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Structure and trophic interactions in anuran metacommunities in Midwestern Brazil

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**A todos os brasileiros que perderam sua vida
para o Coronavírus, pandemia severamente
agravada no Brasil devido ao negacionismo
científico pregado pelo atual governo,
dedico.**

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General abstract

Communities and metacommunities vary in composition over time and space. Likewise, species interactions can also vary along these dimensions. In this way my objective in this thesis is to understand the effects of time and space in anuran metacommunities as well as in anuran-prey interactions. In the first chapter I analyzed the structural patterns in anuran–prey antagonistic interaction networks in different parts of the world. I suggest that different processes, mediated mainly by latitude, are shaping the architecture of anuran–prey networks across the globe. In the second chapter, I examined anuran seasonal patterns of local contributions to beta diversity (LCBD) in different ecoregions of Western Brazil, and assessed their correlation with species richness and if environmental and/or spatial predictors would drive patterns of LCBD. I found that LCBD patterns were similar between seasons with sites tending to contribute in the same way for community composition uniqueness during the dry and rainy season. Among studied ecoregions, Cerrado showed higher LCBD values in both seasons. In addition, LCBD was negatively correlated with species richness in the dry season. We also found that LCBD variation was explained by ecoregion in the dry season, but in the rainy season both environmental and spatial global models were non-significant. Finally, in the third chapter I assessed the turnover of anuran-prey interactions between seasons and among four ecoregions in western Brazil. My results indicated that the variation in interaction beta diversity between seasons and among areas were generated by differences in prey availability. Interaction turnover between ecoregions and seasons were high and driven primarily by interaction rewiring. In addition, beta diversity of species was positively related to geographical distance, but not to interaction beta diversity. I propose that fluctuations in prey abundance along with limited dispersal abilities of anurans and their prey are responsible for the temporal and spatial pattern that emerged in my anuran-prey metaweb. Thus, anuran metacommunities and

interactions vary in time and space but the processes that are driving these patterns are unique and differ depending on the ecoregion.

Resumo Geral

Comunidades e metacomunidades variam em composição no tempo e no espaço. Da mesma forma, as interações entre as espécies também podem variar ao longo dessas dimensões. Meu objetivo nesta tese é compreender os efeitos do tempo e do espaço nas metacomunidades de anuros, bem como nas interações anuro-presa. No primeiro capítulo, analisei os padrões estruturais das redes de interação anuros-presas em diferentes partes do mundo. Como resultado sugiro que diferentes processos, mediados principalmente pela latitude, estão moldando a arquitetura das redes anuros-presas em todo o mundo. No segundo capítulo, examinei os padrões sazonais da contribuição local para a diversidade beta (LCBD) de anuros em diferentes ecorregiões do Oeste do Brasil e avaliei sua correlação com a riqueza e se os preditores ambientais e/ou espaciais guiam os padrões de LCBD. Eu descobri que os padrões de LCBD são semelhantes entre as estações, com os locais tendendo a contribuir da mesma forma para a exclusividade da comunidade durante a estação seca e chuvosa. Entre as ecorregiões estudadas, o Cerrado apresentou os maiores valores de LCBD em ambas as estações. Além disso, a LCBD foi negativamente correlacionada com a riqueza de espécies na estação seca. Também descobri que a variação da LCBD foi explicada pela ecorregião na estação seca, mas na estação chuvosa os modelos globais ambientais e espaciais não foram significativos. Finalmente, no terceiro capítulo, avaliei a mudança das interações anuro-presa entre as estações e entre quatro ecorregiões no Oeste do Brasil. Meus resultados indicaram que a variação na beta diversidade das interações entre as estações e entre as áreas foi gerada por diferenças na disponibilidade de presas. A beta diversidade das interações entre ecorregiões e estações do ano foi alta e impulsionada principalmente pela religação das interações. Além disso, a diversidade beta das espécies foi positivamente relacionada à distância geográfica, mas o mesmo não ocorreu com a beta diversidade das interações. Eu proponho que a flutuação na abundância das presas junto com a capacidade limitada de dispersão dos anuros e presas são responsáveis pelo padrão

temporal e espacial das redes entre anuros e presas. Assim, as metacomunidades de anuros e suas interações variam no tempo e no espaço, mas os processos que estão conduzindo esses padrões são únicos e diferem dependendo da ecorregião.

General Introduction

One of the foundational goals in community ecology is to understand patterns of diversity and distributions of species across environmentally heterogeneous landscapes (Hutchinson 1953) and how those patterns change through time (Levin 1992). Ecologists have taken two distinct approaches in studying the distribution and diversity of communities: a species-centric focus and an interaction-network based on the interactions between species (Tylianakis et al. 2008). The species focused approach frequently assesses compositional changes in ecological communities to better understand biodiversity patterns (Legendre & Condit 2019). These compositional changes are often measured with species turnover, the directional dissimilarity in species identity and abundance across spatial, temporal or environmental gradients (Anderson et al. 2011). In this context, β-diversity portrays the variation in species composition among spatially or temporally separated communities (Whittaker 1960; Whittaker 1972). Alternatively, the ecological network approach typically investigates the structural dynamics of species interaction networks to explore community structure, function, or ecological processes like predation (Poisot et al. 2012; Guimarães 2020). In addition, a current frontier in community-level studies of ecological systems is the integration of the species and interaction network by investigating both simultaneously; this can be achieved by evaluating the contribution of species turnover to interaction turnover (Poisot et al. 2012).

These biodiversity patterns studied by species-centric focus and an interaction-network based are centered to determine conditions necessary for conservation of group models. Neotropical anurans are considered excellent ecological models because they are locally abundant and their sampling is relatively easy (Leão-Pires et al. 2018). Anurans are particularly susceptible to environmental and spatial factors because they have permeable skin, a biphasic life cycle, unshelled eggs, limited dispersal and most of them are dependent on water bodies for tadpoles development and adult reproduction (Green 2003). Moreover, anurans play an important role in food webs as they represent a link between terrestrial and aquatic environments (Duré et al. 2009) and can act both as predators (Vignoli & Luiselli 2012) and as prey (Stewart & Woolbright 1996; Toledo et al. 2007). As predators, anurans have a diet based mainly on arthropods, but most species are opportunistic (Wells 2007), consuming any resource that is available in the environment (Duellman & Trueb 1986). Given the generality of the diet combined with its biphasic life cycle, several studies show the efficiency of amphibians, both tadpoles and adults, in the population control of disease-transmitting mosquitoes (e.g., DuRant & Hopkins 2008; Salinas et al. 2018; Thorp et al. 2018) as well as in agricultural pest control (Khatiwada et al. 2016). Considering that anuran biodiversity is highly threatened, suffering a severe global decline by virtue of diseases, climate change, and habitat loss (Becker et al. 2007; Lion et al. 2014; Scheele et al. 2019), understanding spatial and temporal patterns of species composition and interactions may be highly useful for biodiversity conservation, as well as detecting sites and species that disproportionally contribute to species richness and interaction networks, respectively.

In this sense this thesis is structured into three chapters: In Chapter 1 I performed a global-scale literature analysis to build up a database of interactions between anuran communities and their preys, from a wide range of geographical areas, using a network approach. After, I tested the influence of latitude, as well as anuran taxonomic, functional and phylogenetic richness on network metrics. In Chapter 2 I examined anuran seasonal patterns (dry and rainy seasons) of compositional uniqueness (LCBD) in different ecoregions of Western Brazil and their correlation with species richness, thus elucidating possible keystone communities. I also assessed if environmental (climatic variables, pond area and ecoregions) and/or spatial predictors (spatial configuration of sampling sites captured by distance-based Moran’s Eigenvector Maps) would drive patterns of LCBD. Finally, in the Chapter 3, I quantified the species turnover and interaction rewiring components of the beta diversity of anuran-prey interactions and tested how they varied across ecoregions and between wet and dry seasons.

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Chapter 1. Global patterns in anuran-prey networks: structure mediated by latitude

Abstract

Life on Earth is supported by a huge number of interactions among organisms. Species interactions in these networks are influenced by latitude, evolutionary history and species traits. We performed a global-scale literature analysis to build up a database of interactions between anuran communities and their preys, from a wide range of geographical areas, using a network approach. For this purpose, we compiled a total of 55 weighted anuran-prey interaction networks, 39 located in the tropics and 16 in temperate areas. We tested the influence of latitude, as well as anuran taxonomic, functional and phylogenetic richness on network metrics. We found that anuran-prey networks are not nested, exhibit low complementary specialization and modularity, and high connectance when compared to other types of networks. The main effects on network metrics were related to latitude, followed by anuran taxonomic, functional and phylogenetic richness, a pattern similar to the emerging in mutualistic networks. Our study is the first integrated analysis of the structural patterns in anuran-prey antagonistic interaction networks in different parts of the world. We suggest that different processes, mediated mainly by latitude, are modeling the architecture of anuran-prey networks across the globe.

Keywords: amphibia, ecological networks, food webs, macroecology

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Resumo

A vida na Terra é sustentada por um número infinito de interações entre organismos. As interações entre as espécies nessas redes são influenciadas pela latitude, história evolutiva e características das espécies. Realizamos uma análise da literatura em escala global para construir um banco de dados de interações entre comunidades de anuros e suas presas, em uma ampla área geográfica, usando a abordagem de rede. Compilamos um total de 55 redes de interação anuro-presa ponderadas, 39 localizadas nos trópicos e 16 em áreas temperadas. Testamos a influência da latitude, bem como a riqueza taxonômica, funcional e filogenética dos anuros nas métricas da rede. Descobrimos que as redes anuro-presa não são aninhadas, exibem baixa especialização e modularidade e alta conectância quando comparadas a outros tipos de redes. Os principais efeitos nas métricas de rede foram relacionados à latitude, seguida pela riqueza taxonômica, funcional e filogenética dos anuros, um padrão semelhante ao emergente em redes mutualísticas. Nosso estudo é a primeira análise integrada dos padrões estruturais em redes de interação anuro-presa em diferentes partes do mundo. Sugerimos que diferentes processos, mediados principalmente pela latitude, estão modelando a arquitetura das redes anuros-presas em todo o mundo.

Palavras-chave: amphibia, redes ecológicas, teias alimentares, macroecologia.

Introduction

Maintenance of life on Earth is supported by a huge number of interactions among organisms (Jordano 2016), which also play an important role in the origin and evolution of species diversity (Bascompte et al. 2006; Schemske et al. 2009). Such interactions among organisms are not evenly distributed throughout the globe (Olesen et al. 2007). Some recent studies have made substantial efforts to describe the structure and to understand ecological community assembling (Pires & Guimarães 2013). The complex web of interactions that structures biotic communities is the study focus of ecological networks. This science aims to describe and evaluate patterns of species interactions and their effects on ecological processes (Dáttilo & Rico-Gray 2018). The most commonly studied networks are unipartite food webs (i.e., those where species are not divided into groups such as plants and pollinators) and bipartite networks of two interacting guilds (Dáttilo & Rico-Gray 2018). However, in nature, interactions gather multiple interaction types, which vary in space and time and are interconnected such as networks of networks, which are represented by multilayer networks (Pilosof et al. 2017). Interaction networks can be mutualistic, if they involve species that have mutual benefits, as in pollination and seed-dispersal networks (Bascompte & Jordano 2007); or antagonistic, when one member in the pair of interacting species can be negatively affected while the other benefits, such as in predation, parasitism and competition (Morris et al. 2014; Kéfi et al. 2015). Food webs are antagonistic networks which represent the trophic connections among species, a central role in the study of biological communities (McClanahan & Branch 2008; Kéfi et al. 2015).

Different aspects of network structure are measured by specific metrics like network size, connectance, nestedness and modularity (Dormann et al. 2009; Zanata et al. 2017). Patterns on these metrics usually differ between antagonistic and mutualistic networks (e.g., Morris et al. 2014; Estes et al. 2016), and they tend to change along biogeographical scales, such as latitudinal and climatic gradients (Schleuning et al. 2012; Zanata et al. 2017). The gradient of latitudinal diversity is a prominent pattern on Earth (Fischer 1960) and, in accordance, the majority of taxonomic groups, including anurans and invertebrates, exhibits richer communities in the tropics decreasing towards the poles (Hillebrand 2004; Wiens 2007). Species richness has been shown to affect networks metrics, as detected, for example, in plant-hummingbird networks, which are more specialized in richer communities (Dalsgaard et al. 2011). Accordingly, species richness strongly influences network architecture, reducing nestedness, and increasing modularity in plant-pollinator networks (Spiesman & Inouye 2013). These findings support the idea that network metrics also vary in response to latitude. For example, in plant-pollinator networks specialization increases towards the tropics (Zanata et al. 2017), whereas in plant-frugivore networks the opposite occurs (Schleuning et al. 2012). On the other hand, antagonistic networks, as plant-herbivore and host-parasitoid networks, seem to be structured independently of latitude (Morris et al. 2014; Araújo 2016). These contrasting results suggest that biotic interactions respond differently to latitude (Schemske et al. 2009), according to the taxonomic group or type of interaction.

Environmental conditions vary according to latitude and these abiotic conditions can act for molding morphologies (Schöb et al. 2012). Ecological processes mediated by species interactions are suitable systems to investigate whether species' traits affect their functional roles (Dáttilo & Rico-Gray 2018). The use of trait-based and phylogenetic tree-based proxies lies in the idea of niche complementarity, whereby species with similar functional traits and thus partially overlapping niches are expected to perform similar and, to a certain degree, redundant, ecological roles (Pigot et al. 2016). Frugivores with distinct traits tend to be more functionally specialized, interacting with plants that are less frequently visited by other members of the community, thus increasing specialization (Junker et al. 2013; Maglianesi et al. 2015; Watts et al. 2016; Tinoco et al. 2017) and modularity (Maruyama et al. 2014; Morente-

López et al. 2018) of networks. On the other hand, it was not detected an effect of species' traits on metrics of host-parasitoid networks (Morris et al. 2014). Regarding food-webs, it was demonstrated that species traits affect their trophic structure (Petchey et al. 2008), although there is no study testing their influence on network metrics. The architecture of an interaction network can also be influenced by the phylogeny of the component species (Cattin et al. 2004; Brito et al. 2014). Species that are phylogenetically closely related may have more similar dietary preferences or parasite communities than unrelated species (Krasnov et al. 2012; Fontaine & Thébault 2015). In addition, if interspecific differences in species traits is a result of differences on phylogenetic histories, it may also affect network metrics (Minoarivelo et al. 2014; Schleuning et al. 2014). Indeed, it was demonstrated that phylogenetic distance among species affects nestedness and modularity in mutualistic networks (Rezende et al. 2007; Schleuning et al. 2014, but see Ponisio & M'Gonigle 2017), as well as in antagonistic plant-herbivore networks (Fontaine & Thébault 2015) and in host-parasitoid networks (Krasnov et al. 2012; Brito et al. 2014, but see Campião et al. 2015). In spite of the possible relation between phylogeny and species traits, these drivers can influence network metrics in different ways (Ponisio & M'Gonigle 2017), according to the network type and location.

Regardless of the growing number of network studies in the last decade, few evaluated the structure of antagonistic networks in large spatial scales (Morris et al. 2014). And those which did it focused mainly on marine and freshwater food-webs involving fishes (Belgrano 2005; McClanahan & Branch 2008; Kéfi et al. 2015), evidencing the need for further studies for terrestrial organisms (Dobson 2009). Anurans play an important role in the food webs as they represent a link between terrestrial and aquatic environments (Duré et al. 2009). Despite the fact that there are several studies of anuran diets, mainly in the tropics (Duellman 1978; Toft 1980; Vignoli et al. 2009; Menin et al. 2015), most of these studies are locally constrained in space and time and aimed to describe the food repertoire of a small subset of anurans. Therefore, this abundance of scattered empirical evidence asks for broader approaches that unravel the structure of anurans-prey networks in a wider context, indicating the main forces that determine their structure on a global scale.

Herein, we describe the structure of antagonistic anuran-prey interactions from a wide range of geographical areas, using a network approach. We expect that anuran-prey networks will present high connectance and low values of nestedness, modularity and complementary specialization in relation to other types of interaction networks. Connectance would be elevated because anuran's diet are usually highly generalized (Vignoli & Luiselli 2012). Anurans usually eat what is available in the environment with no preference for any type of prey(Duellman & Trueb 1986). The only constraint is the relationship prey/mouth-size, because mouth dimensions tend to restrict the upper limit of prey size they can consume (Duellman & Trueb 1986). Thus, the number of links between anurans and preys would be high, increasing connectance. In addition, network metrics can be driven by different ecological factors (see Dáttilo & Rico-Gray 2018). Here we tested the influence of latitude, and of anuran taxonomic, functional and phylogenetic richness on networks structure. We expect: 1) a latitudinal effect on networks metrics, because there are more species of anurans (Wiens 2007), prey availability (Novotny et al. 2006; Roslin et al. 2017), and biotic interactions (Schemske et al. 2009) in the tropics, which would lead to lower values of nestedness, complementary specialization and modularity in networks of high latitudes when compared to their low latitudes counterparts. This expected pattern agrees to the those recorded for mutualistic networks and other food-web systems (e.g., Schleuning et al. 2012; Saporiti et al. 2015). 2) As in the tropical region species richness, as well as functional and phylogenetic diversity are higher (Petchey & Gaston 2002) than in the temperate communities, we expect that the abundance of specialists' would be higher in tropical region, leading these networks to be more nested than in the temperate region. Nestedness indicates that specialists' diet would be a subset of the generalists' diets. On the other hand, this higher abundance of specialists in the tropics would result in higher values of complementary specialization and modularity in relation to the temperate region.

Methods

We compiled interactions using a globally distributed database of anurans and their preys, after a comprehensive review of the literature (Supplementary material Appendix 1, Table A1). We searched for studies in the Web of Science (<https://webofknowledge.com/ >) and Scopus (< https://www.scopus.com >) databases, using the keywords "Trophic ecology OR Feed* OR Diet*" and "assemblage structure" and "trophic overlap OR trophic plasticity OR niche breadth OR Autoecol*" up to 2017. In addition, we gather all data from direct searches of references in Google Scholar (https://scholar.google.com.br/), and got unpublished data by private correspondence with researchers active within the subject field. Among these compiled references, we selected only studies presenting data on diet and including at least three syntopic species of anurans. This minimum value was established because studies on anurans' diet are scarce in the temperate region, and species richness are characteristically low (Wiens 2007; Marin & Hedges 2016). From each of the selected studies data on taxonomic information on anurans (only species identified at least to genus level) and prey categories (usually to order, with exception of the Formicidae and Isoptera suborders), prey abundance in stomachs as well as country and geographical coordinates of the study site were recorded. In studies of anurans diets, preys are usually identified only to the level of order (categories) because of their fragmentation after consumption, turning a finer identification hard to achieve (Duellman 1978; Toft 1980; Ceron et al. 2018).

We compiled a total of 55 weighted anuran-prey interaction networks, with 39 located in tropical and 16 in temperate regions (Figure 1, Supplementary material Appendix 1, Table A1). For each study site, we built up weighted matrices of interactions containing the anuran species as columns and their prey categories as rows. In these matrices, predation interaction was represented by their interaction abundance. Interaction abundance represents the number of each specific prey ingested by the anuran. We used weighted networks because they better reflect dependencies among species and the structure of interaction networks (Vázquez et al. 2005; Lewinsohn et al. 2006). Additionally, metrics based on weighted networks have been shown to be less sensitive to sampling bias than those based on binary networks (Banašek-Richter et al. 2004; Dormann et al. 2009; Vizentin-Bugoni et al. 2016). Additionally, for data visualization, we also built up a meta-network compiling all these 55 networks together, one meta-network combining the 39 tropical sites, and another one combining the 16 temperate sites (Figure 2). For graphical representation of the networks, we used the PAJEK software (http://pajek.imfm.si/doku.php?id=pajek).

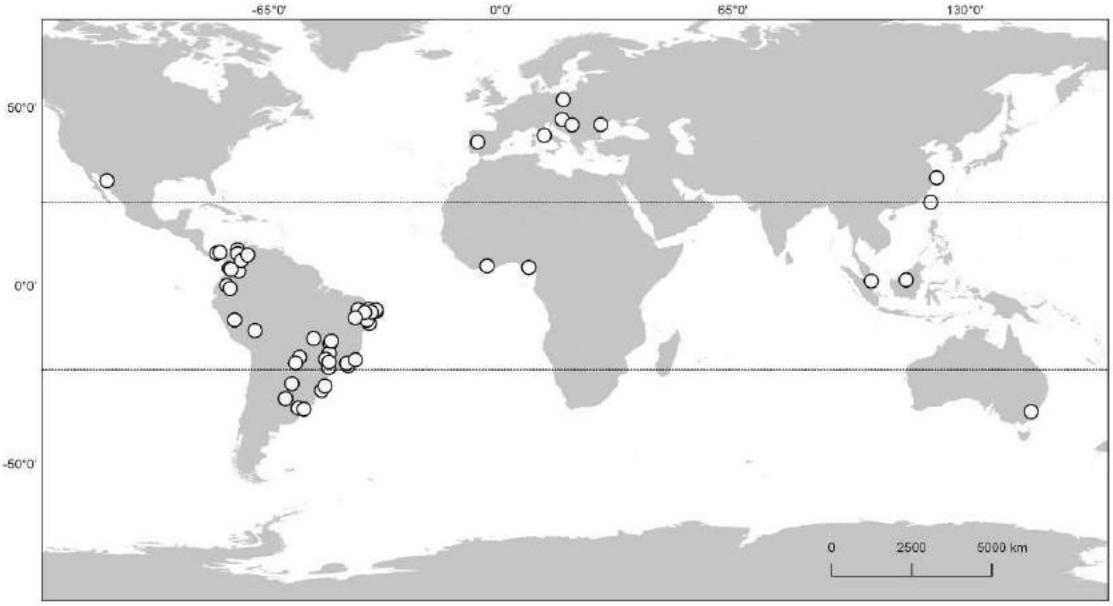

Figure 1. Distribution of 55 anuran–prey interaction networks included in the analysis of this study.

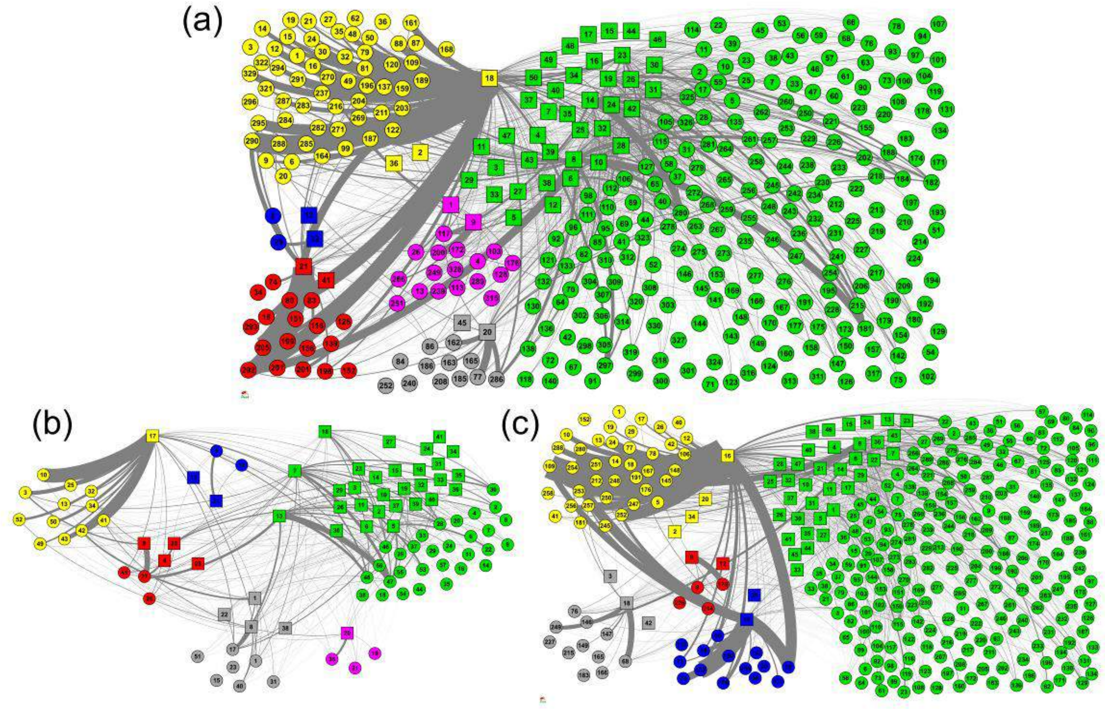

Figure 2. (a) Graphs showing modules in the compiled anuran-prey meta-network including 55 networks worldwide, (b) the meta-network combining 16 temperate sites and (c) the meta-network combining 39 tropical sites. Boxes represent prey categories and circles denote anuran species. Widths of connecting lines (grey) indicate the relative number of observed interactions (See Supplementary material Appendix 1, Table A2 to number legend).

