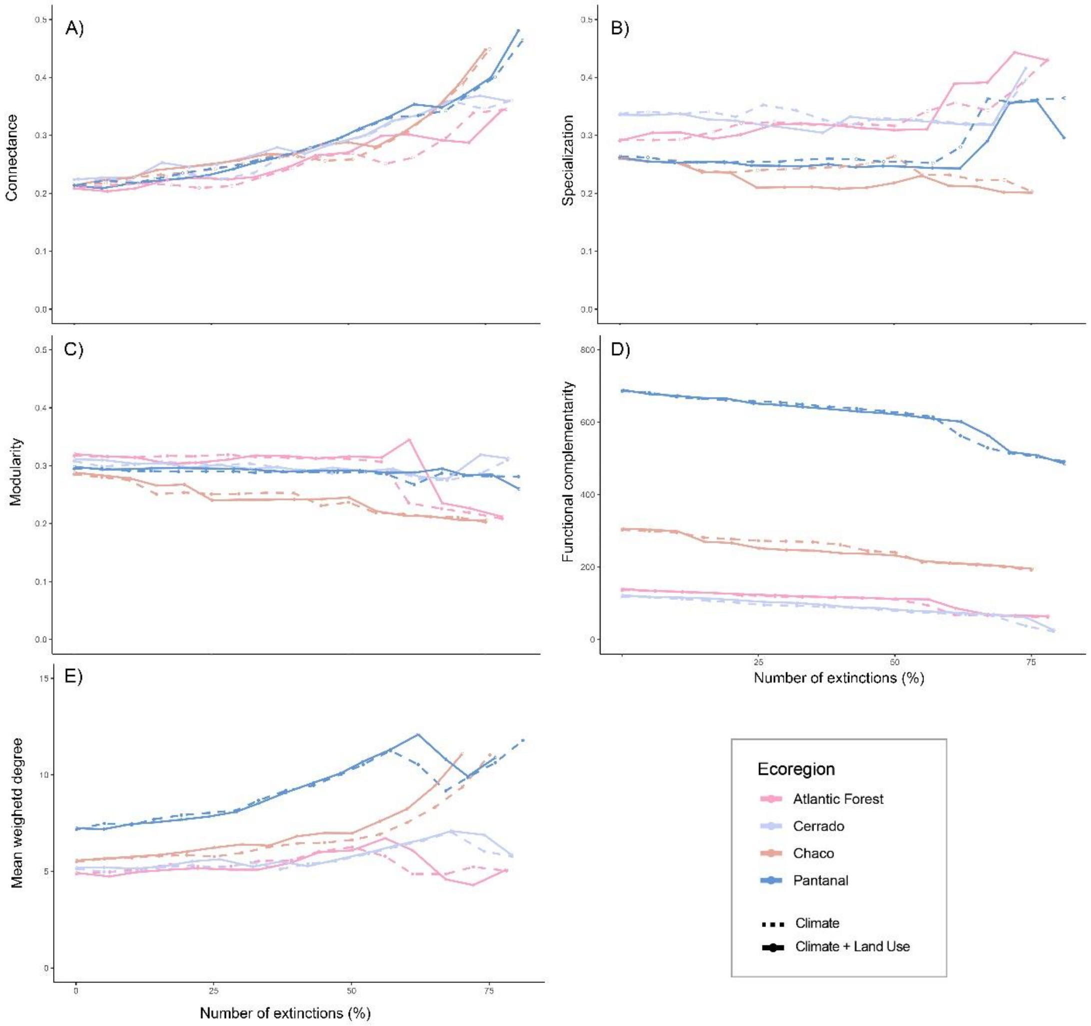

Figure 5: Variation in the structure of anuran-prey networks under varying levels species extinctions in each ecoregion. Extinction sequence was determined according to species vulnerability estimated under the climate and land use scenario SSP 8.5.

Discussion

Changes in climate/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 the anuran vulnerability according to projected changes in distribution was generally associated with the level of trophic specialization, signaled 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.

The reduction of suitable environment driven by climate change and land use threat anurans around the world (Newbold 2018). 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 (Vasconcelos *et al.* 2018; Alves-Ferreira *et al.* 2022). Because anurans are disproportionately sensitive to land use changes, the synergetic effects of climate/land use projections have a high impact on their distributions (Newbold 2018). Such high vulnerability of anurans to land use change is also associated with the limited dispersal ability of anurans, which reduces their ability to reach suitable areas. That is why fragmentation, degradation, and habitat split are among the main causes of amphibian declines (Becker *et al.* 2007; Lion *et al.* 2014).

The three facets of biodiversity showed little variation among ecoregions. The functional diversity was higher in the Atlantic Forest and the Pantanal, showing greater variation in traits like size/mass and reproductive mode. These regions do not have severe droughts like the Chaco and the Cerrado, which may act by filtering species traits and homogenizing communities (Pennington *et al.* 2009). Instead, their water supply is more abundant and distributed throughout the year, allowing anurans to explore unique microhabitats to breed, varying reproductive modes, and increasing functional diversity. Nevertheless, once abiotic variables affect the relationship between species diversity and functional diversity, reductions in precipitation or temperature in Chaco and Cerrado may restrict the pool of viable growth habits, lowering species richness and thus functional diversity (Cadotte *et al.* 2011). Conversely, interaction diversity was higher in Chaco, indicating that anurans in this region had more unique diets. Among the studied regions, Chaco experiences the most prolonged and severe drought period, which reduces the availability of food throughout the year (Adamoli *et al.* 1990). When food is scarce, anurans may shift their diets by including less-preferred items. In fact, the Chaco presented higher levels of specialization, with certain species feeding mainly on one or a few prey categories (e.g., Formicidade, Acari). On contrary, in more stable environments, when resources are abundant, optimal feeding might favor selectivity (Emlen 1966; Robinson & Wilson 1998). Thus, the combination of different levels of diet specialization leads to diverse interaction patterns, which results in more unique diets in this region.

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., Ripple *et al.* 2017; Anjos *et al.* 2020;

Fontana *et al.* 2021]. Yet, we found no relationship between specific trait combinations and vulnerability to climate and land use. This lack of trait-selectivity combined with the high functional redundancy among the anurans explains the robustness of functional diversity. This result highlights that functional redundancy safeguards functional diversity even at moderate levels of species loss (Sura *et al.* 2021). Likewise, phylogenetic diversity 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 (harboring 45% of species), and Leptodactylidae (harboring 34% of species), a pattern in many Neotropical anuran assemblages (Segalla *et al.* 2021) that may be a result of large radiations of few lineages generated by *in situ* diversification after few initial immigration events (Fritz & Rahbek 2012).

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., *E. matogrosso*, *E. bicolor*, *R. 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, 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 is 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 favoring the rewiring of interactions, altering the ecosystem functioning and its associated services.

Functional diversity is often viewed as a proxy for interaction diversity and 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 biodiversity 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 extremely 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 (Valiente-Banuet *et al.* 2015; Schleuning *et al.* 2020). 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.

Funding

KC thanks São Paulo Research Foundation (FAPESP) by Postdoctoral Fellowship (#2020/12558-0). DJS thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico [CNPq proceeses 404239/2021-8, 402519/2016-7] and Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia do Estado de Mato Grosso do Sul [FUNDECT process 054/2017] for financial support. DJS also thanks CNPq for his research fellowship [CNPq 309420/2020-2]. LPS acknowledges the receipt of a Banting Postdoctoral Fellowship from the National Sciences and Engineering Research Council of Canada (Application #454219).

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