Measuring network metrics - We calculated six network metrics commonly used to describe distinct aspects of the network structure. These metrics were calculated separately for each of the 55 networks.

Network size refers to the total number of anurans and the prey categories they consumed. It can be calculated as species richness and indicates the maximum possible number of interactions (Olesen & Jordano 2002). We also measured the Mean number of links per species, which corresponds to the total number of links observed in the network divided by the total number of species (Dormann et al. 2008).

Connectance describes the ratio between the total number of realized 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 distributed within the community (Jordano 1987).

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 corresponds to a subset of the interaction partners of generalist species (Bascompte et al. 2003). We calculated the weighted nestedness (wNODF), which is based on the overlap and decreasing fill in the weighted matrix (Almeida-Neto & Ulrich 2011). Nestedness values ranges from 0 (non-nested network) to 100 (perfect nestedness).

Modularity is a network property that emerges when groups of species are densely connected and have sparser connections to other groups of interacting species. The organization of interactions into modules may reflect similarity of traits, phylogeny, biogeography and climate among species, providing information on how the interactions are partitioned in the community (Maruyama et al. 2014; Araujo et al. 2018). We analyzed modularity using the recently implemented LPAwb + algorithm (Liu & Murata 2010; Beckett 2016). LPAwb+ algorithm uses label propagation and multi-step agglomeration to attempt to maximize modularity in networks (see Beckett 2016). Also, it is currently the most used algorithm to calculate modularity in biological systems such as interactions between plants and pollinators and food webs. Besides that, the LPAwb+algotithm robustly identify partitions with high modularity scores, showing to be efficient for the detection of subgroups in ecological networks (Beckett 2016).

Complementary specialization (H2’) is derived from two-dimensional Shannon entropy, and quantifies the niche partitioning among species considering partner availability (Blüthgen et al. 2006; Zanata et al. 2017). Thus, it is interpreted as a measure of interactions´

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 H2’ range from 0 to 1 indicating the extremes of generalization and specialization, respectively.

In order to compare network metrics obtained for the anuran-prey networks with those recorded for other network types, we applied linear mixed models (LMMs) following the same procedures adopted by Naranjo et al. (2019). For this purpose, we used data on epiphyte-phorophyte, as well as on mutualistic (seed dispersal, pollination, ant-myrmecophyte) and parasitic networks (bat-fly and fish-parasite), obtained in Naranjo et al. (2019) and specific literature (Lima et al. 2012; Bellay et al. 2015; Zarazúa-Carbajal et al. 2016; Durán et al. 2018; Vizentin-Bugoni et al. 2019; Urbieta et al. 2020). Linear mixed models were fitted using the ‘lme4’ package in R (Bates et al. 2007).

Null-model corrections of network metrics

To assess the significance of the network metrics wNODF, modularity and H2’, we compared the observed values to those generated by null models. We used the Patefield algorithm (Patefield 1981) to generate simulated matrices with the same marginal totals as the original network so that species interacting with highest or lowest frequencies in the observed matrices were the same in the simulated ones (Patefield 1981). We used the Patefield algorithm because it keeps the number of interactions constant (i.e. the same as in the original matrix) when simulating the null models. For each of the observed networks, we generated 1,000 randomized matrices to estimate nestedness and complementary specialization and 100 to estimate the modularity. We used fewer randomizations for modularity because their calculation requires excessively time-consuming algorithms (Olesen et al. 2007; Zanata et al. 2017). For each of the randomized networks, we calculated the network metrics following the same procedure as adopted for the observed networks. To quantify the departure of the observed network values from the null expectation, we calculated null-model corrected values by subtracting the observed metric value from the mean value across all randomized networks (Δ – transformation). Then, the Δ – transformed value was divided by the standard deviation of values across all randomized networks (z – transformation; Zanata et al. 2017). All network metrics and null models were calculated with the "bipartite" 2.08 package (Dormann et al. 2008) in R 3.4.0 (R Core Team 2019).

Sampling completeness and intensity

Food web metrics are useful for comparisons to other food webs in order to detect regularities in respect to their structure (Banašek-Richter et al. 2004). Detected network patterns may be biased depending on the sampling effort employed and the metrics considered (see Vizentin-Bugoni et al. 2016). To avoid such bias we estimated sampling intensity following Schleuning et al. (2012) and sampling completeness following Chacoff et al. (2012) and Vizentin-Bugoni et al. (2016). Sampling intensity was defined as the square-root of the number of interaction events in the network divided by the square-root of the product of the number of anuran and preys in the network (Schleuning et al. 2012). Using abundance data and the Chao 1 estimator of species richness (Magurran 2013), we estimated the total number of anurans-prey interactions in each community. After, we calculated sampling completeness dividing the observed by the estimated richness of interactions (Chacoff et al. 2012). The Chao 1 estimator was calculated with the "iNEXT" 2.0.12 package (Hsieh et al. 2016) in R 3.4.0 (R Core Team 2019).

Path analysis for the association between network metrics and their predictors

Given that networks are influenced by structural factors like latitude (Zanata et al. 2017), richness (Jordano 1987), phylogeny (Schleuning et al. 2014), species traits (Bastazini et al. 2017) and sampling (Vizentin-Bugoni et al. 2016), our main goal was to split the effects of different factors on the network metrics based on a priori causal assumptions (Table 1). In order to calculate the functional richness of sites, data on species traits such as habitat use (fossorial terrestrial, aquatic or arboreal), body size (snout-vent length, SVL), breeding strategy (development direct, larvae or viviparous) and reproductive modes (number of reproductive mode, see Crump (2015) from anurans were obtained from AmphiBIO_v1. (Oliveira et al. 2017) and specific literature (e.g., Duellman & Trueb 1986; Haddad et al. 2013; Crump 2015). Pairwise functional distances between all functional entities were computed using the Gower distance, which allows mixing different types of variables while giving them equal weight (Borcard et al. 2018). For evolutionary history, we use a phylogeny proposed by Jetz & Pyron (2018), which includes all 304 anuran species registered in our dataset. We calculated pairwise phylogenetic distances among all pairs of anurans using the cophenetic distance (PDist) based on branch lengths (Sneath & Sokal 1962; Parker et al. 2015). Then, Principal Coordinates Analysis (PCoA) were performed using the functional distance and phylogenetic distance matrix separately. Functional and phylogenetic entities coordinates on the first three principal axes (PC) of this PCoA were kept to build a multidimensional functional and phylogenetic space (Villéger et al. 2011; Mouillot et al. 2014). After, we calculate the volume of the multidimensional functional and phylogenetic space using the package ‘geometry’ (Habel et al. 2015) in R 3.4.0 (R Core Team 2019). Similarly, functional and phylogenetic richness of each site were measured as the volume inside the convex hull shaping all of the functional and phylogenetic richness recorded worldwide. These raw volumes were then standardized by the volume filled by the global pool of taxa to obtain values constrained (Villéger et al. 2011). Thus, functional and phylogenetic richness represents the amount of functional or phylogenetic space filled by each network in relation to the total volume filled by the global pool of taxa (see Villéger et al. 2008 for details on method). Therefore, we performed a path analysis using the sampling metrics as control variable to observe the raw effect of structural factors (latitude, species richness, functional and phylogenetic richness) on network metrics. The path analysis was performed using ‘lava’ package (Holst & Budtz-Jørgensen 2013) in R 3.4.0 (R Core Team 2019). In order to detect spatial autocorrelation in our data we checked the path analysis residuals using Moran’ I with ‘ape’ package (Paradis et al. 2004) in R 3.4.0 (R Core Team 2019).

Table 1. Overview of the path model components showing the influence of explicative variables (path from) on network metrics.

Path from	Rationale	Reference
Anuran richness	The tropical region harbors a higher diversity of anurans than the temperate region. Besides that, adaptations to some combination of abiotic conditions and biotic interactions allow tropical species to be more specialized, dividing resources more finely among more species. This niche separation in the tropics leads to different levels of complementary specialization, modularity and nestedness in the networks.	Jordano 1987; Hillebrand 2004; Wiens 2007; Brown 2014
Latitude	Network metrics tend to be influenced by latitude in mutualistic systems and in food-webs, but not in bipartite antagonistic networks like host-parasitoid and plant-herbivore.	Guilhaumon et al. 2012; Trøjelsgaard & Olesen 2013; Morris et al. 2014; Saporiti et al. 2015; Araújo 2016
Functional richness	It is well established that species' traits influence networks metrics through complementary specialization in mutualistic networks. As anurans' functional traits influence their diet, we expect such traits to reflect in the network metrics as complementary specialization.	Bascompte et al. 2003; Petchey et al. 2008; Bastazini et al. 2017; Maruyama et al. 2018
Phylogenetic richness	Phylogenetic richness, the phylogenetic volume filled by the global pool of taxa calculated from the phylogenetic distance between species, may influence their position in networks. In mutualistic systems and in antagonistic plant-herbivore networks, the phylogenetic signal can affect network metrics.	Schleuning et al. 2014; Fontaine & Thébault 2015
Control variable	**Rationale**	**Reference**
Sampling effort	Different sampling efforts bias network metrics. Given that our data fits such scenario with different sampling efforts, we have controlled this effect in the network metrics.	Vizentin-Bugoni et al. 2016

Results

Anuran richness for the 55 networks analyzed separately ranged from three to 64 species (x̄ = 10.01 ± 12.1), and the prey richness ranged from four to 30 categories (x̄ = 17.89 ± 5.88). Among the 50 prey categories registered, 42 are Arthropoda, six are Chordata, one is an Annelida and one a Mollusca. Coleoptera was the most frequent category (62.57%) and Hymenoptera (Formicidae) was the most abundant item (ca. 56000 items), followed by termites (Isoptera) (ca. 20000 items). The size of networks varied from 27 to 1539 nodes (x̄ = 196.7 ± 286.3). The number of links per anuran species varied from 1.36 to 4.94 (x̄ = 2.42 ± 0.16).

Mean connectance for the 55 networks analyzed varied from 0.25 to 0.89 (x̄ = 0.55 ± 0.16). Nestedness varied from 25.29 to 67.29 (x̄ = 44.2 ± 7.45), but none of the communities were significantly nested. On the other hand, networks were significantly modular ($p < 0.05$) with values ranging between 0.04 to 0.56 (x̄ = 0.24 ± 0.12). The number of modules varied from 2 to 6 (x̄ = 3.1 ± 0.83). Complementary specialization ranged from 0.04 to 0.67 and was significant ($p < 0.05$) for most (96.36%) of the networks (n = 53). However, the mean specialization observed on networks was low (x̄ = 0.32 ± 0.15). Sampling completeness of networks was high (x̄ = 81.08 ± 13.13 %), ranging from 40.65 to 100%. Intensity varies from 0.7 to 5.96 (x̄ = 2.49 ± 1.37).

Modularity and complementary specialization varied significantly among the different types of networks analyzed (all LMM tests; $P< 0.0001$; Figure 3, see Supplementary material Appendix 1, Table A3). They were significantly lower in the anuran-prey networks than in the rest of the networks, with the exception of epiphyte-phorophyte networks (Figure 3, all tests: $P< 0.01$). Network size influenced specialization values (LMM tests: $P=0.09$; see

Supplementary material Appendix 1, Table A3), but did not significantly affect modularity (LMM tests: all P=0.1; see Supplementary material Appendix 1, Table A3). The variance explained by the entire model (Rc2) ranged between 0.46 and 0.54 [Supplementary material Appendix 1, Table A3], with the variance explained by fixed factors (Rm2) representing a large fraction in all cases (53–54 %).

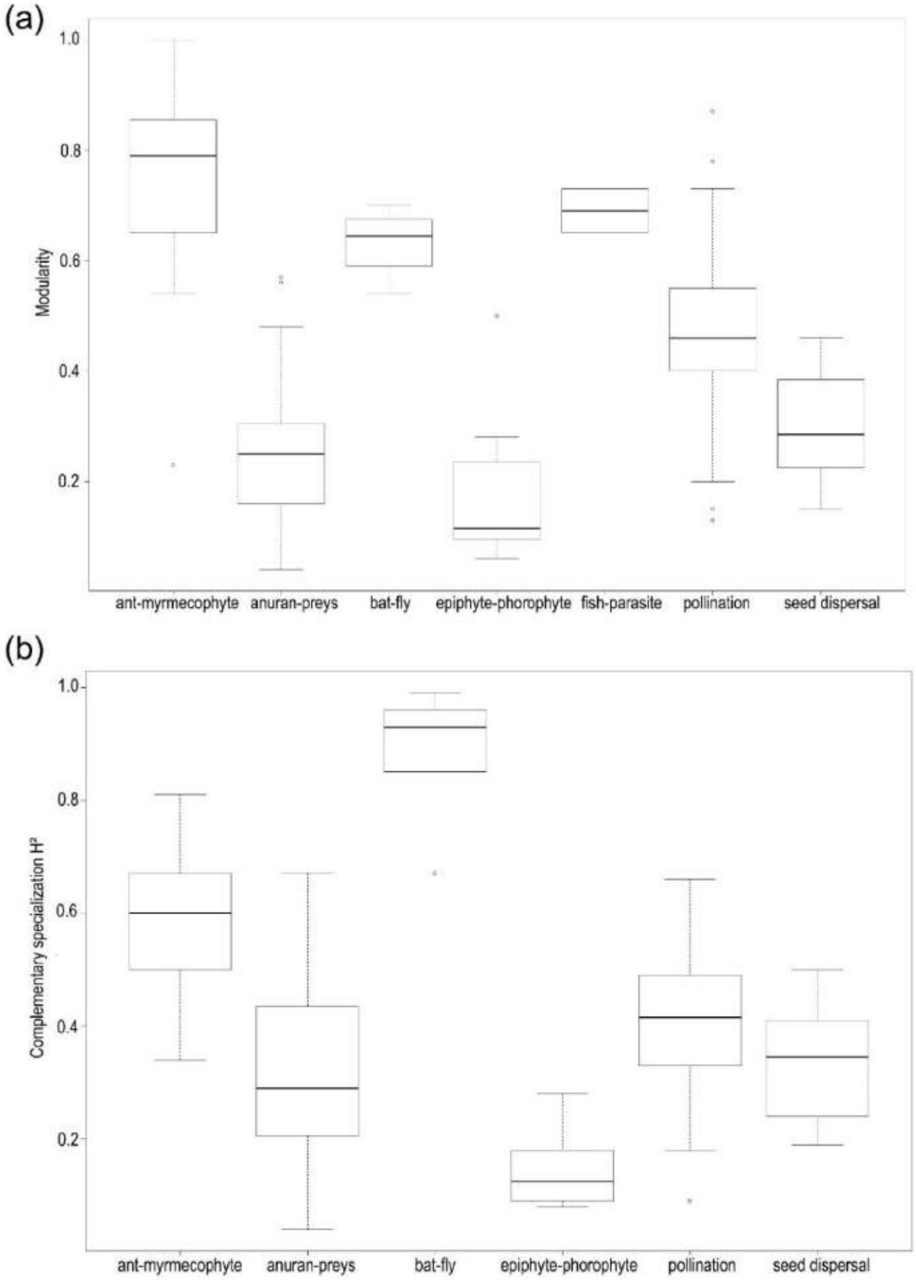

Figure 3. Variation in network metrics across network interaction types: anuran-prey, commensalistic epiphyte–phorophyte, bat-fly, fish-parasite, seed dispersal, pollination, ant–myrmecophyte, networks. (a) Modularity, (b) complementary specialization.

Path analysis showed that part of the effects of complementary specialization, nestedness and modularity are mediated by changes in latitude, sampling metrics, anuran richness, functional and phylogenetic richness (Figure 4, Supplementary material Appendix 1, Table A3). We did not detect any spatial structure for none of the response variables in our model ($p>0.33$ for all variables). The fit index indicated a good fit between the model and the data (RMSEA = 0.515; $p < 0.05$). Sampling metrics (completeness and intensity, respectively) directly influenced complementary specialization ($\beta = 3.79$; $\beta = 1.99$) and modularity ($\beta = 2.36$; $\beta = 2.25$). Anuran richness was spatially structured, being higher towards the tropics ($\beta = - 2.46$) and had effects on the functional and phylogenetic richness ($\beta = 6.68$; $\beta = 5.44$, respectively), with richer communities tending to be phylogenetic and functionally richer.

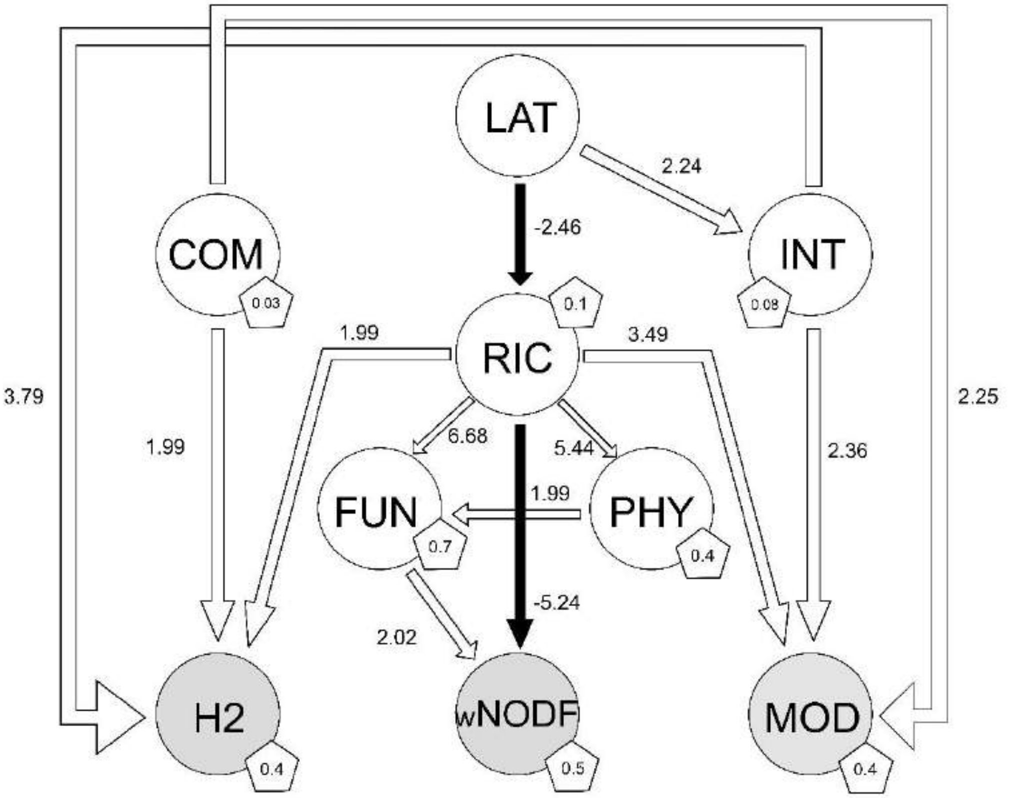

Figure 4. Path diagram showing statistically significant positive (white arrow) and negative (black arrow) influences of variables on network metrics (grey circles), where: LAT (latitude), RIC (anuran richness), FUN (functional richness), PHY (phylogenetic richness), INT (sampling intensity), COM (sampling completeness), H2 (complementary specialization), wNODF (weighted nestedness) and MOD (modularity). Numbers in diamonds represent the r^2 values and numbers on arrows represent beta values.

Latitude indirectly affected complementary specialization via richness ($\beta = -2.46 * 1.99 = -4.89$), with tropical communities tending to be richer and to present greater specialization than the temperate ones. Likewise, latitude influenced complementary specialization mediated by sampling intensity ($\beta = 2.24 * 3.79 = 8.48$), causing a total effect of 3.59 (β = -4.89 + 8.48), which indicates that temperate communities are better sampled, resulting in higher values of complementary specialization.

Nestedness was also indirectly affected by latitude, mediated by anuran richness (β = -2.46 * -5.24 = 12.89). Temperate communities showed lower anuran richness, which resulted in higher values of nestedness. Similarly, latitude negatively influenced nestedness mediated by anuran richness and functional richness (β = -2.46 * 6.68 * 2.02 = - 33.19), as well as by functional and phylogenetic richness, resulting in a total effect of – 53.79 (β = -2.46 * 5.44 * 1.99 * 2.02). Richer communities tend to be phylogenetic and functionally more diverse, resulting in lower values of nestedness.

Modularity was indirectly affected by latitude, mediated by anuran richness (β = -2.46 * 3.49 = - 8.58). Poor communities tended to be less modular than richer communities. In addition, latitude indirectly affected modularity via sampling intensity (β = 2.24 * 2.36 = 5.28), with temperate communities tending to be better sampled as denoted by their higher values of sampling intensity and completeness (β = 2.25). These resulted in higher values of modularity.

Discussion

We found that anuran-prey networks are not nested, exhibit high connectance and low complementary specialization and modularity when compared to other network types. The main effects on network metrics were mediated by changes in latitude, anuran richness, functional and phylogenetic richness.

The diet of anurans is generally based on arthropods (Duellman 1978). Among prey categories, Coleoptera was the most frequent and connected with a great number of anuran species, both in temperate and tropical networks. In addition, Formicidae and Isoptera were the most consumed prey categories. The worldwide elevated richness of Coleoptera, allied to the fact that ants and termite have eusocial habits and form big colonies, make these orders locally abundant, probably explaining their high abundance in the networks (Davidson et al. 2003; Rafael et al. 2012).

The pattern that emerged in the anuran-prey networks in a global scale is different from that reported for other antagonistic networks, such as host-parasitoid (e.g., Morris et al. 2014; Bellay et al. 2015) and marine food-webs (e.g, Dunne et al. 2004). The anuran-prey networks presented low complementary specialization and modularity in relation to other networks types and high values of connectance, as we hypothesized. However, contrary to our expectations, our networks were not nested. These results can be attributed to the community structure of anurans resulting in effects on their diversity and local abundance (Jordano 1987; Lewinsohn et al. 2006), as well as on their generalist and opportunistic food habits (Vignoli & Luiselli 2012). Community structure affects the connectance, as elevated values occur when the number of links in a network is close to the network size, indicating high generalization (Jordano 1987), as observed herein. Likewise, the generalist and opportunistic habits of anurans result in wide and non-restrictive diets and, consequently, in low values of complementary specialization (Blüthgen et al. 2006). In addition, the more specialized anurans did not feed exclusively on one item, but feed it more frequently than others, which lead to low values of complementary specialization and modularity (Toft 1980). This finding is similar to the recorded for epiphyte-phorophyte networks, which are modular, in spite of their low values of specialization (Naranjo et al. 2019). However, values of complementary specialization should be used for comparisons with care, because this metric is highly sensitive to sampling bias (Blüthgen 2010).

Anuran and insect richness are both affected by latitude (Hillebrand 2004; Wiens 2007). And we did detect a direct effect of latitude on anuran richness and sampling intensity. The latitudinal effect on richness is a well-known pattern, with the tropical region harboring higher diversity than temperate regions (Fischer 1960). In this sense, the number of anuran species and interactions are expected to be lower in temperate areas (Wiens 2007; Schemske et al. 2009). Consequently, sampling intensity tends to be higher in temperate than in tropical regions, where interactions tend to be more numerous due to higher species richness. Indeed, networks metrics have already been reported to be sensitive to sampling intensity (Fründ et al. 2016). In the same way, the influence of anuran richness on functional and phylogenetic richness was expected because richer communities tend to harbor higher phylogenetic and trait diversities (Diamond 1975).

The results of the latitudinal effect confirm our hypothesis, since we found indirect effects of latitude in all networks metrics. This result was similar to those that emerged in mutualistic networks, where some networks metrics tend to be influenced by latitude (Schleuning et al. 2012; Trøjelsgaard & Olesen 2013; Schleuning et al. 2014; Dalsgaard et al. 2017). Instead, in host-parasite networks, latitude did not influence network metrics

(Guilhaumon et al. 2012; Morris et al. 2014). The indirect effect of latitude mediated by anuran richness on complementary specialization is explained because tropical communities tend to be richer than their temperate counterparts, resulting in higher specialization, because there are more chances of a species to be a specialist in a diverse community (Schemske et al. 2009), as indicated by path-analysis.

None of the communities were significantly nested. Nestedness occurs when interactions of less connected elements form proper subsets of the interactions of more connected elements. Thus, nestedness decrease when there is high connectance (Cantor et al. 2017), as observed in this study. The high generalization of anuran networks emerged from anurans generalist habits minimizing nestedness.

As predicted, we detected a positive effect of functional richness on nestedness, although values were not significant. We did not find any direct effect of phylogenetic richness on nestedness as hypothesized. However, phylogenetic richness indirectly influenced nestedness via functional richness. This effect starts with latitude, passing by anuran richness and phylogenetic richness. The relation and effects of phylogenetic similarity and species traits are a recurrent pattern in food webs (Cattin et al. 2004; Naisbit et al. 2012). In fact, in a study performed with 13 food-webs, it was demonstrated that body size and phylogenetic similarity are correlated and determine the trophic structure of those webs (Naisbit et al. 2012). Moreover, phylogenetic constraints can explain some empirical food web patterns as intervality, and species abundance mediated by body size (Cattin et al. 2004). Thus, these evidences suggest that the combined effects of phylogenetic and functional richness on nestedness are stronger than the effect of functional richness alone.

Modularity is an emerged pattern in pollination and seed-dispersal networks (Olesen et al. 2007; Schleuning et al. 2014). One of the possible explanations for creating modules in these networks is that modules are composed by groups of species with convergent traits and with the functional interdependence (Schleuning et al. 2014). The detected effect of richness on modularity can be explained because greater species richness can be associated with a high range of anuran sizes and habits. These differences may lead to the formation of modules, assembling some species (e.g. specialists, small sized and terrestrial species) with different characteristics from that in other modules (e.g. generalists, big-sized and arboreal species; (Woodward & Hildrew 2002; Woodward et al. 2005; Olesen et al. 2007). A possible explanation for the detected modularity in the anuran-prey networks is that small-sized species may behave like specialists, preying only upon small insects, because of the relationship among frog body/mouth size and prey volume and size (Toft 1980). And big-sized anurans act as generalist species, preying upon insects of a different size range, causing modularity. Similarly, terrestrial species will prey upon different categories compared to arboreal species, being these groups assigned to different modules. Besides, communities most highly connected tend to exhibit nestedness or modularity properties (Fortuna et al. 2010), a pattern confirmed here, where anuran-prey communities exhibited high connectance and a modular pattern (even if lower than the detected in other types of interaction networks) with no nestedness. Despite this, the detected influence of latitude in modularity for our anuran-prey networks is similar to the recorded in pollination and frugivore networks, where modularity increases with latitude (Dalsgaard et al. 2013; Schleuning et al. 2014). This is also related to the greater species richness in low latitudes (Hillebrand 2004; Wiens 2007).

Our study is the first integrated analysis of structural patterns among networks of antagonistic interactions between anuran and their preys, including information from different parts of the world. In conclusion, our results show that anuran-preys networks have high connectance and low complementary specialization and modularity in relation to other network types, and that they are shaped by latitude, anuran richness, functional and phylogenetic richness. Altogether, our results indicate that there is a latitudinal pattern in anuran-preys network metrics, as previous mutualistic macroecological studies have shown. Latitude indirectly influenced network metrics via anuran richness and functional and/or phylogenetic richness. Furthermore, the pattern emerged in anuran-prey networks metrics reflect the generalist and opportunistic habits of anurans diets. We provide novel information on predator-prey interaction networks in a global scale, concluding that different processes are modeling the architecture of anuran-prey networks, mainly mediated by latitude.

Supporting Information

Table A1: Information on the country, geographical coordinates (decimal degrees), number of recorded anurans species and prey orders, network size (number of anurans + number of preys), sampling completeness and climatic region of the 55 anuran-prey networks. Reference numbers refer to data source.

Reference	Country	Latitude	Longitude	No. of anurans	No. of preys	Network size	Completeness	Region
1	Argentina	-31.6719	-60.6252	6	18	108	92.99	Temperate
2	Argentina	-31.6667	-60.5000	6	18	108	87.95	Temperate
3	Argentina	-27.5002	-58.7502	16	24	384	89.5	Temperate
4	Australia	-35.3112	148.6557	5	14	70	92.5	Temperate
5	Brazil	-22.4334	-42.9833	3	25	75	88.24	Tropical
6	Brazil	-16.2306	-48.0803	3	14	42	80.02	Tropical
7	Brazil	-22.9833	-48.4167	4	19	76	72.34	Tropical
8	Brazil	-7.1804	-35.0942	3	22	66	81.96	Tropical
9	Brazil	-10.5417	-37.0584	16	20	320	72.67	Tropical
10	Brazil	-9.6500	-37.6667	11	20	220	60.64	Tropical
11	Brazil	-6.5860	-37.2673	16	23	368	79.21	Tropical
12	Brazil	-6.6650	-40.2086	16	20	320	75.18	Tropical
13	Brazil	-6.7215	-35.1893	26	21	546	79.35	Tropical
14	Brazil	-7.4167	-36.5144	16	27	432	85.01	Tropical
15	Brazil	-20.0272	-56.6024	4	11	44	100	Tropical
16	Brazil	-18.9167	-48.3000	4	26	104	92.31	Tropical
17	Brazil	-21.7323	-43.3702	3	16	48	85.3	Tropical
18	Brazil	-14.7988	-52.6420	4	15	60	98.59	Tropical
19	Brazil	-29.3833	-50.3833	7	20	140	88.72	Temperate
20	Brazil	-20.7500	-40.9501	3	15	45	91.87	Tropical
21	Brazil	-7.4744	-38.3442	13	25	325	88.09	Tropical
22	Brazil	-20.5769	-49.3167	3	20	60	81.62	Tropical
23	Brazil	-21.6645	-57.7179	12	17	204	52.01	Tropical
24	Brazil	-9.0000	-41.0000	3	15	45	75.58	Tropical
25	Brazil	-15.4867	-47.6892	5	17	85	86.3	Tropical
26	Brazil	-21.4099	-48.3509	7	10	70	77.57	Tropical
27	Brazil	-28.1344	-49.4797	3	23	69	66.69	Temperate
28	China	30.2916	122.1710	3	14	42	84.48	Temperate
29	Colombia	10.0810	-74.0012	5	19	95	70.33	Tropical
30	Colombia	4.1321	-73.6416	24	21	504	80.45	Tropical
31	Colombia	9.0000	-73.9667	4	15	60	84.27	Tropical

Reference	Country	Latitude	Longitude	No. of anurans	No. of preys	Network size	Completeness	Region
32	Colombia	7.0500	-72.9501	6	14	84	40	Tropical
33	Colombia	4.8333	-76.2500	17	20	340	67.1	Tropical
34	Colombia	4.5927	-75.8209	8	18	144	66.44	Tropical
35	Ecuador	0.0500	-76.9836	64	20	1280	71.66	Tropical
36	Ecuador	-0.7669	-76.1000	38	22	836	75.22	Tropical
37	Hungary	46.6373	17.1428	3	21	63	62.18	Temperate
38	Italy	42.1392	12.1025	6	21	126	87.41	Temperate
39	Ivory Coast	5.5286	-4.0194	4	15	60	96.31	Tropical
40	Malaysia	1.6167	113.5833	10	10	100	95.24	Tropical
41	Mexico	29.4621	-110.6140	3	9	27	71.44	Temperate
42	Nigeria	5.1172	7.7875	4	22	88	73.72	Tropical
43	Panama	9.0833	-79.8333	8	4	32	86.5	Tropical
44	Panama	9.3333	-78.9167	20	4	80	95.89	Tropical
45	Peru	-9.5833	-74.8000	13	4	52	99.1	Tropical
46	Peru	-12.5833	-69.0833	57	27	1539	73.42	Tropical
47	Poland	52.2031	17.4896	3	12	36	80.06	Temperate
48	Romania	45.1691	27.9472	4	12	48	91.49	Temperate
49	Serbia	45.1064	19.9106	3	23	69	90	Temperate
50	Singapore	1.3152	103.8163	6	22	132	94.34	Tropical
51	Spain	40.2824	-6.6610	7	30	210	87.46	Temperate
52	Taiwan	23.4283	120.4850	5	19	95	54.02	Tropical
53	Uruguay	-34.3336	-57.0002	3	12	36	97.41	Temperate
54	Uruguay	-34.6167	-55.3667	4	13	52	100	Temperate
55	Venezuela	8.6167	-71.1500	6	26	156	60.71	Tropical

Table A2: Prey categories and anuran species according to numbers represented in the compiled meta-network combining all the 55 studies together, and the meta-networks combining the 16 temperate sites and the 39 tropical sites (Figure 2).

	Compiled		**Temperate**		**Tropical**	
Numbers	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**
1	Acari	*Adelphobates quinquevittatus*	Acari	*Alytes obstetricans*	Acari	*Adelphobates quinquevittatus*
2	Amblypygi	*Adenomera andreae*	Amphipoda	*Bombina bombina*	Amblypygi	*Adenomera andreae*
3	Amphipoda	*Adenomera* sp.	Annelidae	*Bufo bufo*	Amphipoda	*Adenomera* sp.
4	Annelidae	*Adenomera* sp.1	Anura	*Bufo calamita*	Annelidae	*Agalychnis hulli*
5	Anura	*Agalychnis hulli*	Araneae	*Bufo gargarizans*	Anura	*Allobates cepedai*
6	Araneae	*Allobates cepedai*	Blattaria	*Crinia signifera*	Araneae	*Allobates femoralis*
7	Blattaria	*Allobates femoralis*	Coleoptera	*Dendropsophus minutus*	Blattaria	*Allobates juanii*
8	Coleoptera	*Allobates juanii*	Collembola	*Dendropsophus nanus*	Coleoptera	*Allobates marchesianus*
9	Collembola	*Allobates marchesianus*	Crustaceae	*Discoglossus galganoi*	Collembola	*Allobates talamancae*
10	Crustaceae	*Allobates talamancae*	Dermaptera	*Elachistocleis bicolor*	Crustaceae	*Amazophrynella minuta*
11	Dermaptera	*Alytes obstetricans*	Dictyoptera	*Epidalea viridis*	Dermaptera	*Ameerega braccata*
12	Dictyoptera	*Amazophrynella minuta*	Diplura	*Fejervarya limnocharis*	Diplura	*Ameerega petersi*
13	Diplura	*Ameerega braccata*	Diptera	*Hyla arborea*	Diptera	*Ameerega picta*
14	Diptera	*Ameerega petersi*	Embioptera	*Hyla intermedia*	Ephemeroptera	*Ameerega trivittata*
15	Embioptera	*Ameerega picta*	Ephemeroptera	*Hypsiboas faber*	Fish	*Amietophrynus maculatus*
16	Ephemeroptera	*Ameerega trivittata*	Fish	*Hypsiboas leptolineatus*	Formicidae	*Anaxyrus debilis*
17	Fish	*Amietophrynus maculatus*	Formicidae	*Hypsiboas pulchellus*	Hemiptera	*Anaxyrus punctatus*
18	Formicidae	*Anaxyrus debilis*	Hemiptera	*Hypsiboas punctatus*	Hymenoptera	*Andinobates fulguritus*
19	Hemiptera	*Anaxyrus punctatus*	Hymenoptera	*Leptodactylus bufonius*	Isoptera	*Andinobates minutus*
20	Hymenoptera	*Andinobates fulguritus*	Isoptera	*Leptodactylus chaquensis*	Isopoda	*Aromobates alboguttatus*
21	Isoptera	*Andinobates minutus*	Isopoda	*Leptodactylus latinasus*	Larvae	*Atelopus oxyrhynchus*
22	Isopoda	*Aromobates alboguttatus*	Larvae	*Leptodactylus latrans*	Lepidoptera	*Atelopus varius*
23	Larvae	*Atelopus oxyrhynchus*	Lepidoptera	*Litoria verreauxii*	Mantodea	*Brachycephalus garbeanus*

	Compiled		**Temperate**		**Tropical**	
Numbers	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**
24	Lepidoptera	*Atelopus varius*	Mantodea	*Lysapsus limellum*	Mollusca	*Bufo typhonius*
25	Mantodea	*Bombina bombina*	Mollusca	*Melanophryniscus cupreuscapularis*	Myriapoda	*Centrolene robledoi*
26	Mollusca	*Brachycephalus garbeanus*	Myriapoda	*Pelobates fuscus*	Nymph	*Ceratophrys cornuta*
27	Myriapoda	*Bufo bufo*	Neuroptera	*Pelophylax esculentus*	Neuroptera	*Chalcorana chalconota*
28	Nymph	*Bufo calamita*	Odonata	*Pelophylax lessonae*	Odonata	*Chiasmocleis alagoanus*
29	Neuroptera	*Bufo gargarizans*	Opiliones	*Pelophylax nigromaculatus*	Opiliones	*Chiasmocleis bassleri*
30	Odonata	*Bufo typhonius*	Orthoptera	*Pelophylax ridibundus*	Orthoptera	*Chiasmocleis ventrimaculata*
31	Opiliones	*Centrolene robledoi*	Phalangida	*Physalaemus albonotatus*	Ovocyte anura	*Colostethus fraterdanieli*
32	Orthoptera	*Ceratophrys cornuta*	Phasmatodea	*Physalaemus biligonigerus*	Phalangida	*Colostethus ingunialis*
33	Ovocyte anura	*Chalcorana chalconota*	Plecoptera	*Physalaemus gracilis*	Phasmatodea	*Colostethus pratti*
34	Phalangida	*Chiasmocleis alagoanus*	Protura	*Physalaemus lisei*	Phthiraptera	*Colostethus* sp.
35	Phasmatodea	*Chiasmocleis bassleri*	Pseudoscorpionida	*Physalaemus riograndensis*	Plecoptera	*Corythomantis greeningi*
36	Phthiraptera	*Chiasmocleis ventrimaculata*	Psocoptera	*Physalaemus santafesinus*	Protura	*Craugastor fitzingeri*
37	Plecoptera	*Colostethus fraterdanieli*	Scorpionida	*Pseudis cardosoi*	Pseudoscorpionida	*Craugastor golmeri*
38	Protura	*Colostethus ingunialis*	Solifugae	*Pseudis paradoxa*	Psocoptera	*Craugastor longirostris*
39	Pseudoscorpionida	*Colostethus pratti*	Thysanoptera	*Pseudopaludicola boliviana*	Pupae	*Craugastor talamancae*
40	Psocoptera	*Colostethus* sp.	Trichoptera	*Pseudopaludicola falcipes*	Rodentia	*Ctenophryne geayi*
41	Pupae	*Corythomantis greeningi*	Vertebrata	*Pseudophryne bibroni*	Scorpionida	*Dendrobates auratus*
42	Rodentia	*Craugastor bransfordii*		*Pseudophryne corroboree*	Siphonaptera	*Dendrophryniscus minutus*
43	Scorpionida	*Craugastor fitzingeri*		*Pseudophryne dendyi*	Tadpole	*Dendropsophus allenorum*
44	Solifugae	*Craugastor golmeri*		*Rana arvalis*	Thysanoptera	*Dendropsophus bifurcus*
45	Siphonaptera	*Craugastor longirostris*		*Rana dalmatina*	Thysanura	*Dendropsophus bokermanni*
46	Tadpole	*Craugastor talamancae*		*Rana esculenta* complex	Trichoptera	*Dendropsophus branneri*
47	Thysanoptera	*Crinia signifera*		*Rana iberica*	Vertebrata	*Dendropsophus brevifrons*
48	Thysanura	*Ctenophryne geayi*		*Rana perezi*		*Dendropsophus columbianus*
49	Trichoptera	*Dendrobates auratus*		*Rhinella bergi*		*Dendropsophus elegans*

Compiled			Temperate		Tropical	
Numbers	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**
50	Vertebrata	*Dendrophryniscus minutus*		*Rhinella fernandezae*		*Dendropsophus koechlini*
51		*Dendropsophus allenorum*		*Rhinella gr. granulosa*		*Dendropsophus leali*
52		*Dendropsophus bifurcus*		*Rhinella granulosa*		*Dendropsophus leucophyllatus*
53		*Dendropsophus bokermanni*		*Rhinella schneideri*		*Dendropsophus marmoratus*
54		*Dendropsophus branneri*		*Scinax acuminatus*		*Dendropsophus mathiassoni*
55		*Dendropsophus brevifrons*		*Scinax granulatus*		*Dendropsophus microcephalus*
56		*Dendropsophus columbianus*		*Scinax nasicus*		*Dendropsophus minutus*
57		*Dendropsophus elegans*		*Scinax perereca*		*Dendropsophus nanus*
58		*Dendropsophus koechlini*				*Dendropsophus oliveirai*
59		*Dendropsophus leali*				*Dendropsophus parviceps*
60		*Dendropsophus leucophyllatus*				*Dendropsophus rhodopeplus*
61		*Dendropsophus marmoratus*				*Dendropsophus riveroi*
62		*Dendropsophus mathiassoni*				*Dendropsophus sanborni*
63		*Dendropsophus microcephalus*				*Dendropsophus sarayacuensis*
64		*Dendropsophus minutus*				*Dendropsophus schubarti*
65		*Dendropsophus nanus*				*Dendropsophus triangulum*
66		*Dendropsophus oliveirai*				*Dermatonotus muelleri*
67		*Dendropsophus parviceps*				*Diasporus vocator*
68		*Dendropsophus rhodopeplus*				*Duttaphrynus melanostictus*
69		*Dendropsophus riveroi*				*Edalorhina perezi*
70		*Dendropsophus sanborni*				*Elachistocleis cesarii*
71		*Dendropsophus sarayacuensis*				*Elachistocleis ovalis*
72		*Dendropsophus schubarti*				*Eleutherodactylus bransfordi*
73		*Dendropsophus triangulum*				*Eleutherodactylus* cf. *juipoca*
74		*Dermatonotus muelleri*				*Engystomops petersi*

	Compiled		Temperate		Tropical	
Numbers	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**
75		*Diasporus vocator*				*Engystomops pustulosus*
76		*Discoglossus galganoi*				*Fejervarya limnocharis*
77		*Duttaphrynus melanostictus*				*Hamptophryne alios*
78		*Edalorhina perezi*				*Hamptophryne boliviana*
79		*Elachistocleis bicolor*				*Hemiphractus proboscideus*
80		*Elachistocleis cesarii*				*Hoplobatrachus occipitalis*
81		*Elachistocleis ovalis*				*Hyalinobatrachium munozorum*
82		*Eleutherodactylus* cf. *juipoca*				*Hyloscirtus albopunctulatus*
83		*Engystomops petersi*				*Hyloscirtus estevesi*
84		*Engystomops pustulosus*				*Hyloscirtus jahni*
85		*Epidalea viridis*				*Hyloscirtus platydactylus*
86		*Fejervarya limnocharis*				*Hyloxalus bocagei*
87		*Hamptophryne alios*				*Hyloxalus sauli*
88		*Hamptophryne boliviana*				*Hypodactylus nigrovittatus*
89		*Hemiphractus proboscideus*				*Hypsiboas* aff. *pulchellus*
90		*Hoplobatrachus occipitalis*				*Hypsiboas alboguttata*
91		*Hyalinobatrachium munozorum*				*Hypsiboas albomarginatus*
92		*Hyla arborea*				*Hypsiboas albopunctatus*
93		*Hyla intermedia*				*Hypsiboas bifurca*
94		*Hyloscirtus albopunctulatus*				*Hypsiboas boans*
95		*Hyloscirtus estevesi*				*Hypsiboas calcaratus*
96		*Hyloscirtus jahni*				*Hypsiboas cinerascens*
97		*Hyloscirtus platydactylus*				*Hypsiboas crepitans*
98		*Hyloxalus bocagei*				*Hypsiboas faber*
99		*Hyloxalus sauli*				*Hypsiboas fasciatus*
100		*Hypodactylus nigrovittatus*				*Hypsiboas geographicus*

	Compiled		Temperate		Tropical	
Numbers	Preys categories (boxes)	Anuran species (circles)	Preys categories (boxes)	Anuran species (circles)	Preys categories (boxes)	Anuran species (circles)
101		*Hypsiboas aff. pulchellus*				*Hypsiboas lanciformis*
102		*Hypsiboas alboguttata*				*Hypsiboas prasinus*
103		*Hypsiboas albomarginatus*				*Hypsiboas pugnax*
104		*Hypsiboas albopunctatus*				*Hypsiboas punctatus*
105		*Hypsiboas bifurca*				*Hypsiboas raniceps*
106		*Hypsiboas boans*				*Incilius coniferus*
107		*Hypsiboas calcaratus*				*Incilius mazatlanensis*
108		*Hypsiboas cinerascens*				*Ischnocnema ramagii*
109		*Hypsiboas crepitans*				*Kaloula pulchra*
110		*Hypsiboas faber*				*Leptobrachium nigrops*
111		*Hypsiboas fasciatus*				*Leptodactus latrans*
112		*Hypsiboas geographicus*				*Leptodactylus bolivianus*
113		*Hypsiboas lanciformis*				*Leptodactylus bufonius*
114		*Hypsiboas leptolineatus*				*Leptodactylus caatingae*
115		*Hypsiboas prasinus*				*Leptodactylus chaquensis*
116		*Hypsiboas pugnax*				*Leptodactylus colombiensis*
117		*Hypsiboas pulchellus*				*Leptodactylus elenae*
118		*Hypsiboas punctatus*				*Leptodactylus fragilis*
119		*Hypsiboas raniceps*				*Leptodactylus furnarius*
120		*Incilius coniferus*				*Leptodactylus fuscus*
121		*Incilius mazatlanensis*				*Leptodactylus hylaedactylus*
122		*Kaloula pulchra*				*Leptodactylus latrans*
123		*Leptobrachium nigrops*				*Leptodactylus leptodactyloides*
124		*Leptodactylus bolivianus*				*Leptodactylus lineatus*
125		*Leptodactylus bufonius*				*Leptodactylus macrosternum*
126		*Leptodactylus caatingae*				*Leptodactylus marmoratus*

	Compiled		Temperate		Tropical	
Numbers	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**
127		*Leptodactylus chaquensis*				*Leptodactylus mystaceus*
128		*Leptodactylus colombiensis*				*Leptodactylus mystacinus*
129		*Leptodactylus elenae*				*Leptodactylus natalensis*
130		*Leptodactylus fragilis*				*Leptodactylus pentadactylus*
131		*Leptodactylus furnarius*				*Leptodactylus petersii*
132		*Leptodactylus fuscus*				*Leptodactylus podicipinus*
133		*Leptodactylus hylaedactylus*				*Leptodactylus rhodonotus*
134		*Leptodactylus latinasus*				*Leptodactylus* sp.
135		*Leptodactylus latrans*				*Leptodactylus troglodytes*
136		*Leptodactylus leptodactyloides*				*Leptodactylus vastus*
137		*Leptodactylus lineatus*				*Limnonectes blythii*
138		*Leptodactylus macrosternum*				*Limnonectes ibanorum*
139		*Leptodactylus marmoratus*				*Limnonectes kuhlii*
140		*Leptodactylus mystaceus*				*Limnonectes macrodon*
141		*Leptodactylus mystacinus*				*Lithobates catesbeianus*
142		*Leptodactylus natalensis*				*Lithobates palmipes*
143		*Leptodactylus pentadactylus*				*Lithodytes lineatus*
144		*Leptodactylus petersii*				*Meristogenys jerboa*
145		*Leptodactylus podicipinus*				*Microhyha butleri*
146		*Leptodactylus rhodonotus*				*Microhyla fissipes*
147		*Leptodactylus sp.*				*Microhyla heymonsi*
148		*Leptodactylus troglodytes*				*Microhyla heynamii*
149		*Leptodactylus vastus*				*Micryletta stejnegeri*
150		*Limnonectes blythii*				*Nyctimantis rugiceps*
151		*Limnonectes ibanorum*				*Odorrana hosii*
152		*Limnonectes kuhlii*				*Oreobates cruralis*

	Compiled		Temperate		Tropical	
Numbers	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**
153		*Limnonectes macrodon*				*Oreobates quixensis*
154		*Lithobates catesbeianus*				*Osteocephalus buckleyi*
155		*Lithobates palmipes*				*Osteocephalus cabrerai*
156		*Lithodytes lineatus*				*Osteocephalus carri*
157		*Litoria verreauxii*				*Osteocephalus deridens*
158		*Lysapsus limellum*				*Osteocephalus fuscifacies*
159		*Melanophryniscus cupreuscapularis*				*Osteocephalus leprieurii*
160		*Meristogenys jerboa*				*Osteocephalus planiceps*
161		*Microhyha butleri*				*Osteocephalus* sp.
162		*Microhyla fissipes*				*Osteocephalus taurinus*
163		*Microhyla heymonsi*				*Osteocephalus yasuni*
164		*Microhyla heynamii*				*Phitecopus azureus*
165		*Micryletta stejnegeri*				*Phrynobatrachus ghanensis*
166		*Nyctimantis rugiceps*				*Phrynobatrachus phyllophilus*
167		*Odorrana hosii*				*Phrynoidis asper*
168		*Oreobates cruralis*				*Phyllomedusa atelopoides*
169		*Oreobates quixensis*				*Phyllomedusa hypochondrialis*
170		*Osteocephalus buckleyi*				*Phyllomedusa nordestina*
171		*Osteocephalus cabrerai*				*Phyllomedusa palliata*
172		*Osteocephalus carri*				*Phyllomedusa sauvagii*
173		*Osteocephalus deridens*				*Phyllomedusa tarsius*
174		*Osteocephalus fuscifacies*				*Phyllomedusa tomopterna*
175		*Osteocephalus leprieurii*				*Phyllomedusa vaillanti*
176		*Osteocephalus planiceps*				*Physalaemus albifrons*
177		*Osteocephalus* sp.				*Physalaemus biligonigerus*

	Compiled		Temperate		Tropical	
Numbers	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**
178		*Osteocephalus taurinus*				*Physalaemus centralis*
179		*Osteocephalus yasuni*				*Physalaemus cicada*
180		*Pelobates fuscus*				*Physalaemus cuvieri*
181		*Pelophylax esculentus*				*Physalaemus marmoratus*
182		*Pelophylax lessonae*				*Physalaemus nattereri*
183		*Pelophylax nigromaculatus*				*Pipa carvalhoi*
184		*Pelophylax ridibundus*				*Pipa pipa*
185		*Phrynobatrachus ghanensis*				*Pleurodema brachyops*
186		*Phrynobatrachus phyllophilus*				*Pleurodema diplolister*
187		*Phrynoidis aspera*				*Polypedates leucomystax*
188		*Phyllomedusa atelopoides*				*Pristimantis palmeri*
189		*Phyllomedusa hypochondrialis*				*Pristimantis acatallelus*
190		*Phyllomedusa nordestina*				*Pristimantis achatinus*
191		*Phyllomedusa palliata*				*Pristimantis acuminatus*
192		*Phyllomedusa sauvagii*				*Pristimantis altae*
193		*Phyllomedusa tarsius*				*Pristimantis altamazonicus*
194		*Phyllomedusa tomopterna*				*Pristimantis angustilineatus*
195		*Phyllomedusa vaillanti*				*Pristimantis brevifrons*
196		*Physalaemus albifrons*				*Pristimantis calcaratus*
197		*Physalaemus albonotatus*				*Pristimantis carlossanchezi*
198		*Physalaemus biligonigerus*				*Pristimantis conspicillatus*
199		*Physalaemus centralis*				*Pristimantis croceoinguinis*
200		*Physalaemus cicada*				*Pristimantis cruentus*
201		*Physalaemus cuvieri*				*Pristimantis erythropleura*
202		*Physalaemus gracilis*				*Pristimantis fenestratus*
203		*Physalaemus lisei*				*Pristimantis frater*

Compiled			Temperate		Tropical	
Numbers	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**
204		*Physalaemus marmoratus*				*Pristimantis hectus*
205		*Physalaemus nattereri*				*Pristimantis imitatrix*
206		*Physalaemus riograndensis*				*Pristimantis juanchoi*
207		*Physalaemus santafesinus*				*Pristimantis jubatus*
208		*Pipa carvalhoi*				*Pristimantis lacrimosus*
209		*Pipa pipa*				*Pristimantis lanthanites*
210		*Pleurodema brachyops*				*Pristimantis lutitus*
211		*Pleurodema diplolister*				*Pristimantis martiae*
212		*Plyllomedusa azureua*				*Pristimantis medemi*
213		*Polypedates leucomystax*				*Pristimantis merostictus*
214		*Pristimantis acatallelus*				*Pristimantis miyatai*
215		*Pristimantis achatinus*				*Pristimantis myops*
216		*Pristimantis acuminatus*				*Pristimantis ockendeni*
217		*Pristimantis altae*				*Pristimantis orpacobates*
218		*Pristimantis altamazonicus*				*Pristimantis palmeri*
219		*Pristimantis angustilineatus*				*Pristimantis paululus*
220		*Pristimantis brevifrons*				*Pristimantis peruvianus*
221		*Pristimantis calcaratus*				*Pristimantis pseudoacuminatus*
222		*Pristimantis carlossanchezi*				*Pristimantis quantus*
223		*Pristimantis conspicillatus*				*Pristimantis quaquaversus*
224		*Pristimantis croceoinguinis*				*Pristimantis ramagii*
225		*Pristimantis cruentus*				*Pristimantis savagei*
226		*Pristimantis erythropleura*				*Pristimantis* sp.
227		*Pristimantis fenestratus*				*Pristimantis* sp.1
228		*Pristimantis frater*				*Pristimantis toftae*
229		*Pristimantis hectus*				*Pristimantis vanadise*

	Compiled		Temperate		Tropical	
Numbers	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**
230		*Pristimantis imitatrix*				*Pristimantis variabilis*
231		*Pristimantis juanchoi*				*Pristimantis vinhai*
232		*Pristimantis jubatus*				*Pristimantis w-nigrum*
233		*Pristimantis lacrimosus*				*Proceratophrys cristiceps*
234		*Pristimantis lanthanites*				*Proceratophrys renalis*
235		*Pristimantis lutitus*				*Proceratophrys* sp.
236		*Pristimantis martiae*				*Pseudis platensis*
237		*Pristimantis medemi*				*Pseudopaludicola pocoto*
238		*Pristimantis merostictus*				*Pseudopaludicola pusilla*
239		*Pristimantis miyatai*				*Psudopaludicola* aff. *saltica*
240		*Pristimantis myops*				*Ptychadena aequiplicata*
241		*Pristimantis ockendeni*				*Ptychadena mascareniensis*
242		*Pristimantis orpacobates*				*Ptychadena oxyrhynchus*
243		*Pristimantis palmeri*				*Ptychadena pumilio*
244		*Pristimantis paululus*				*Pulchrana signata*
245		*Pristimantis peruvianus*				*Rentapia hosii*
246		*Pristimantis pseudoacuminatus*				*Rhaebo glaberrimus*
247		*Pristimantis quantus*				*Rhaebo haematiticus*
248		*Pristimantis quaquaversus*				*Rheobates palmatus*
249		*Pristimantis ramagii*				*Rhinella bergi*
250		*Pristimantis savagei*				*Rhinella crucifer*
251		*Pristimantis* sp.				*Rhinella* gr. *typhonius*
252		*Pristimantis* sp.1				*Rhinella granulosa*
253		*Pristimantis toftae*				*Rhinella icterica*
254		*Pristimantis vanadise*				*Rhinella jimi*
255		*Pristimantis variabilis*				*Rhinella major*

	Compiled		Temperate		Tropical	
Numbers	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**
256		*Pristimantis vinhai*				*Rhinella margaritifera*
257		*Pristimantis w-nigrum*				*Rhinella marina*
258		*Proceratophrys cristiceps*				*Rhinella ocellata*
259		*Proceratophrys renalis*				*Rhinella schneideri*
260		*Proceratophrys sp.*				*Rulyrana flavopunctata*
261		*Pseudis cardosoi*				*Scarthyla goinorum*
262		*Pseudis paradoxa*				*Scarthyla vigilans*
263		*Pseudis platensis*				*Scinax acuminatus*
264		*Pseudopaludicola* aff. *saltica*				*Scinax crospedospilus*
265		*Pseudopaludicola boliviana*				*Scinax cruentommus*
266		*Pseudopaludicola falcipes*				*Scinax euridyce*
267		*Pseudopaludicola pocoto*				*Scinax funereus*
268		*Pseudopaludicola pusilla*				*Scinax fuscomarginatus*
269		*Pseudophryne bibroni*				*Scinax garbei*
270		*Pseudophryne corroboree*				*Scinax ictericus*
271		*Pseudophryne dendyi*				*Scinax nebulosus*
272		*Ptychadena aequiplicata*				*Scinax pachicrus*
273		*Ptychadena mascareniensis*				*Scinax pedromedinae*
274		*Ptychadena oxyrhynchus*				*Scinax rostratus*
275		*Ptychadena pumilio*				*Scinax ruber*
276		*Pulchrana signata*				*Scinax wandae*
277		*Rana arvalis*				*Scinax x-signatus*
278		*Rana dalmatina*				*Silverstoneia nubicola*
279		*Rana esculenta complex*				*Sphaenorhynchus carneus*
280		*Rana iberica*				*Sphaenorhynchus lacteus*
281		*Rana perezi*				*Sphaenorhynchus planicola*

	Compiled		Temperate		Tropical	
Numbers	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**
282		*Rentapia hosii*				*Strabomantis biporcatus*
283		*Rhaebo glaberrimus*				*Strabomantis bufoniformis*
284		*Rhaebo haematiticus*				*Strabomantis sulcatus*
285		*Rheobates palmatus*				*Tachiramantis douglasi*
286		*Rhinella bergi*				*Teratohyla midas*
287		*Rhinella crucifer*				*Trachycephalus coriaceus*
288		*Rhinella fernandezae*				*Trachycephalus typhonius*
289		*Rhinella* gr. *granulosa*				*Zachaenus carvalhoi*
290		*Rhinella granulosa*				
291		*Rhinella icterica*				
292		*Rhinella jimi*				
293		*Rhinella major*				
294		*Rhinella margaritifera*				
295		*Rhinella marina*				
296		*Rhinella ocellata*				
297		*Rhinella schneideri*				
298		*Rulyrana flavopunctata*				
299		*Scarthyla goinorum*				
300		*Scarthyla vigilans*				
301		*Scinax acuminatus*				
302		*Scinax crospedospilus*				
303		*Scinax cruentommus*				
304		*Scinax euridyce*				
305		*Scinax funereus*				
306		*Scinax fuscomarginatus*				
307		*Scinax garbei*				

	Compiled		Temperate		Tropical	
Numbers	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**	**Preys categories (boxes)**	**Anuran species (circles)**
308		*Scinax granulatus*				
309		*Scinax ictericus*				
310		*Scinax nasicus*				
311		*Scinax nebulosus*				
312		*Scinax pachicrus*				
313		*Scinax pedromedinae*				
314		*Scinax perereca*				
315		*Scinax rostratus*				
316		*Scinax ruber*				
317		*Scinax wandae*				
318		*Scinax x-signatus*				
319		*Silverstoneia nubicola*				
320		*Sphaenorhynchus carneus*				
321		*Sphaenorhynchus lacteus*				
322		*Sphaenorhynchus planicola*				
323		*Strabomantis biporcatus*				
324		*Strabomantis bufoniformis*				
325		*Strabomantis sulcatus*				
326		*Tachiramantis douglasi*				
327		*Teratohyla midas*				
328		*Trachycephalus coriaceus*				
329		*Trachycephalus typhonius*				
330		*Zachaenus carvalhoi*				

Table A3: Summary of the path analysis model showing the effects of latitude on network metrics.

Driver	Response	Indirect effect	Mediated by	Total effect
Latitude	Nestedness	12.89	Anuran richness	-74.09
		-33.19	Anuran and functional richness	
		-53.79	Anuran, functional and phylogenetic richness	
	Complementary specialization	-4.89	Anuran richness	3.59
		8.48	Intensity	
	Modularity	-8.58	Anuran richness	-3.3
		5.28	Intensity	

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Chapter 2. Seasonal patterns of ecological uniqueness of anuran metacommunities along different ecoregions in Western Brazil

Abstract

Beta diversity can be portioned into local contributions to beta diversity (LCBD), which represents the degree of community composition uniqueness of a site compared to regionally sampled sites. LCBD can fluctuate among seasons and ecoregions according to site characteristics, species dispersal abilities, and biotic interactions. In this context, we examined anuran seasonal patterns of LCBD in different ecoregions of Western Brazil, and assessed their correlation with species richness and if environmental (climatic variables, pond area and ecoregions) and/or spatial predictors (spatial configuration of sampling sites captured by distance-based Moran's Eigenvector Maps) would drive patterns of LCBD. We sampled anurans in 19 ponds in different ecoregions in the Mato Grosso do Sul state, Western Brazil, during one dry and one rainy season. We found that LCBD patterns were similar between seasons with sites tending to contribute in the same way for community composition uniqueness during the dry and rainy season. Among studied ecoregions, Cerrado showed higher LCBD values in both seasons. In addition, LCBD was negatively correlated with species richness in the dry season. We also found that LCBD variation was explained by ecoregion in the dry season, but in the rainy season both environmental and spatial global models were non-significant. Our results reinforce the compositional uniqueness of the Cerrado ecoregion when compared to the other ecoregions in both seasons, which may be caused by the presence of species with different requirements that tolerate different conditions caused by seasonality.

Keywords: Beta diversity, LCBD, biomes, ponds.

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Resumo

A diversidade beta pode ser dividida em contribuições locais para a diversidade beta (LCBD), que representa o grau de exclusividade da composição da comunidade de um local em comparação com locais amostrados regionalmente. O LCBD pode flutuar entre estações e ecorregiões de acordo com as características do local, habilidade de dispersão das espécies e interações bióticas. Neste contexto, examinamos os padrões sazonais do LCBD dos anuros em diferentes ecorregiões do Oeste do Brasil, e avaliamos sua correlação com a riqueza de espécies e se o ambiente (variáveis climáticas, área das lagoas e ecorregião) e / ou preditores espaciais (configuração espacial dos pontos de amostragem capturado pelos Mapas de Autovetores de Moran baseados na distância) conduziriam os padrões de LCBD. Amostramos anuros em 19 lagoas em diferentes ecorregiões no estado de Mato Grosso do Sul, Oeste do Brasil, durante as estações seca e chuvosa. Descobrimos que os padrões de LCBD foram semelhantes entre as estações com os locais tendendo a contribuir da mesma forma para a exclusividade da composição da comunidade durante a estação seca e chuvosa. Entre as ecorregiões estudadas, o Cerrado apresentou maiores valores de LCBD em ambas as estações. Além disso, o LCBD foi correlacionado negativamente com a riqueza de espécies na estação seca. Também descobrimos que a variação do LCBD foi explicada pela ecorregião na estação seca, mas na estação chuvosa os modelos globais ambientais e espaciais não foram significativos. Nossos resultados reforçam a singularidade composicional do Cerrado quando comparado às demais ecorregiões em ambas as estações, o que pode ser causado pela presença de espécies com diferentes exigências que toleram diferentes condições causadas pela sazonalidade.

Palavras-chave: Beta diversidade, LCBD, biomas, poças.

Introduction

Understanding the organization of species diversity through space and time is one of the main scopes of community ecology (Ricklefs 2004). Species diversity can be divided into gamma (regional diversity), alpha (local diversity), and beta components (Whittaker 1972). The latter (beta diversity) is the variation in species composition among sites within a region, first described by Whittaker (Whittaker 1960; Whittaker 1972). Such variation can be related to ecological processes, so analyzing beta diversity patterns can shed light on the mechanisms underlying biodiversity patterns (Anderson et al. 2011). Beta diversity can be measured in different ways, including additive and multiplicative indices, dissimilarity measures, and beta diversity as variation in community structure among sampling units (Anderson et al. 2011). These methods include the partition of the variance of community data into species contributions to beta diversity (SCBD) and into local contributions to beta diversity (LCBD) (Legendre & De Cáceres 2013). LCBDs represent the degree of community composition uniqueness of a site compared to regionally sampled sites (Legendre & De Cáceres 2013) and constitute an important tool to detect more unique sites in terms of community composition that can be used to guide conservation strategies and to detect keystone communities (Mouquet et al. 2013; Ruhí et al. 2017; Valente-Neto et al. 2020). Keystone community is defined as communities with a disproportional positive impact relative to their weight in the metacommunity. One simple way to detect keystone communities is through the correlation between LCBD (a measure of the relative site impact in the metacommunity) and species richness (a measure of weight or size of local communities) (Mouquet & Loreau 2003; Ruhí et al. 2017; Valente-Neto et al. 2020). Keystone communities would be those communities with high impact on metacommunity (high value of LCBD) and low value of species richness (Valente-Neto et al. 2020).

Local contributions to beta diversity can also be used to test if selection and/or dispersal-related processes explain biodiversity patterns (Tonkin et al. 2016; Heino & Grönroos 2017; da Silva et al. 2018). Selection by both site characteristics and biotic interactions filters species from the regional species pool to occur in local communities. For example, in a study performed in Brazilian Atlantic Forest, Almeida-Gomes et al. (2016) found that larger forest patch sizes are important for amphibian persistence in fragmented landscapes. Dispersal also affects local community dynamics (Mouquet & Loreau 2003; Chase et al. 2011). High dispersal can reduce beta diversity among sites, homogenizing the metacommunity (Mouquet & Loreau 2003). In contrast, low dispersion or dispersal limitation may increase beta diversity, because organisms cannot reach suitable sites and may increase the role of drift (Soininen et al. 2007), as observed in the Brazilian Atlantic Forest (Lion et al. 2014; da Silva et al. 2014).

An increasing number of studies used the partitioning of beta diversity into LCBD and SCBD in a variety of plant and animal taxa to better understand biodiversity patterns (Qiao et al. 2015; Vad et al. 2017; Krasnov et al. 2018; da Silva et al. 2018; Legendre & Condit 2019). However, this method is still poorly explored among ecoregions, which are large units of land containing a distinct assemblage of natural communities and species (Olson et al. 2001; Dinerstein et al. 2017). Typically, a given ecoregion is similar in structure along its extent, but shares few species with other ecoregions due to biogeographic barriers, species turnover caused by geographical distance, or by environmental and biotic selection (Dinerstein et al. 1995; Nekola & White 1999). On a global scale, the relationship between dissimilarity in species composition and productivity varied according to ecoregion (He & Zhang 2009), but information on a finer scale is still scarce. The dissimilarity in species composition in a given region composed of different ecoregions can vary according to climate, vegetation type, disturbance regimes (e.g., fires), and migrations (Olson et al. 2001).

Besides the spatial variation in community composition, beta diversity can fluctuate over time in the same site, known as temporal beta diversity (Legendre & Gauthier 2014). Understanding the temporal dynamics of communities can solve fundamental ecological processes, including effects of individual life histories on ecosystem change, the relative importance of biotic and abiotic factors in determining community structure, or how taxa and the networks in which they are embedded respond to environmental change (Tilman 1999). Community composition changes through time occur due to gains and losses of species, as well as changes in species abundance, resulting from different ecological processes, including environmental seasonality (Legendre & Gauthier 2014; Tolonen et al. 2017). As consequence, LCDB value also fluctuate among seasons and its association with environmental and spatial factors can change among periods (Tolonen et al. 2018). For example, Tolonen et al. (2018) found that drivers of compositional uniqueness of aquatic macroinvertebrates change between spring and autumn, which was mainly related to species life cycle events. The explained variation of compositional uniqueness by environmental variables (e.g., pH, particle size and stream width) decreased from spring to autumn, while the explained variation by the spatial variables increased notably (Tolonen et al. 2018). Similarly, Kong et al. (2017) shown that compositional uniqueness of fish changes between the dry and rainy seasons because of the presence of particular species moving back and forth from floodplain habitats. Thus, seasonal variation in compositional uniqueness depend on the life history of organism model and physical characteristics of the study area.

Understanding compositional uniqueness variation between seasons and its drivers may help to identify sites and species with high conservation values or sites that need to be restored (Legendre & De Cáceres 2013). Indeed, assessing variation in composition uniqueness among sites and seasons can improve our understanding on processes that generate and maintain biodiversity. The mid-western Brazil location has a highly seasonal variation in environmental conditions in the Atlantic Forest, Cerrado, Chaco and, Pantanal ecoregions. This region allows us to explore seasonal patterns of compositional uniqueness and compare the relative importance of the potential mechanisms explaining those patterns.

Neotropical anurans are considered excellent ecological models because they are locally abundant and their sampling is relatively easy (Leão-Pires et al. 2018). Anurans are particularly susceptible to environmental and spatial factors because they have permeable skin, a biphasic life cycle, unshelled eggs and limited dispersal (Green 2003). Most of them are dependent on ponds or water bodies for tadpoles development and adults reproduction. Considering that anuran biodiversity is highly threatened, suffering a severe global decline by virtue of diseases, climate change, and habitat loss (Becker et al. 2007; Lion et al. 2014; Scheele et al. 2019), understanding spatial and temporal patterns may be highly useful for biodiversity conservation and for detecting sites that disproportionally contribute to regional species pool relative to species richness (Legendre & De Cáceres 2013; Ruhí et al. 2017; Valente-Neto et al. 2020).

We examined anuran seasonal patterns (dry and rainy seasons) of compositional uniqueness (LCBD) in different ecoregions of Western Brazil and their correlation with species richness, thus elucidating possible keystone communities. We also assessed if environmental (climatic variables, pond area and ecoregions) and/or spatial predictors (spatial configuration of sampling sites captured by distance-based Moran’s Eigenvector Maps) would drive patterns of LCBD. We expected that LCBD would differ among ecoregions for the dry season, and no difference would be found in LCBD for the rainy season. This expectation is based on the low water availability in dry season compared to the rainy season, when all ecoregions tended to be equal in terms of water availability. This water restriction in the dry season would filter species in naturally seasonally dry ecoregions, such as the Cerrado and Chaco (Pennington et al. 2009), where water availability is a constraint for many species in the dry season (Pennington et al. 2009), leading to more unique communities. We also expected that this filter would be more intensive in the Cerrado because this ecoregion is not close to floodplains that may maintain water availability during the dry season. The Chaco region is close to the Pantanal and both occupy the area under influence of Paraguay Basin flood pulses, which would provide water to anuran reproduction throughout the year. In this way, we expected that the Cerrado ecoregion would have higher values of LCBD compared to other ecoregions in the dry season. We also hypothesized that LCBD variation would be driven by environmental variables in the dry and rainy seasons, but the total amount of variation would be higher in the dry season.

Methods

Study area

We sampled anurans in 19 ponds located in Mato Grosso do Sul state, covering the Atlantic Forest, Chaco, Cerrado, and Pantanal ecoregions in Brazil (sensu Olson et al. 2001), Fig 1, Table S1). Typically, the dry season ranges from April to September, and the rainy season extends from October to March in the region. The Atlantic Forest and Cerrado ecoregions support the highest species richness and rates of endemism, and they have been undergoing huge forest loss, being classified as hotspots of biodiversity (Myers et al. 2000; Ribeiro et al. 2009). Atlantic Forest is characterized by heterogeneous and highly diverse plant species, with lowland, montane, semideciduous, and deciduous forests, but most of them are represented by small fragments (Morellato & Haddad 2000; Ribeiro et al. 2009). Semideciduous parts of the domain shared many species with neighbouring ecoregions (e.g., Cerrado) (Cantidio & Souza 2019) and receive in the study region around 1313 mm/year of rainfall (Fick & Hijmans 2017).

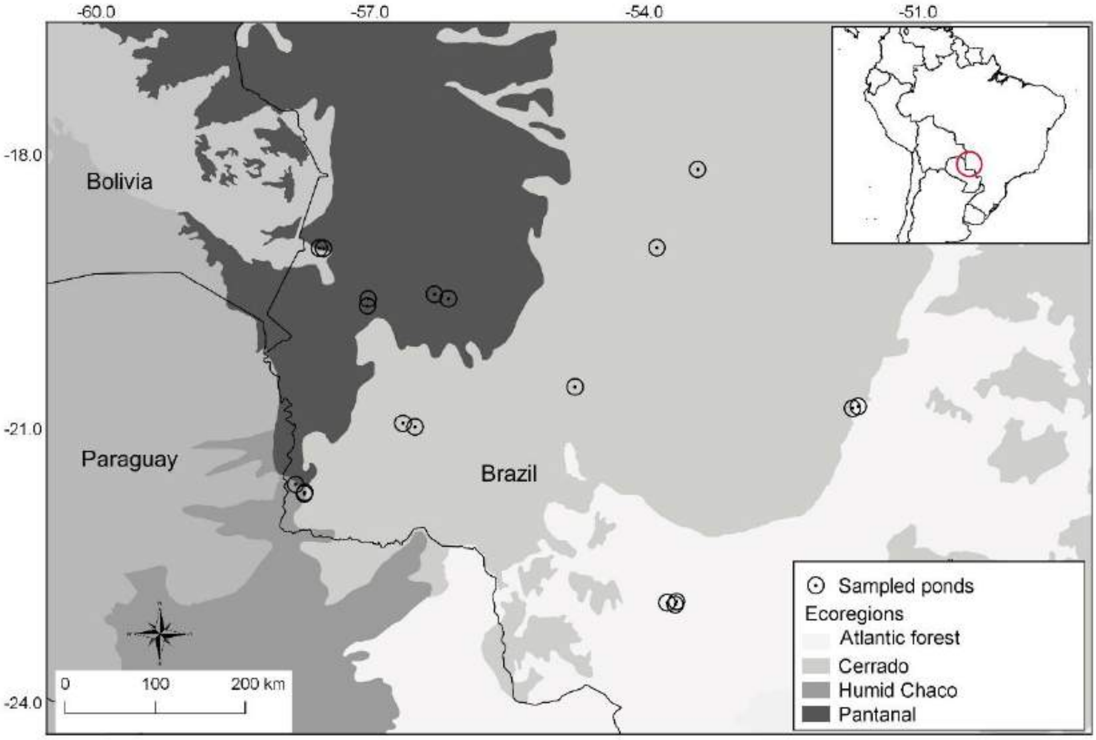

Figure 1. Location of the sampled ponds in West Brazil for each ecoregion (Atlantic Forest, Chaco, Cerrado, and Pantanal).

The Cerrado ecoregion is characterized by an extremely variable physiognomy, ranging from open grassland to forest with a discontinuous grass layer (Strassburg et al. 2017). The overall amount of rainfall in the study region of the Cerrado is 1,424 mm/year (Fick & Hijmans 2017). The Chaco ecoregion is one of the most threatened subtropical woodland savannas in the world (Zak et al. 2004; Nori et al. 2016). Vegetation comprises xerophytic forests, alternating with patches of secondary woodlands and scrubs, and in temporarily flooded areas; the vegetation is typically composed of sclerophyllous grasslands. The Chaco ecoregion receive in the study region around 1,161 mm per year of rainfall (Fick & Hijmans 2017). The Cerrado and Chaco ecoregions are considered 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). Pantanal is one of the largest wetlands in the world and is comprised of major vegetation formations: flood-free ridges (ancient levees) inhabited by trees, seasonally flooded plains with grasslands, and water bodies with aquatic macrophytes (Pott & Pott 2004). Although species diversity is not particularly high and endemism is practically absent, the region is notable for its abundance of wildlife (Harris et al. 2005). Annual rainfall in the studied area of the Pantanal is around 1,177 mm (Fick & Hijmans 2017). Among the sampled sites, Cerrado is the only one that did not exhibit flood pulses during the rainy season. Cerrado and Pantanal ecoregions show the higher values of precipitation seasonality (55.54 and 59.01 coefficient of variation, respectively) in relation to Atlantic Forest (46.64 coefficient of variation) and Chaco (45.45 coefficient of variation) (Fick & Hijmans 2017).

We sampled three ponds in Chaco (CH), five each in Cerrado (CE) and Atlantic Forest (semideciduous forest) (AF), and six in Pantanal (PA), during 2017 and 2018 (Fig 2, Table S1). Each pond constituted a replicate. The minimum distance among ponds was 500 m between CE3 and CE4. The remaining ponds were far more than 1 km distance from each other. Each area was surveyed for one day per season during one dry and one rainy season, totalizing six hours of sampled effort per pond per season. We sampled anurans by active search (Scott Jr & Woodward 1994) and visual and acoustic encounters conducted during time limited transects (Zimmerman 1994). Samplings started on sunset and extended through midnight.

Ethics statement

Anuran sampling was conducted under the permission of Brazilian wildlife regulatory service (SISBIO # 56729-1). The specimen manipulation was carried out following the recommendations of CEUA-UFMS protocol (# 838/2017). The collected individuals were sacrificed with the application of 5% lidocaine on the skin and fixed in 10% formalin, with later conservation in 70% alcohol.

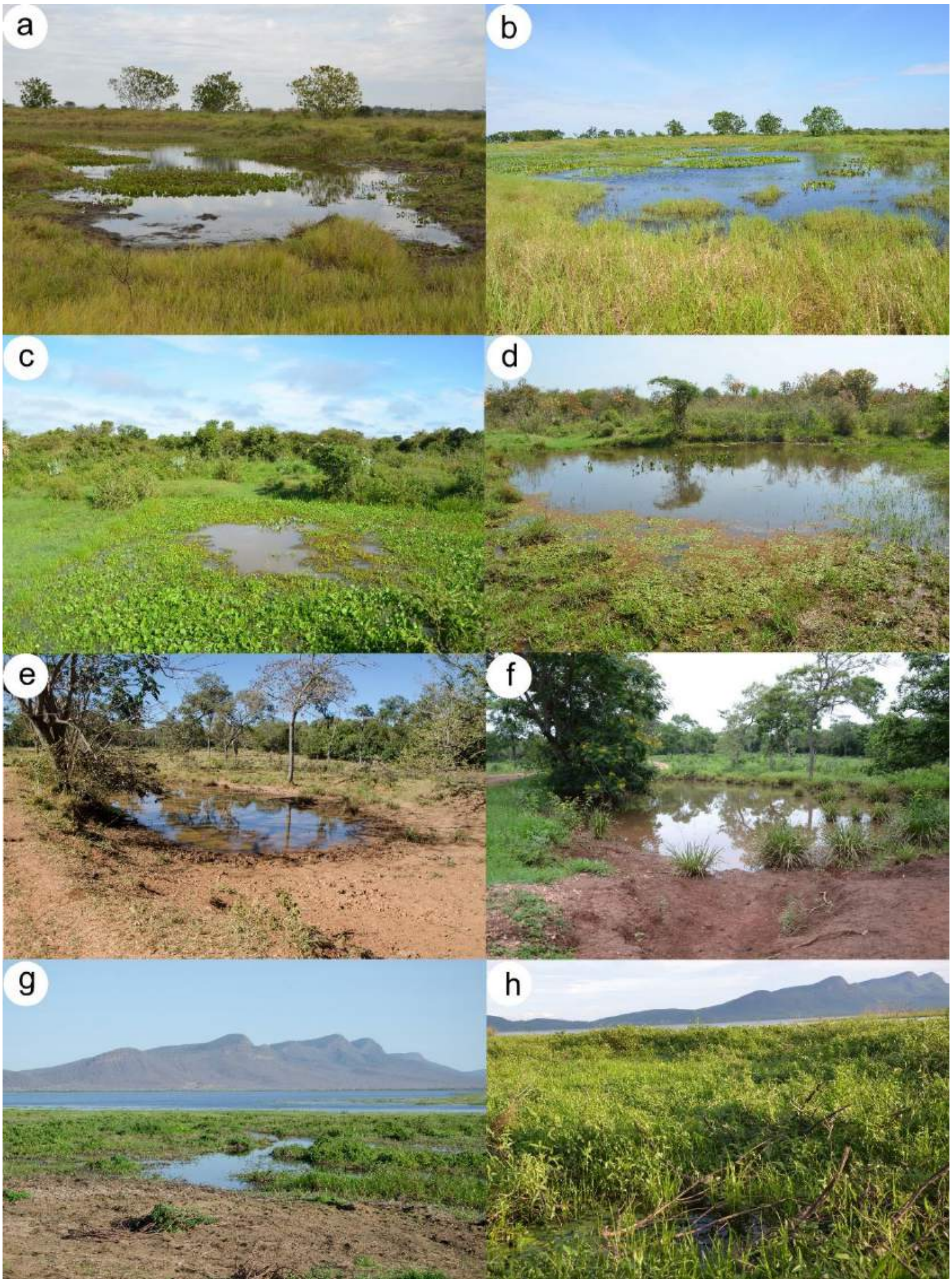

Figure 2. Some sampled sites during the dry and rainy season respectively in a–b) Atlantic Forest, c–d) Chaco, e–f) Cerrado, and g–h) Pantanal.

Environmental predictors

We used the location of each pond to extract 19 climatic variables from the BioClim database (Fick & Hijmans 2017). These variables cover different aspects of the mean and seasonal variability of temperature and precipitation (for more details see Table S2). Climate predictors were extracted from raster files with 30 arc-second resolution using ‘raster’ package (Hijmans & Van Etten 2016) in R version 3.5.0 (R Core Team 2019). For each location, we averaged each climatic variable over a 2000 m buffer zone to reduce the effect of uncertainty in study location. In addition, we chose this radius because the home range size of anurans can reach up to 2000 m (Wells 2007).

Climatic variables were summarized by local contribution to environmental heterogeneity (LCEH), method developed by Castro et al. (2019). To estimate LCEH for each site, we used standardized Euclidean distance (Borcard et al. 2018). Similar to LCBD, sites with high LCEH have singular environmental conditions while sites with low values have common environmental conditions. In addition to LCEH, we also included three dummy variables representing ecoregion specificities other than climatic (e.g., vegetational structure) and pond area as environmental predictors.

Spatial predictors

We used distance-based Moran’s eigenvector maps (dbMEM) on sampling sites’ latitude and longitude (Borcard & Legendre 2002; Dray et al. 2006). First, the minimum spanning tree distance that keeps all sites connected was calculated and used as a truncation threshold to construct the truncated matrix. This matrix was submitted to a Principal Coordinate Analysis (PCoA), and we selected the eigenvectors with significant patterns of spatial autocorrelation, i.e., with significant ($P < 0.05$) and positive Moran’s I (Sokal & Oden 1978). The eigenvectors represent spatial structures of relationships among the sampled sites, from broad to fine-scale patterns (Sokal & Oden 1978; Griffith & Peres-Neto 2006). We used the selected eigenvectors (MEMs) as spatial predictors in data analyses.

Data analysis

We used the method described by Legendre & De Cáceres (2013) to estimate both total beta diversity (BDtotal) and local contribution to beta diversity (LCBD). A community composition matrix (abundance data) was Hellinger transformed and then used to estimate BDtotal as the unbiased total sum of square of the species composition data. The BDtotal will assess LCBD, which is the relative contribution of each sampling unit to beta diversity, i.e., the division of sum of squares corresponding to each sampling unit by the total sum of squares. LCBD was calculated for dry (LCBDdry) and rainy (LCBDrainy) seasons independently.

We used Pearson correlation to assess if LCBD patterns of dry and rainy seasons were correlated. We also used Pearson correlation to assess the relationship between LCBD and species richness. If a negative correlation between LCBD and richness is found, we may detect keystone communities as those that have high LCBD (impact) and low richness (weight) (Mouquet et al. 2013; Valente-Neto et al. 2020).

We used forward selection as implemented by Blanchet et al. (2008) for significant global models. To select variables from an explanatory matrix, forward selection requires significance ($p<0.05$) and R2adj have to be below the global R2adj (Blanchet et al. 2008). In this way, the explained variance is not overestimated, preventing the inflation of Type I error (Blanchet et al. 2008). For non-significant global, we did not proceed with forward selection and variation partitioning, reporting just significant global model after forward selection. If both global models were significant, we used variation partitioning to divide the LCBD variation of each season into four components: pure environmental component [a], the amount of variation shared by environmental component and spatial component [b], pure specific spatial component

[c] and non-explained variation (residual) [d]. The significance [a] and [c] were tested via permutation-based (1000 permutations) tests of partial multiple regressions models.

To perform all analyses, we used R language and the packages ‘vegan’ (Oksanen et al. 2017) ‘packfor’ (Dray et al. 2009) and ‘adespatial’ (Dray et al. 2016).

Results

We sampled a total of 43 species and 1488 individuals distributed in Atlantic Forest (species= 20; individuals=296), Cerrado (n= 25; 297), Chaco (n= 21; 289) and in Pantanal (n= 23; 606). On average, species richness tended to be higher in the Chaco ecoregion ($\bar{x}$=10.3), followed by Atlantic Forest ($\bar{x}$=8.8), Cerrado ($\bar{x}$=7.4), and Pantanal ($\bar{x}$=6.3) (Table S1). *Dendropsophus nanus* was the most abundant species in Atlantic Forest (n=64), Cerrado (n=63), and in Pantanal (n=138), and *Lysapsus limellum* was the most abundant species in Chaco (n=62). Overall, species richness was higher during the wet season (n=37) than the dry season (n=32), as well as the total abundance (772 and 716, respectively). Atlantic Forest had 19 species in the wet season and 11 species in the dry season, while Cerrado had 21 and 14 species, in the wet season and dry seasons, respectively. Chaco had 18 and 14 species, and Pantanal 16 and 17 species, respectively for the rainy and the dry seasons. Of the sampled species, *Boana albopunctata*, *B. geographica*, *Leptodactylus furnarius*, *L. labyrinthicus*, *Phyllomedusa sauvagii*, *Pristimantis dundeei* were registered only in the Cerrado ecoregion, *Adenomera dyptix*, *L. latrans*, *L.* aff. *fuscus*, and *Scinax acuminatus* were registered only in the Pantanal, *Physalaemus biligonigerus*, *L. elenae*, *L. bufonius* and *Rhinella major* were registered only in the Chaco and *Dendropsophus sanborni*, *Elachistocleis bicolor* and *Scinax squalirostris* were registered only in the Atlantic Forest. The total beta diversity for the dry period was 0.60. The mean local contribution to beta diversity in this season was 0.052 (ranging from 0.024 to 0.097) (Fig 3a). Sites with the highest values (LCBD>=0.080) had significant LCBDs (four sites, all in the Cerrado ecoregion), whereas sites with values lower than 0.080 had non-significant LCBDs. Cerrado sites had higher LCBD values than sites in other ecoregions. LCBD was negatively correlated with species richness in the dry season (Pearson correlation =-0.46, p=0.04) (Fig S2). In the rainy period, the total beta diversity was slightly lower compared to the dry season (BD total=0.55). The mean local contribution to beta diversity in the rainy period was 0.052 (ranging from 0.030 to 0.100) (Fig 3b). Sites with the highest values in this period (LCBD>=0.080) had significant LCBDs (two sites, one in the Cerrado and the other in the Pantanal ecoregions), whereas sites with values lower than 0.080 had no significant LCBDs. The pattern of higher LCBD in Cerrado sites was maintained in the rainy season (Fig 3). Contrary to the dry period, the relationship between LCBD and richness was not significantly correlated in the rainy season (Pearson correlation=0.09, p=0.69) (Fig S2). LCBD values from dry period were significantly correlated with rainy season (Pearson correlation=0.56, p=0.01) (Fig S1), demonstrating that similar sites contribute in the same way to compositional uniqueness (Fig 3).

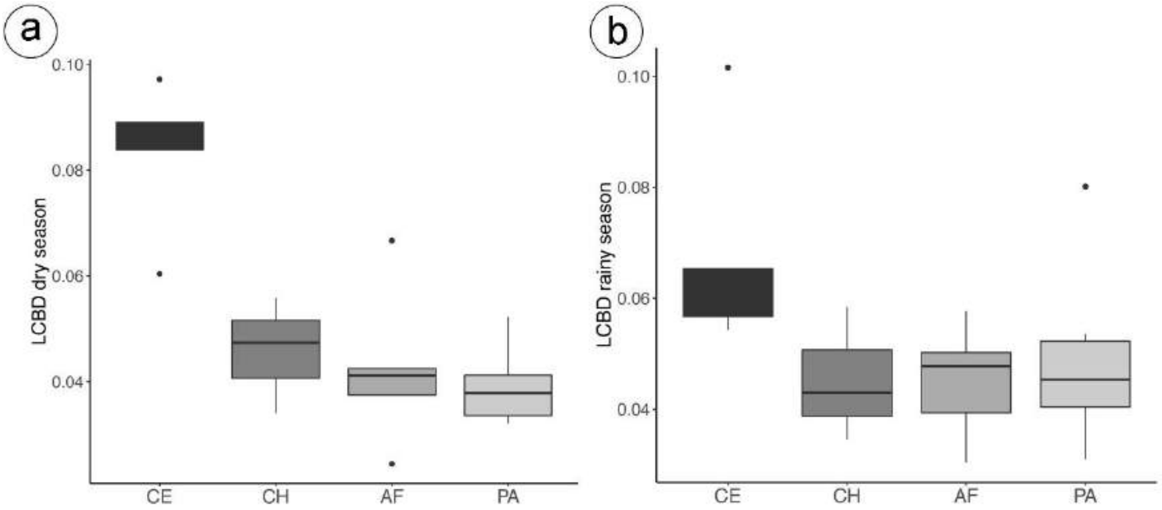

Figure 3. Local contributions to beta diversity (LCBD) values for the dry and rainy seasons from the four ecoregions sampled (AF=Atlantic Forest, CH=Chaco, CE=Cerrado, and PA=Pantanal).

The environmental global model was significant for the dry period, ($p=0.001$) and the Cerrado ecoregion was the variable selected. Distance-based Moran's eigenvector maps generated three eigenvectors, all of them with positive and significant spatial correlation. Spatial global model was also significant ($p=0.008$) and MEM3 was selected to be included in the variation partitioning. Pure environmental component composed by Cerrado ecoregion [a] significantly explained variance in LCBD values ($p=0.002$; adjusted $R^2=0.29$), whereas pure spatial component composed by MEM3 [c] was not significant to explain LCBD variation in the four ecoregions ($p=0.20$; adjusted $R^2=0.01$). The shared component between environmental and spatial components explained 42% of variation in LCBD values and the unexplained variation in LCBD values corresponded to 27%. In the rainy season, both environmental and spatial global models were not significant (environmental: $F=2.15$, $p=0.22$; spatial: $F=2.37$, $p=0.11$), and, consequently, we did not proceed with variation partitioning (Table 1).

Table 1. Results of the partial redundancy analysis of site uniqueness for anurans during the dry season, where [a] pure environmental component, [b] the amount of variation shared by environmental component and spatial component, [c] pure specific spatial component and [d] non-explained variation (residual). Bold: represents significant fractions. Results for the rainy season were omitted because both environmental and spatial global models were non-significant

			[a]		[b]	[c]		[d]
	Env selected	Spa selected	R2adj	F	R2adj	R2adj	F	R2adj
LCBD Dry	Dummy_Cerrado	MEM3	**0.29**	**19.33****	0.42	0.01	1.80	0.27

[a] The explained variation for component b was -0.21 and for this reason the residual presented in the table is 0.50. According to Legendre & Legendre (2012) negative explained variance should be interpreted as 0.00. * $0.05<p<0.01$; * $0.01<p<0.001$

Discussion

In this study we found that LCBD patterns were similar between seasons, i.e., sites tended to contribute in the same way for community composition uniqueness during the dry and rainy season, contrary to our hypothesis. In addition, LCBD was negatively correlated with species richness in the dry season. Among studied ecoregions, Cerrado showed higher LCBD values in both seasons, despite lower values during the rainy season. We also found that LCBD variation was explained by pure environmental variables (ecoregion) in the dry season, but models were non-significant during the rainy season.

For both seasons, local contributions to beta diversity were higher in Cerrado sites than in Atlantic Forest, Chaco and Pantanal, partially confirming our hypothesis. Cerrado is considered one of the world's ‘hotspots’ for biodiversity conservation because of its high endemism and its high rates of habitat conversion and biodiversity loss (Myers et al. 2000). In relation to anurans, Cerrado has high species richness and endemism with assemblages from different lineages, which is likely a result of its contact with four South American ecoregions: Amazonia, Atlantic Forest, Caatinga, and Chaco (Oliveira & Marquis 2002; Valdujo et al. 2012).

On the other hand, the similarity of LCBD values among Atlantic Forest, Chaco, and Pantanal might be related to their similarity in floodplain areas and by the elevated number of common and well-distributed species, such as *L. limellum*. In the study area, these ecoregions are strongly influenced by great rivers such as the Paraná and Paraguay, which flood seasonally and can act as migration routes for modern floras and faunas (Spichiger et al. 2004). Moreover, sites of Atlantic Forest, Chaco, and Pantanal in this study can be considered transition zones because they are located at the boundaries between biogeographic regions and represent areas of biotic overlap, which are promoted by historical and ecological changes that allow the mixture of different biotic elements (Prado et al. 1992; Morrone 2014). Thus, each area could allow the entrance of well-distributed species coming from the surrounding ecoregions, in turn affecting the distribution of species and LCBD values in the core of the study sites.

We detected that sites tended to contribute in the same way to beta diversity in both seasons. Sampled sites in Atlantic Forest, Chaco, and Pantanal are composed of ponds that are more connected to adjacent ponds in the rainy season and isolated during the dry season. Conversely, in dry season Cerrado ponds experience the decreasing water availability in ponds, forcing anurans to aestivate or seek shelter (Silva & Rossa-Feres 2007), and favour species that do not depend on water or are more adapted to desiccation (e.g., *P. dundeei* and *L. furnarius*) (Giaretta & Kokubum 2004; Hedges et al. 2008), increasing LCBD values. In the rainy season, the greater water availability in Cerrado sites tends to decrease the difference between LCBD values from those values of other ecoregions. As a result, the seasonal LCBD patterns in the Cerrado ecoregion between seasons may be driven by drought periods and species requirements. Considering all these patterns, Cerrado sites may be keystone areas because of their disproportional contribution to regional species pool relative to their species richness in the dry season (Ruhí et al. 2017; Valente-Neto et al. 2020).

Environmental heterogeneity is an important driver in metacommunity structure and dynamics, with organisms tracking environmental variation across the region via dispersal (Leibold et al. 2004). In our study, sites tended to contribute in the same way for community composition uniqueness during the dry and rainy season, but the factors explaining each seasonal pattern differed. These results indicate that understanding the mechanisms responsible for beta diversity patterns is distant from to be cleared, as more unique habitats and marked seasons are not necessarily the ones harbouring more unique communities (Castro et al. 2019). The different requirements among species can lead to some differences in community responses to environmental variables, when dispersal is limited or restrained by seasons (Varpe 2017). In the dry season, our results indicated that LCBD variation was related to pure environmental variables (ecoregion characteristics) and by shared component (spatially structured environmental variables). The effect of environmental filters is stronger during the dry than the rainy season, filtering species that tolerate water restrictions (Córdova-Tapia et al. 2018). Anurans can minimize energy use during dry periods and may aestivate or hibernate once the availability of resources and reproductive habitats decrease due to lower humidity or temperatures (Valenzuela-Sánchez et al. 2015). Also, species that require less water (e.g., viviparous species that do not depend on water for reproduction, *P. dundeei*) tend to appear in the dry season, mainly in Cerrado, increasing LCBD values in this ecoregion. Similar results were obtained for anurans from Amazonian sites, where the compositional uniqueness was more strongly associated with the environment (Landeiro et al. 2018), and for macrophytes in China when diversity patterns were driven mainly by spatially structured environmental determinism (He & Zhang 2009). Therefore, pronounced seasonal environments may impose a fluctuating selection on life history traits, selecting species according to their requirements in the dry season due to desiccation.

During the rainy season, optimal conditions are experienced by the majority of anurans and environmental selection is less pronounced. The elevated rainfall triggers breeding in the majority of anurans (Duellman & Trueb 1986), many of them widely distributed and habitat generalists, like *Dendropsophus nanus* and *D. minutus*. Anuran communities are more similar in this season, leading to similar LCBD values. For example, ponds in Pantanal and Chaco are more connected to adjacent sites in the rainy season, where flood pulses are more pronounced (Scarabotti et al. 2011). Flood pulses are also an important force for semideciduous areas of Atlantic forest near the Paraná River, promoting dispersion and the homogenization of communities. These pulses tend to connect ponds, favoring species dispersal among sites within each ecoregion (Pantanal, Chaco, and Atlantic Forest) (Delatorre et al. 2015; Almeida-Gomes et al. 2016) and potentially between some of them, such as Pantanal and Chaco. This connection provides large areas available for breeding, which minimizes resource competition among individuals, favoring dispersion of species. These factors may be related to the non-significance of environmental and spatial models during this season. Besides to provide large areas for breeding the rainy season also provide a great amount of prey to anurans (Michelin et al. 2020), because the composition of invertebrates in an environment change throughout a year in relation to climatic variations, different requirements among species, and life history stages (Santana et al. 2015). Thus, the non-significance of environmental and spatial models can be related to the optimal conditions of species during this season, with species not being constrained by environmental or spatial filters.

Combining site-specific contributions to beta diversity in different seasons, we identified sites that consistently harbored unique communities, contributing to the maintenance of a regional species pool. Based on our analyses, Cerrado sites can be considered as keystone communities, because they have a disproportional contribution to the regional species pool in the dry season. The presence of a unique set of species composition, derived from its high endemism relative to the other ecoregions, increases the local contribution to beta diversity of Cerrado. Despite its enormous importance for species conservation and the provision of ecosystem services, only 19.8% of the native vegetation of Cerrado remains undisturbed (Strassburg et al. 2017). The change in land uses as livestock and pastures is the main driver to deforestation of this hotspot and will drive ~480 endemic plant species to extinction (Ratter et al. 1997; Strassburg et al. 2017). Thus, this elevated exploitation may reduce biodiversity in Cerrado sites, and consequently, would cause great effects in the anuran metacommunity. Therefore, to maintain the role of Cerrado as keystone areas, we suggest the identification and mapping highly unique sites in order to preserve the regional biodiversity. In addition, through environmental education, owners of these areas should be made aware of the importance of these areas for regional diversity and should help to maintain the ecological process associated with these species.

Supporting Information

Table S1. Ponds sampled during the years of 2017 and 2018 in West Brazil.

Name site	Site	Formation	Lat	Long	Pond área (m²)	Wet richness	Dry richness	Sample coverage
Brejo Bonito	CE1	Cerrado	-20.5377	-54.7548	6617	7	2	61.15
Camapuã	CE2	Cerrado	-19.0142	-53.8591	866	5	4	78.41
Mimosa 01	CE3	Cerrado	-20.9659	-56.524	1355	12	5	100.00
Mimosa 02	CE4	Cerrado	-20.9685	-56.5211	1018	7	5	73.09
Taquari	CE5	Cerrado	-18.1571	-53.413	5770	6	5	89.21
Chaco 01	CH1	Chaco	-21.6929	-57.7169	1736	11	7	53.09
Chaco 02	CH2	Chaco	-21.6065	-57.8163	802	9	8	94.17
Chaco 03	CH3	Chaco	-21.71	-57.7209	1146	11	11	92.64
Três Lagoas 01	AF1	Atlantic Forest	-20.7513	-51.6544	839	5	2	73.17
Três Lagoas 02	AF2	Atlantic Forest	-20.7727	-51.7158	2888	4	4	83.57
Ivinhema 01	AF3	Atlantic Forest	-22.9218	-53.6571	1809	12	6	60.48
Ivinhema 02	AF4	Atlantic Forest	-22.9008	-53.7471	652	12	5	60.30
Ivinhema 03	AF5	Atlantic Forest	-22.889	-53.6439	797	11	8	65.10
Barranco Alto 01	PA1	Pantanal	-19.5724	-56.1548	2061	7	7	100.00
Barranco Alto 02	PA2	Pantanal	-19.5719	-56.144	4250	4	8	100.00
BEP 01	PA3	Pantanal	-19.5752	-57.0217	1116	6	5	53.25
BEP 02	PA4	Pantanal	-19.5765	-57.0187	434	6	6	97.33
Baía Negra 01	PA5	Pantanal	-19.0222	-57.5106	6670	7	9	74.47
Baía Negra 02	PA6	Pantanal	-19.0184	-57.5564	4052	8	8	75.30

Table S2. Raw climatic variables. All temperature and precipitation values were extracted from BioClim (http://worldclim.org/current) for each studied community. All values were averaged over the surrounding 2km to help buffer uncertainty in the reported locations. Variables indicates the name of the climatic variable in the respective date source.

Bioclimatic variables	**Units**	**Description**
BIO1	$C^{0}\times 10$	Annual Mean Temperature
BIO2	$C^{0}\times 10$	Mean Diurnal Range
BIO3	ratio	Isothermality (BIO2/BIO7) (* 100)
BIO4	stdev ×100	temperature seasonality
BIO5	$C^{0}\times 10$	Max Temperature of Warmest Month
BIO6	$C^{0}\times 10$	Min temperature of coldest month
BIO7	$C^{0}\times 10$	Temperature Annual Range (BIO5-BIO6)
BIO8	$C^{0}\times 10$	Mean Temperature of Wettest Quarter
BIO9	$C^{0}\times 10$	Mean Temperature of Driest Quarter
BIO10	$C^{0}\times 10$	Mean Temperature of Warmest Quarter
BIO11	$C^{0}\times 10$	Mean Temperature of Coldest Quarter
BIO12	mm	Annual Precipitation
BIO13	mm	Precipitation of Wettest Month
BIO14	mm	Precipitation of Driest Month
BIO15	coef var	Precipitation Seasonality
BIO16	mm	Precipitation of Wettest Quarter
BIO17	mm	Precipitation of Driest Quarter
BIO18	mm	Precipitation of Warmest Quarter
BIO19	mm	Precipitation of Coldest Quarter

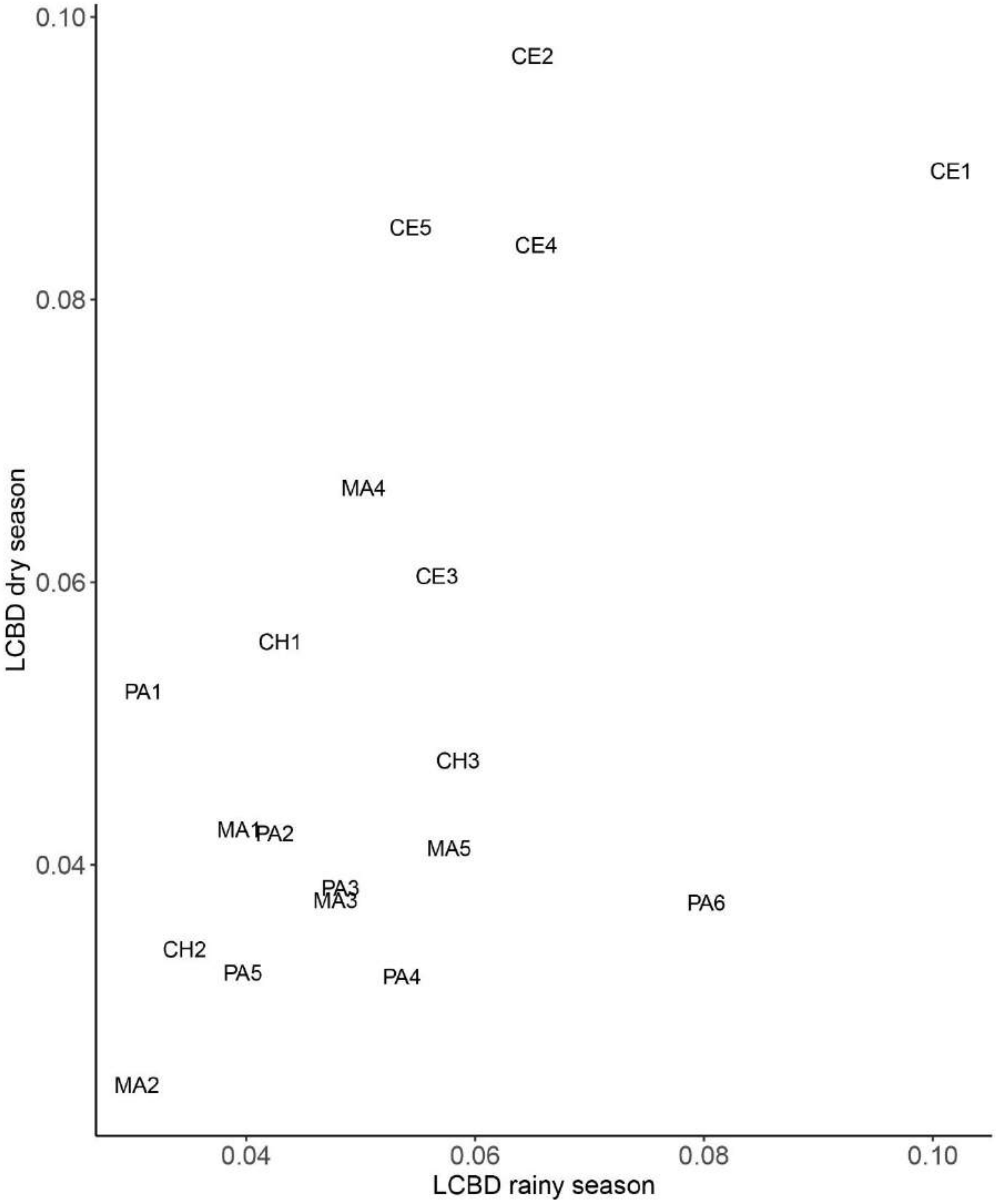

Fig S1. Pearson correlation between LCBD values during dry and rainy seasons. Sites abbreviation can be seen in the Table S1.

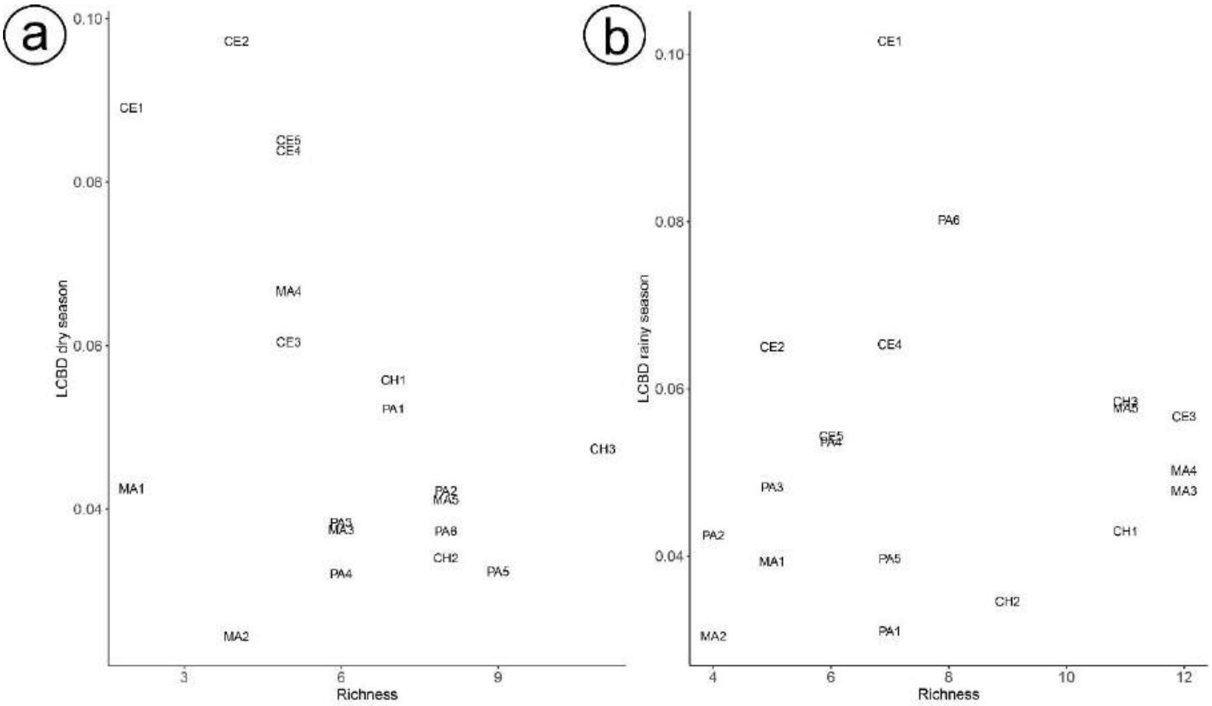

Fig S2. Pearson correlation between richness and LCBD values during dry (a) and rainy seasons (b). To studied sites abbreviation see Table S1.

Chapter 3. Prey availability and interaction rewiring drive the spatial and seasonal structure of an anuran-prey metaweb

Abstract

Space and time promote variation in network structure by affecting the likelihood of potential interactions. Interaction beta diversity can help disentangling ecological and biogeographical processes that regulate community assembly. Examining how the interactions vary throughout space and time may help understanding how the relative role of bottom-up and top-down processes depend on the environmental context. Here, we assessed the turnover of anuran-prey interactions between seasons and among four ecoregions in western Brazil. The variation in interaction beta diversity between seasons and among areas were generated by differences in prey availability. Interaction turnover between ecoregions and seasons were high and driven primarily by interaction rewiring. In addition, beta diversity of species was positively related to geographical distance, but not to interaction beta diversity. We propose that fluctuations in prey abundance along with limited dispersal abilities of anurans and their prey are responsible for the temporal and spatial pattern that emerged in our anuran-prey metaweb.

Keywords: Beta diversity, community assembly, ecological networks, food web, interaction turnover, metacommunities, trophic ecology, Eltonian Niche.

Resumo

O espaço e o tempo promovem a variação na estrutura da rede, afetando a probabilidade de potenciais interações. A beta diversidade das interações pode ajudar a desemaranhar os processos ecológicos e biogeográficos que regulam a montagem de uma comunidade. Ainda, verificar como as interações variam ao longo do espaço e do tempo pode ajudar a entender como o papel relativo dos processos de baixo para cima (*bottom-up*) e de cima para baixo (*top-down*) dependem do contexto ambiental. Neste capítulo, avaliei a mudança das interações anuro-presa entre as estações e entre quatro ecorregiões no Oeste do Brasil. A variação na beta diversidade das interações entre estações e entre áreas foi gerada por diferenças na disponibilidade de presas. A mudança da interação entre ecorregiões e estações do ano foi alta e impulsionada principalmente pela religação das interações. Além disso, a diversidade beta das espécies foi positivamente relacionada à distância geográfica, mas o mesmo não ocorreu com a beta diversidade das interações. Eu proponho que a flutuação na abundância das presas junto com a capacidade limitada de dispersão dos anuros e presas são responsáveis pelo padrão temporal e espacial das redes entre anuros-presas.

Palavras-chave: Beta diversidade, montagem de comunidades, redes ecológicas, teias alimentares, mudanças de interações, metacomunidades, ecologia trófica, nicho Eltoniano.

Introduction

Communities vary in composition over time and space. Likewise, species interactions can also vary along these dimensions. Space and time may promote variation in network structure by affecting the likelihood of potential interactions (Guimarães 2020). The sources of variation in networks have been addressed in the context of networks (e.g., CaraDonna *et al.* 2020) and in classical metacommunity theory. The theory of metacommunities is only starting to incorporate biotic interactions into its framework (Livingston et al. 2017; Leibold et al. 2020; Thompson et al. 2020). For an interaction to occur between individuals, they must first meet, then interact. In the context of network theory, the neutral hypothesis predicts that locally abundant species should have more interactions and that locally rare species should establish fewer interactions. In this case, the variation in species abundance regionally would be more important than species-specific traits in determining structure (Poisot et al. 2015). Conversely, multiple mechanisms can produce turnover in species composition. For example, differences in timing of arrival of a species at a local community can lead to priority effects and multiple stable equilibria under identical environmental conditions (Fukami 2015; Rudolf 2019). Also, community composition can be stable regionally, but fluctuate locally as a result of frequency-dependence interactions and nontransitive interactions between species (Leibold & Chase 2017). Frequency dependence can create spatially structured metacommunities that fluctuate through time, owing to the variation in local interactions among species at different frequencies in the landscape. For each case, the patterns of spatiotemporal variation in species composition support dispersal-limited models of metacommunity organization event thought a mechanism that involves primarily deterministic processes (Leibold & Chase 2017). Therefore, testing how the interactions between predators and their prey vary throughout space and time may help understanding how the relative role of bottom-up and top-down processes depend on the environmental context (Leibold & Chase 2017). Antagonistic metawebs sampled over a large environmental gradient are the ideal construct to explore those ideas.

The dissimilarity of species interaction over time, space or environments, called interaction beta diversity, may offer deeper insights on community assembly dynamics (Poisot et al. 2012). Interaction beta diversity can be partitioned into two components: species turnover and interaction rewiring. Species turnover measures how interactions are lost or gained as a function of differences in species composition, through space or time. Interaction rewiring shows how interactions are reassembled over space and/or time because of changes in pairwise interactions in the same set of co-occurring species. The gain or loss of interactions will depend on which species co-occur spatially and/or temporally (reviewed in CaraDonna *et al.* 2020). For example, species turnover was the main driver of plant-pollinator interaction turnover across space (Carstensen et al. 2014; Simanonok & Burkle 2014). In contrast, interaction rewiring was the major component of the week-to-week turnover in plant-pollinator interactions (CaraDonna et al. 2017). In another example, the interaction turnover of an ant-plant network was mainly driven by rewiring between day-night periods, whereas both interaction rewiring and species turnover contributed to network dissimilarity among plant physiognomies (Luna et al. 2018). To the best of our knowledge, interaction beta diversity has been evaluated only for mutualistic plant-pollinator and ant-plant interactions. Therefore, investigating how dissimilarity between interaction networks can shed light on which processes organize these systems.

Most South American ecoregions have a seasonal climate, varying specially in rainfall regime, which may cause temporal changes in species composition (Grimm 2011). The Brazilian Midwest region comprises the ecoregions of Atlantic Forest, Cerrado, Chaco and Pantanal, each one presenting unique characteristics. The Atlantic Forest and Cerrado ecoregions support the highest species richness and rates of endemism, and are classified as biodiversity hotspots because of their huge rates of habitat loss (Myers et al. 2000b; Ribeiro et al. 2009). The Chaco ecoregion is one of the most threatened subtropical woodland savanna in the world (Zak et al. 2004; Nori et al. 2016), and the Pantanal is one of the largest wetlands in the planet, notable for its abundance of wildlife (Pott & Pott 2004; Harris et al. 2005).

The high rainfall seasonality in these biomes can be particularly challenging to anurans, which depend on water bodies for reproduction and dispersal (Wells 2007). Anurans and their prey (mainly arthropods) are well known by their limited dispersal abilities (Smith & Green 2005; Winterbourn et al. 2007; Semlitsch 2008). Spatial and temporal variation can also change the prey composition may change throughout the year and across ecoregions in response to climatic variations, differences in requirements among species, and life history stages (Janzen 1973; Kikuchi & Ueida 1998; Michelin et al. 2020). Surprisingly, anuran communities in western Brazil did not change significantly between seasons, but did so among ecoregions (Ceron et al. 2020). The unique features of ecoregions in western Brazil, together with anuran sensitivity to climate, are good models to test hypothesis about temporal and spatial variation in interaction beta diversity of predators and their prey. This scenario allows comparing the relative importance of the species turnover and interaction rewiring components to the variation in anuran-prey interaction networks over ecoregions and seasons.

Here, we quantified the species turnover and interaction rewiring components of the beta diversity of anuran-prey interactions and tested how they varied across ecoregions and between wet and dry seasons. Tropical anuran-prey networks have high connectance, low modularity, and complementary specialization that are explained by the generalist diet of anurans (Ceron et al. 2019). Therefore, we expected that interaction beta diversity of anuran-prey networks between seasons and among ecoregions would be driven by the rewiring of interactions and by the turnover of species composition, respectively. That is, the turnover of interactions between local anurans-prey networks would be generated largely by changes in pairwise interactions across seasons, determined by differences in prey availability. Conversely, changes in species composition among ecoregions would be responsible for the turnover of interactions, because both anurans and their prey have low dispersal abilities. We also expected variations in interaction beta diversity between seasons and across ecoregions to be constrained by physiological requirements (e.g., reproductive modes and thermal tolerance) of anuran species and variation in prey availability (Toft 1981; Moroti et al. 2020). Thus, we predicted a positive relationship between geographical distance and the turnover of species and interactions (Carstensen et al. 2014).

Methods

Sampling design and stomach content analysis

We sampled anurans and invertebrate prey in 19 ponds in the ecoregions of Atlantic Forest, Chaco, Cerrado, and Pantanal in Mato Grosso do Sul, central Brazil in the dry and in the wet season. We sampled three ponds in the Chaco, five in Cerrado and Atlantic Forest, and six in the Pantanal, all with similar surface areas from August 2017 to November 2018. For a full explanation of anuran sampling in ecoregions, see Ceron *et al.* (2020). In order to access the availability of potential prey, we installed 20 pitfalls around each sampled pond. These pitfalls consisted of 1-L plastic flask filled with 70% ethanol, which remained opened for 12 h during the same nights (from 18h until 6h) we collected frogs. We also sampled preys in the herbaceous and shrubby vegetation around the ponds using a beating sheet for 30 minutes before we start to collect the frogs.

We analyzed stomachs under a stereomicroscope and identified each item to operational taxonomic units (OTUs). This classification was employed because invertebrates were normally partially digested in stomachs. The taxonomical unity was usually Order, except for the family Formicidae, and larvae, which are usually included in a separate OTU (e.g., Lepidoptera, Lepidoptera larvae).

Beta diversity of predator-prey interactions

For each study site, we built weighted matrices of interactions containing the predator species as columns and the abundance of prey categories (OTU) as rows. For each area, we constructed one matrix including all recorded interactions and separated matrices for each season (wet and dry). We calculated the turnover of interactions in predator-prey networks using the framework proposed by Poisot *et al.* (2012), by calculating the turnover of species (β_{W}) and the dissimilarity or beta diversity of interactions (β_{WN}) between communities. The dissimilarity of interactions can be partitioned additively into changes due to the turnover of species composition (β_{ST}) and the spatial or temporal rewiring of interactions (β_{OS}) (see Poisot *et al.* 2012; CaraDonna *et al.* 2017). This partitioning allowed us to determine whether the dynamics of the interaction networks are due to (1) changes in species composition *per se* (β_{ST}), (2) reassembly of interactions among shared species (β_{OS}) or (3) a combination of both (CaraDonna et al. 2017).

Comparison of interaction beta diversity among ecoregions and seasons

We compared interaction dissimilarity across multiple spatial scales and between seasons. First, we measured the temporal turnover of interactions within each ecoregion metaweb (i.e., a network including all interactions of a given ecoregion). Then we compared the contribution of interaction rewiring (β_{OS}) and species turnover (β_{ST}) to seasonal turnover of interactions using a two-tailed *t*-test. To measure the turnover of interactions between ecoregions, we compared the networks from each community, combining the data of both seasons. We calculated mean beta diversity by averaging the pairwise beta diversity between the 19 sites. Analysis were conducted using the ‘bipartite’ package (Dormann et al. 2008) in R 3.4.0 (R Core Team 2019). Species beta diversity was calculated for predator species alone ($\beta_{predator}$), to prey species alone (β_{Prey}) and to predators and preys together (β_{Shared}). Relationships between interaction turnover components and $\beta_{Shared,}$ $\beta_{predator,}$ β_{Prey} and geographic distance were tested using linear regression in the R package ‘ecodist’ (Goslee & Urban 2007) in R 3.4.0 (R Core Team 2019).

To test for a difference in prey availability between seasons and ecoregions we use a model-based ordination approach in the manyglm function of the R package ‘mvabund’ (Wang et al. 2012) in R 3.4.0 (R Core Team 2019). This approach allows us to identify multivariate patterns by fitting a separate Generalized Linear Model (GLM) using a common set of explanatory variables (Wang et al. 2012). We fit a Poisson GLM with season, ecoregion and their interaction as predictors and prey availability as response and then we checked our model assumptions by analyzing a plot of residuals. To test if the variation in interaction beta diversity among areas and between season results from differences in prey availability, we built a null model based on prey availability per season in each area and calculated the interaction beta diversity. To do that we build theoretical networks where the same number of observed interactions per predator are sampled according to the proportions each has prey been detected in that area in that particular season. Next, we compute pairwise beta diversity across all these theoretical networks (630-paired comparisons) to obtain a distribution of beta diversity under the hypothesis that beta diversity is fully determined by differences in prey availability (Table S1). Afterwards, we compared the interaction beta diversity of the null model against our real interaction beta diversity among areas and between seasons using a Z-test in R 3.4.0 (R Core Team 2019).

Results

We recorded 43 anuran species, belonging to 14 genera, and 42 prey categories. Interaction turnover between seasons was consistently high and mostly driven by rewiring of interactions, with exception of Cerrado (Fig. 1, Table S2). The contribution of rewiring to total interaction turnover was higher than that of species turnover in 14 sites (73.68%). Interaction turnover between seasons in all ecoregions was high (0.77 ± 0.15), with Cerrado having the highest values (0.91) and the Chaco the lowest (0.62) (Figure 1).

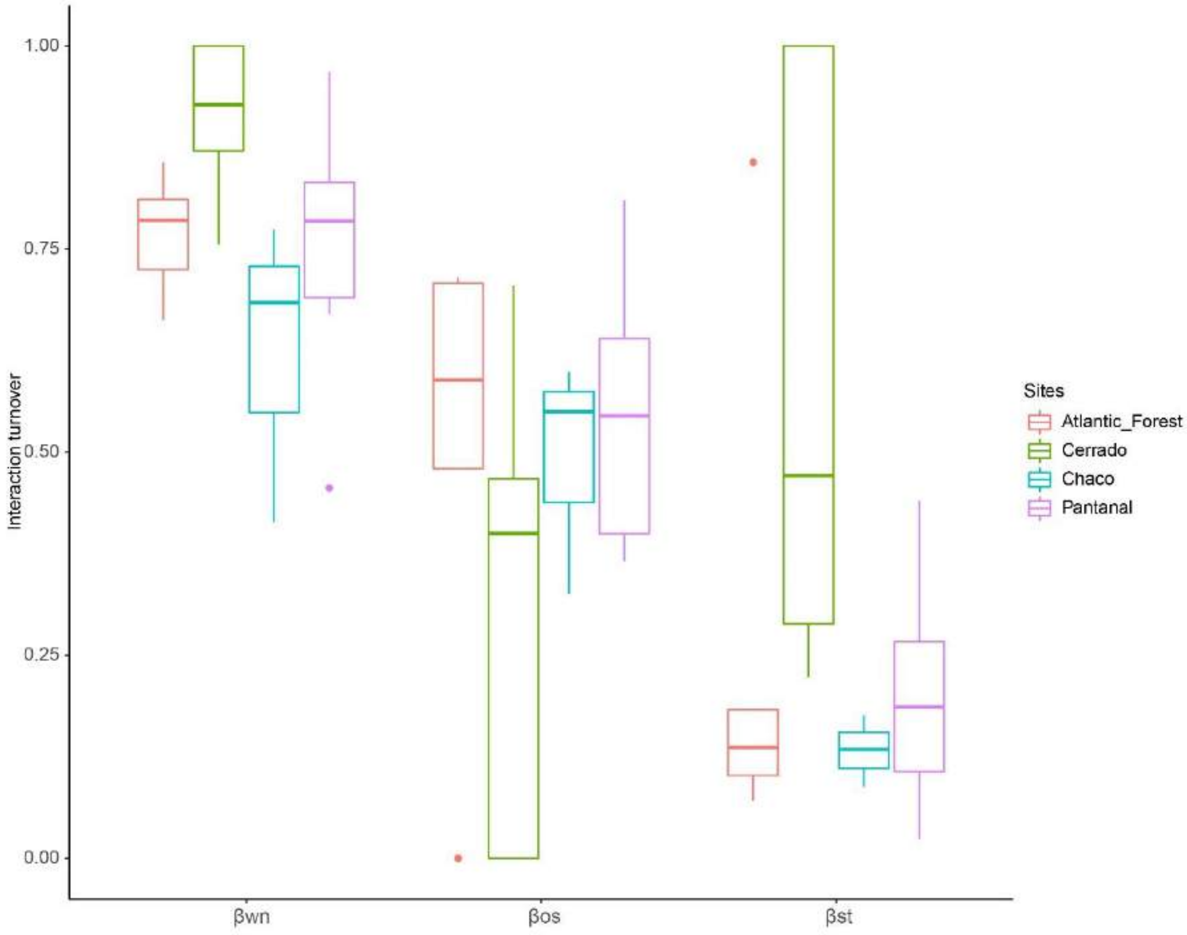

Figure 1. Comparison of the two components of predator-prey interaction turnover (βwn) – rewiring (βos), and species turnover (βst) – between seasons. Values represent raw magnitude of interaction turnover and its components. No significant differences were detected between βst and βos via a two-tailed *t*-test.

Interaction turnover (β_{WN}) was high among ecoregions (0.77 ± 0.15) and primarily driven by interaction rewiring (β_{OS}) (Figure 2; $t_{\text{residuals degrees of freedom}} = 9.81$, $P < 0.0001$). The only exception was between the Atlantic Forest and Pantanal, which was dominated by species turnover ($\beta st = 0.37$). Cerrado and Chaco had the highest values of interaction turnover (0.88), whereas Cerrado and Atlantic Forest the lowest (0.67).

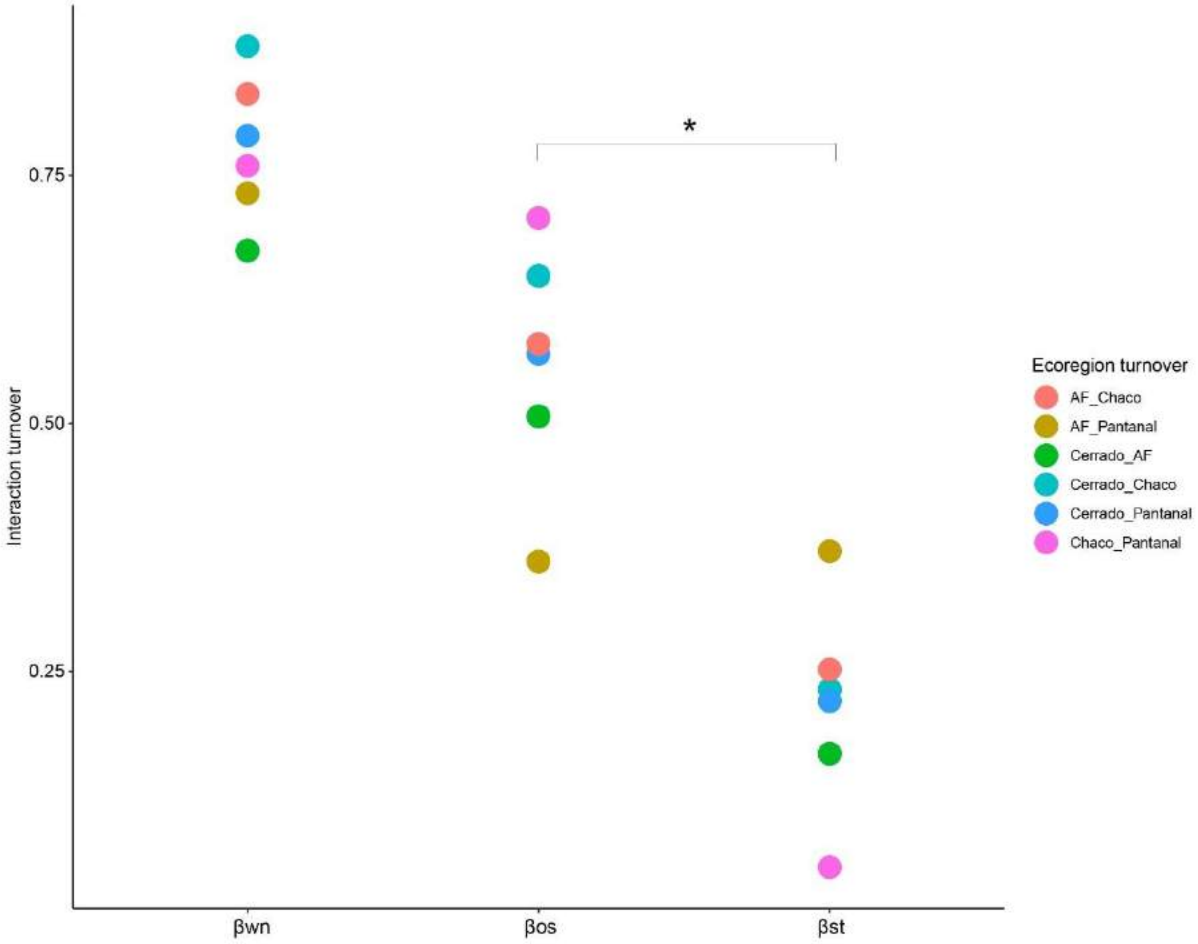

Figure 2. Comparison of the two components of anuran-prey interaction turnover (βwn) – rewiring (βos) and species turnover (βst) – across ecoregions. Values represent the raw magnitude of interaction turnover and its partitioned values. Asterisks indicate statistical significance ($P < 0.05$) between βst and βos via a two-tailed *t*-test. (AF = Atlantic Forest).

Geographical distance was positively correlated with the beta diversity of predators (βpredator) (F = 44.68, df = 170, $R^2 = 0.22$, $P < 0.001$), prey (βprey) (F = 23.44, df = 170, $R^2 = 0.13$, $P < 0.001$) and shared species (βshared) (F = 9.618, df = 170, $R^2 = 0.05$, $P < 0.001$). However, the total beta diversity of interactions (βwn) did not vary with geographical distance (F = 2.61, df = 170, $R^2 = 0.01$, $P = 0.108$, Figure 3). The abundance of prey availability differed between seasons (LRT = 1707, df = 1, $P = 0.001$), among ecoregions (LRT = 4469, df = 3, $P = 0.001$), and the interaction between season and ecoregion was also significant (LRT = 822, df = 3, $P = 0.001$; Figure 4, S1, S2). There was no difference between the observed interaction beta diversity and that derived from the null model based on prey availability between seasons and across ecoregions (Z = -0.482, $P = 0.62$, Fig. 4).

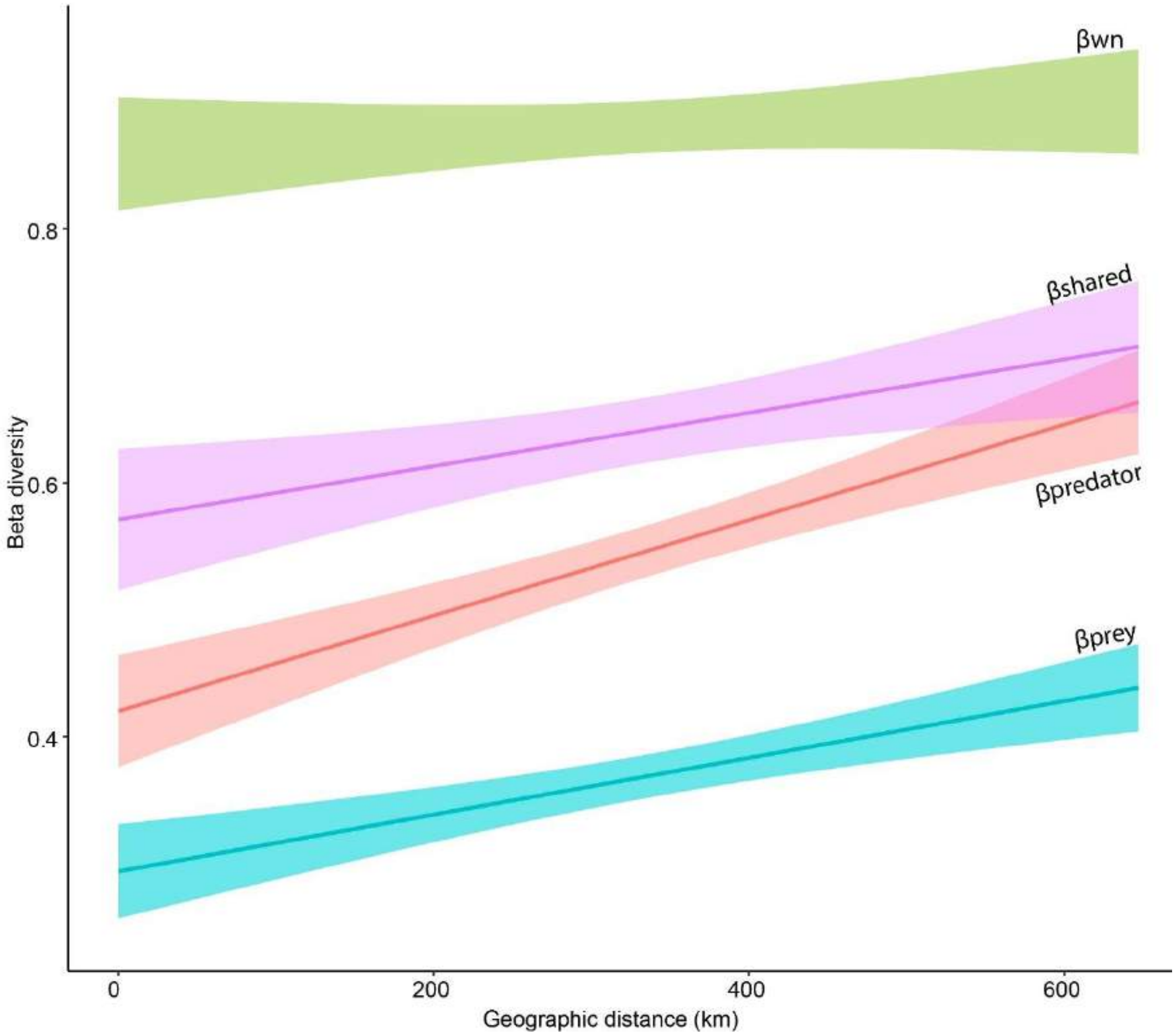

Figure 3. Beta diversity of species and interactions as a function of geographical distance between sites. Total interaction beta diversity βwn (green), predator beta diversity βpredator (red), beta diversity of interactions between shared species βshared (purple), and prey beta diversity βprey (blue). All components, except βwn, relate positively to geographical distance (βshared: F = 9.618, df = 170, $R^2 = 0.05$, $P < 0.001$; βpredator: F = 44.68, df = 170, $R^2 = 0.22$, $P < 0.001$; βprey: F = 23.44, df = 170, $R^2 = 0.13$, $P < 0.001$). Shaded areas represent the corresponding 95% confidence intervals.

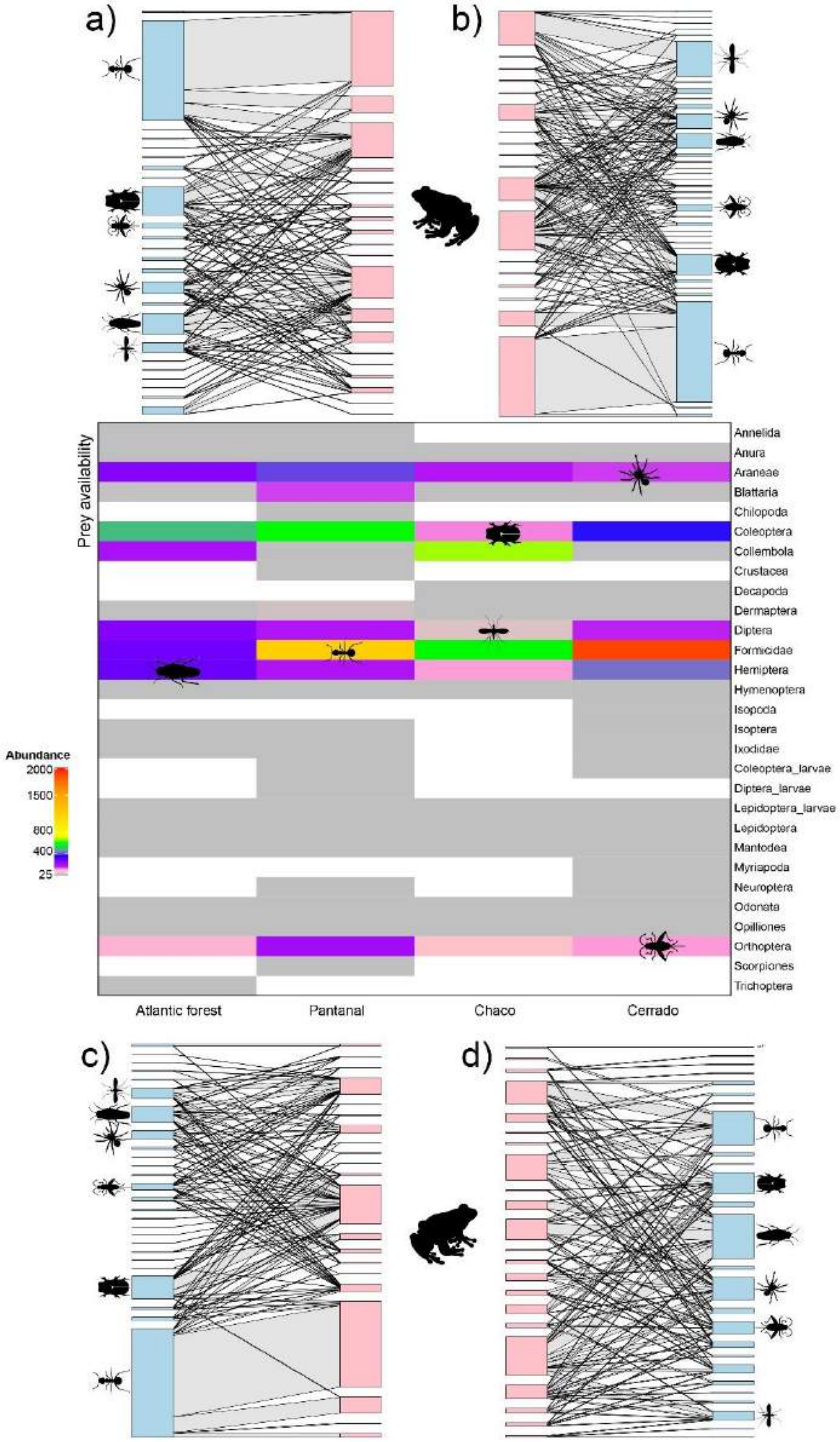

Figure 4. Changes in prey availability influence anuran-prey networks between seasons (Fig. S3) and across ecoregions: a) Atlantic Forest, b) Pantanal, c) Chaco, and d) Cerrado. Available preys are also the most consumed by predators. Blank lines = zero abundance.

Discussion

The variation in interaction beta diversity between seasons and among areas were mainly generated by differences in prey availability. Interaction turnover between both ecoregions and seasons were high and driven primarily by interaction rewiring. In addition, beta diversity of species was positively related to geographic distance but not interaction beta diversity, suggesting that species interactions vary less, across space, than do species identity.

The temporal variation in prey composition was a major driver of the interaction rewiring of anuran-prey networks between seasons (Soares et al. 2013; Michelin et al. 2020). A fundamental asymmetry in composition exists in many ecological communities (Robinson & Wilson 1998). Prey composition changes throughout the year in response to climatic variation, different requirements among species, and life history stages (Janzen 1973; Kikuchi & Ueida 1998; Michelin et al. 2020). Nevertheless, the composition of the predator guild did not change significantly between seasons within the studied sites (Ceron et al. 2020). This pattern was similar to that found in plant-pollinator networks in the Brazilian Cerrado (Carstensen et al. 2014) and in a subalpine area in USA (CaraDonna et al. 2017). These mutualistic networks presented small changes on pollinator species composition, but greater substitution of plants between seasons, possibly related to variation in flowering phenology, leading to a high turnover in plant-pollinator associations across seasons (CaraDonna et al. 2017; Rabeling et al. 2019). In certain sites, however, we did find that both species turnover and interaction rewiring contributed to temporal dynamics. Species turnover will always influence interaction turnover to some extent. When it presents high values, its contribution to interaction turnover will also be high (Poisot et al. 2012).

Interaction rewiring was also the main component of interaction beta diversity of anuran-prey networks among ecoregions. This pattern can be explained by local prey availability, which varied in abundance among ecoregions. Optimal foraging theory predicts that dietary preferences depend on many factors, but are mainly determined by the relative abundances of potential food items and the costs and benefits associated in consuming them (Emlen 1966). For example, the relative abundance of a high-quality resource should determine if an item of lower quality will be used or not (Pyke et al. 1977). This imply on changes in the representativeness of prey in the diet, likely influencing the overall frequency of rewiring (CaraDonna et al. 2017). As most anurans are generalists, their diets are restricted mostly by their mouth size and prey availability (Toft 1980; Ceron et al. 2019; Moroti et al. 2020). Thus, differences in prey composition among ecoregions may lead to considerable changes in interaction patterns, resulting in high interaction rewiring. Species turnover was the most important component of interaction turnover only between Atlantic Forest and Pantanal, which, besides the geographic distance, are quite different in terms of their environmental features, resulting in a low number of shared species (Figure S1).

Beta diversity of species and shared species were related to geographical distance, which is probably related to the low dispersal abilities of both anurans and their prey (Smith & Green 2005; Winterbourn et al. 2007; Semlitsch 2008). Dispersal affects local community composition, because high dispersal rates can reduce beta diversity, homogenizing the metacommunity (Mouquet & Loreau 2003). In contrast, low dispersal increases beta diversity, because organisms cannot reach all suitable sites and may increase the role of drift (Soininen et al. 2007). Similar results were found in plant-pollinator and plant-insect networks (Novotny 2009; Carstensen et al. 2014), in which geographically distant communities tended to be more dissimilar in species composition than communities that were closer in space. However, the absence of an association between interaction beta diversity and geographic distance suggests that species interactions vary less across space, than do species identity. These results support ecological theory suggesting that species interactions play a key role in maintaining a homeostatic state or a relatively low level of dynamical variation on ecological communities despite changes in species composition (Ernest & Brown 2001; Saavedra et al. 2016).

The variation in interaction beta diversity between seasons and across ecoregions was generated by differences in prey availability. Resource availability plays a central role in classical theories of species diversity and resource partitioning (Tilman 1980). Furthermore, Moroti *et al.* (2020) demonstrate the importance of prey availability in the partitioning of trophic resources by anurans. Anurans are mostly generalists and they eat what is available in greater densities in the environment (Ceron et al. 2019; Michelin et al. 2020). Regardless of the identity of species, in the majority of cases, anurans will eat the more abundant preys in, resulting in a complementary trophic role, according as the neutral hypothesis. Consequently, changes in prey availability will affect what anurans eat, with consequences on interaction beta diversity. High levels of generalism also imply that anurans may overlap significantly in their roles in these networks. Yet we do not find totally connected networks indicating that despite the general agreement that these anurans are opportunistic feeders, trophic niche partitioning may exist in some level. Besides differences in body size, which may generate differences in the consumed prey, habitat use may also create heterogeneity in which prey is effectively perceived as the most abundant by different species. For instance, even within the same pond, species that forage in limnetic or littoral zones have access to different sets of prey.

Our findings show how heterogeneous can these different communities be, even within the same region. Preserving multiple habitats is not only a matter of preserving species diversity but also interaction diversity and the ecosystem functions associated with them. Variation across time and space shows how functionally complex interaction networks can be. Documenting this variation is a much necessary step towards a more comprehensive understanding of the processes that determine community assembly, and ultimately shape the functioning of ecosystems. Our work also highlights the potential of anurans to regulate the populations of multiple species of invertebrates underlining that these functions can be quite variable across time and space.

Supporting Information

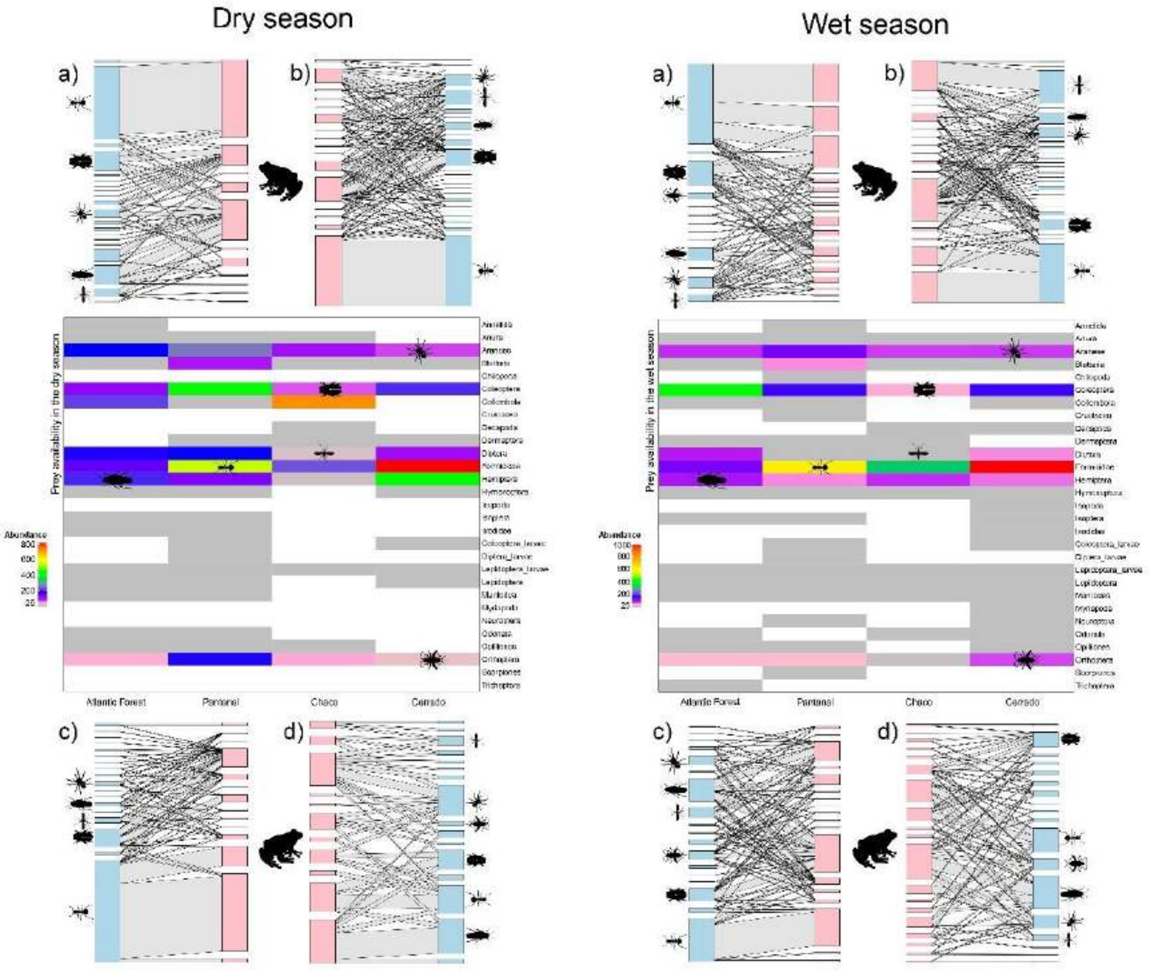

Figure S1. Changes in prey availability and anuran-prey networks of each seasons (left – dry season; right – wet season) and ecoregions: a) Atlantic Forest, b) Pantanal, c) Chaco and d) Cerrado. Most available preys are often the most consumed. Blank lines = zero abundance.

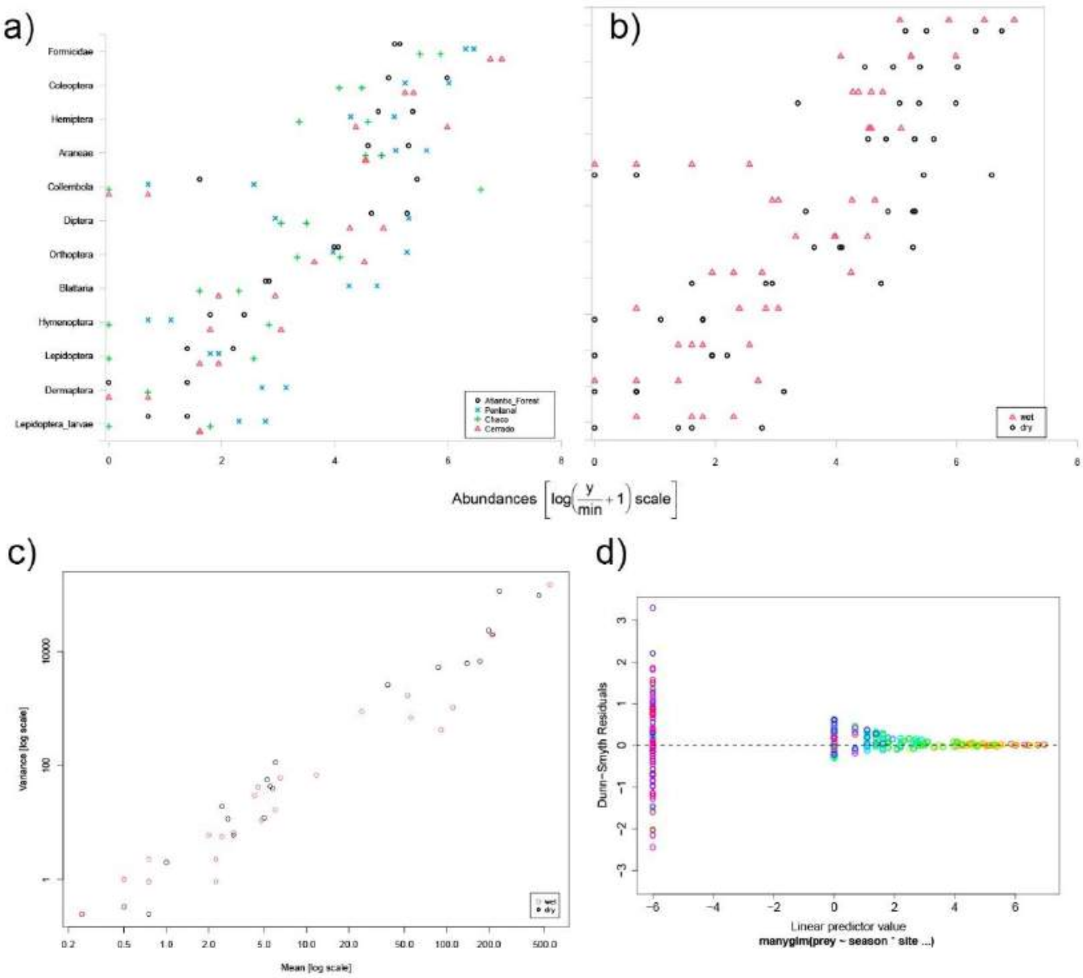

Figure S2: a) Results of multivariate Generalized Linear Model built with *mvabund* showing differences in prey abundance among ecoregions and b) between seasons, c) mean–variance plot of Poisson regression and d) Residual vs. fit diagnostic plot to check the quadratic mean–variance assumption of Poisson regression (with species coded as colors).

Table S1. Mean and standard deviation of pairwise beta diversity across theoretical networks and real networks (CE = Cerrado, CH = Chaco, AF = Atlantic Forest, PA = Pantanal).

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
PA1_wet	PA1_dry	0.797	0.409	0.040
PA1_wet	PA2_wet	0.742	0.265	0.041
PA1_wet	PA2_dry	0.846	0.366	0.040
PA1_wet	PA3_wet	0.688	0.368	0.059
PA1_wet	PA3_dry	0.545	0.498	0.076

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
PA1_wet	PA4_wet	0.556	0.571	0.050
PA1_wet	PA4_dry	0.860	0.445	0.055
PA1_wet	CE2_wet	0.512	0.467	0.084
PA1_wet	CE2_dry	0.733	0.753	0.381
PA1_wet	CH1_wet	0.913	0.481	0.035
PA1_wet	CH1_dry	0.736	0.652	0.067
PA1_wet	CH2_wet	0.854	0.395	0.046
PA1_wet	CH2_dry	0.636	0.502	0.057
PA1_wet	CH3_wet	0.841	0.548	0.040
PA1_wet	CH3_dry	0.931	0.700	0.059
PA1_wet	PA5_wet	0.839	0.627	0.045
PA1_wet	PA5_dry	0.714	0.457	0.041
PA1_wet	PA6_wet	0.614	0.814	0.030
PA1_wet	PA6_dry	0.939	0.486	0.055
PA1_wet	AF3_wet	0.600	0.589	0.066
PA1_wet	AF3_dry	0.800	0.836	0.048
PA1_wet	AF4_wet	0.756	0.418	0.072
PA1_wet	AF4_dry	0.860	0.850	0.071
PA1_wet	AF5_wet	1.000	0.581	0.080
PA1_wet	AF5_dry	0.633	0.611	0.070
PA1_wet	CE3_wet	0.636	0.490	0.070
PA1_wet	CE3_dry	0.633	0.492	0.073
PA1_wet	CE4_wet	0.706	0.517	0.103
PA1_wet	CE4_dry	0.771	1.000	0.000
PA1_wet	CE5_wet	1.000	0.459	0.115
PA1_wet	CE5_dry	0.704	1.000	0.000
PA1_wet	AF1_wet	1.000	1.000	0.000
PA1_wet	AF1_dry	1.000	0.546	0.115
PA1_wet	AF2_wet	0.913	0.558	0.067
PA1_wet	AF2_dry	0.667	0.600	0.049
PA1_dry	PA2_wet	0.516	0.391	0.041
PA1_dry	PA2_dry	0.294	0.296	0.051
PA1_dry	PA3_wet	0.527	0.383	0.072
PA1_dry	PA3_dry	0.558	0.512	0.072
PA1_dry	PA4_wet	0.681	0.641	0.060
PA1_dry	PA4_dry	0.737	0.361	0.062
PA1_dry	CE2_wet	0.757	0.475	0.131
PA1_dry	CE2_dry	0.841	0.786	0.039
PA1_dry	CH1_wet	1.000	0.557	0.045
PA1_dry	CH1_dry	0.698	0.665	0.095
PA1_dry	CH2_wet	0.757	0.499	0.065
PA1_dry	CH2_dry	0.636	0.597	0.057
PA1_dry	CH3_wet	0.667	0.499	0.052
PA1_dry	CH3_dry	0.670	0.688	0.074

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
PA1_dry	PA5_wet	0.853	0.751	0.090
PA1_dry	PA5_dry	0.676	0.405	0.038
PA1_dry	PA6_wet	0.622	0.732	0.074
PA1_dry	PA6_dry	0.939	0.382	0.051
PA1_dry	AF3_wet	0.566	0.710	0.094
PA1_dry	AF3_dry	0.783	0.549	0.087
PA1_dry	AF4_wet	0.946	0.582	0.094
PA1_dry	AF4_dry	0.778	0.798	0.134
PA1_dry	AF5_wet	0.939	0.503	0.083
PA1_dry	AF5_dry	0.756	0.465	0.079
PA1_dry	CE3_wet	0.792	0.428	0.092
PA1_dry	CE3_dry	0.902	0.527	0.138
PA1_dry	CE4_wet	0.761	0.608	0.225
PA1_dry	CE4_dry	0.853	1.000	0.000
PA1_dry	CE5_wet	1.000	0.710	0.090
PA1_dry	CE5_dry	0.933	1.000	0.000
PA1_dry	AF1_wet	1.000	1.000	0.000
PA1_dry	AF1_dry	1.000	0.681	0.101
PA1_dry	AF2_wet	0.857	0.524	0.105
PA1_dry	AF2_dry	0.873	0.431	0.077
PA2_wet	PA2_dry	0.462	0.369	0.040
PA2_wet	PA3_wet	0.379	0.330	0.066
PA2_wet	PA3_dry	0.486	0.448	0.088
PA2_wet	PA4_wet	0.742	0.496	0.057
PA2_wet	PA4_dry	0.826	0.342	0.071
PA2_wet	CE2_wet	0.701	0.550	0.079
PA2_wet	CE2_dry	0.893	0.000	0.000
PA2_wet	CH1_wet	0.959	0.505	0.044
PA2_wet	CH1_dry	0.722	0.645	0.075
PA2_wet	CH2_wet	0.851	0.401	0.050
PA2_wet	CH2_dry	0.679	0.479	0.055
PA2_wet	CH3_wet	0.730	0.486	0.046
PA2_wet	CH3_dry	0.738	0.648	0.071
PA2_wet	PA5_wet	0.841	0.697	0.057
PA2_wet	PA5_dry	0.902	0.455	0.043
PA2_wet	PA6_wet	0.687	0.797	0.054
PA2_wet	PA6_dry	0.864	0.503	0.043
PA2_wet	AF3_wet	0.553	0.614	0.074
PA2_wet	AF3_dry	0.947	0.861	0.056
PA2_wet	AF4_wet	0.851	0.391	0.074
PA2_wet	AF4_dry	0.880	0.820	0.045
PA2_wet	AF5_wet	0.966	0.649	0.080
PA2_wet	AF5_dry	0.840	0.489	0.059
PA2_wet	CE3_wet	0.800	0.396	0.170

Site1/season	**Site2/season**	**Interaction beta-diversity**		
		Real	**Null-model (mean)**	**SD (±)**
PA2_wet	CE3_dry	0.760	0.628	0.070
PA2_wet	CE4_wet	0.867	0.419	0.129
PA2_wet	CE4_dry	0.934	1.000	0.000
PA2_wet	CE5_wet	1.000	0.432	0.171
PA2_wet	CE5_dry	0.887	1.000	0.000
PA2_wet	AF1_wet	1.000	1.000	0.000
PA2_wet	AF1_dry	1.000	0.511	0.074
PA2_wet	AF2_wet	0.918	0.584	0.066
PA2_wet	AF2_dry	0.857	0.606	0.075
PA2_dry	PA3_wet	0.527	0.411	0.062
PA2_dry	PA3_dry	0.500	0.413	0.061
PA2_dry	PA4_wet	0.692	0.626	0.051
PA2_dry	PA4_dry	0.695	0.316	0.062
PA2_dry	CE2_wet	0.754	0.413	0.109
PA2_dry	CE2_dry	0.783	0.801	0.022
PA2_dry	CH1_wet	1.000	0.468	0.047
PA2_dry	CH1_dry	0.652	0.661	0.080
PA2_dry	CH2_wet	0.754	0.435	0.046
PA2_dry	CH2_dry	0.606	0.590	0.053
PA2_dry	CH3_wet	0.595	0.552	0.049
PA2_dry	CH3_dry	0.595	0.676	0.058
PA2_dry	PA5_wet	0.821	0.636	0.080
PA2_dry	PA5_dry	0.725	0.357	0.039
PA2_dry	PA6_wet	0.644	0.763	0.051
PA2_dry	PA6_dry	0.918	0.347	0.047
PA2_dry	AF3_wet	0.576	0.614	0.076
PA2_dry	AF3_dry	0.848	0.619	0.059
PA2_dry	AF4_wet	0.965	0.492	0.071
PA2_dry	AF4_dry	0.781	0.779	0.088
PA2_dry	AF5_wet	0.918	0.484	0.058
PA2_dry	AF5_dry	0.846	0.522	0.062
PA2_dry	CE3_wet	0.767	0.374	0.069
PA2_dry	CE3_dry	0.908	0.547	0.121
PA2_dry	CE4_wet	0.840	0.486	0.120
PA2_dry	CE4_dry	0.882	1.000	0.000
PA2_dry	CE5_wet	1.000	0.597	0.065
PA2_dry	CE5_dry	0.907	1.000	0.000
PA2_dry	AF1_wet	1.000	1.000	0.000
PA2_dry	AF1_dry	1.000	0.652	0.089
PA2_dry	AF2_wet	0.795	0.503	0.069
PA2_dry	AF2_dry	0.870	0.353	0.071
PA3_wet	PA3_dry	0.529	0.448	0.070
PA3_wet	PA4_wet	0.688	0.424	0.096
PA3_wet	PA4_dry	0.857	0.375	0.071

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
PA3_wet	CE2_wet	0.634	0.484	0.091
PA3_wet	CE2_dry	0.831	0.793	0.153
PA3_wet	CH1_wet	0.969	0.589	0.058
PA3_wet	CH1_dry	0.681	0.525	0.098
PA3_wet	CH2_wet	0.854	0.466	0.069
PA3_wet	CH2_dry	0.688	0.488	0.058
PA3_wet	CH3_wet	0.712	0.478	0.059
PA3_wet	CH3_dry	0.778	0.545	0.095
PA3_wet	PA5_wet	0.845	0.523	0.103
PA3_wet	PA5_dry	0.789	0.355	0.060
PA3_wet	PA6_wet	0.612	0.690	0.201
PA3_wet	PA6_dry	0.946	0.417	0.067
PA3_wet	AF3_wet	0.582	0.663	0.105
PA3_wet	AF3_dry	0.868	0.675	0.089
PA3_wet	AF4_wet	0.902	0.470	0.096
PA3_wet	AF4_dry	0.816	0.820	0.107
PA3_wet	AF5_wet	0.946	0.580	0.102
PA3_wet	AF5_dry	0.778	0.501	0.074
PA3_wet	CE3_wet	0.741	0.415	0.102
PA3_wet	CE3_dry	0.689	0.556	0.119
PA3_wet	CE4_wet	0.840	0.490	0.162
PA3_wet	CE4_dry	0.868	1.000	0.000
PA3_wet	CE5_wet	1.000	0.608	0.099
PA3_wet	CE5_dry	0.882	1.000	0.000
PA3_wet	AF1_wet	1.000	1.000	0.000
PA3_wet	AF1_dry	1.000	0.643	0.120
PA3_wet	AF2_wet	0.906	0.549	0.093
PA3_wet	AF2_dry	0.831	0.527	0.073
PA3_dry	PA4_wet	0.545	0.522	0.085
PA3_dry	PA4_dry	0.686	0.466	0.068
PA3_dry	CE2_wet	0.469	0.407	0.116
PA3_dry	CE2_dry	0.737	0.758	0.257
PA3_dry	CH1_wet	0.935	0.431	0.083
PA3_dry	CH1_dry	0.738	0.632	0.087
PA3_dry	CH2_wet	0.878	0.398	0.082
PA3_dry	CH2_dry	0.651	0.534	0.095
PA3_dry	CH3_wet	0.718	0.540	0.092
PA3_dry	CH3_dry	0.758	0.574	0.104
PA3_dry	PA5_wet	0.771	0.537	0.115
PA3_dry	PA5_dry	0.767	0.370	0.072
PA3_dry	PA6_wet	0.569	0.696	0.156
PA3_dry	PA6_dry	0.951	0.454	0.081
PA3_dry	AF3_wet	0.483	0.604	0.102
PA3_dry	AF3_dry	0.828	0.723	0.093

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
PA3_dry	AF4_wet	0.796	0.507	0.084
PA3_dry	AF4_dry	0.815	0.814	0.111
PA3_dry	AF5_wet	0.951	0.538	0.095
PA3_dry	AF5_dry	0.719	0.547	0.083
PA3_dry	CE3_wet	0.577	0.462	0.083
PA3_dry	CE3_dry	0.719	0.620	0.094
PA3_dry	CE4_wet	0.714	0.538	0.125
PA3_dry	CE4_dry	0.907	1.000	0.000
PA3_dry	CE5_wet	1.000	0.503	0.127
PA3_dry	CE5_dry	0.829	1.000	0.000
PA3_dry	AF1_wet	1.000	1.000	0.000
PA3_dry	AF1_dry	1.000	0.587	0.154
PA3_dry	AF2_wet	0.742	0.499	0.103
PA3_dry	AF2_dry	0.632	0.519	0.070
PA4_wet	PA4_dry	0.674	0.441	0.077
PA4_wet	CE2_wet	0.366	0.611	0.116
PA4_wet	CE2_dry	0.667	0.758	0.273
PA4_wet	CH1_wet	0.913	0.591	0.071
PA4_wet	CH1_dry	0.623	0.550	0.098
PA4_wet	CH2_wet	0.756	0.520	0.071
PA4_wet	CH2_dry	0.673	0.516	0.088
PA4_wet	CH3_wet	0.778	0.465	0.071
PA4_wet	CH3_dry	0.793	0.491	0.067
PA4_wet	PA5_wet	0.806	0.707	0.082
PA4_wet	PA5_dry	0.486	0.472	0.048
PA4_wet	PA6_wet	0.579	0.545	0.257
PA4_wet	PA6_dry	0.879	0.691	0.050
PA4_wet	AF3_wet	0.640	0.517	0.045
PA4_wet	AF3_dry	0.760	0.750	0.090
PA4_wet	AF4_wet	0.951	0.407	0.097
PA4_wet	AF4_dry	0.754	0.782	0.097
PA4_wet	AF5_wet	0.879	0.563	0.073
PA4_wet	AF5_dry	0.755	0.474	0.095
PA4_wet	CE3_wet	0.591	0.617	0.124
PA4_wet	CE3_dry	0.796	0.545	0.102
PA4_wet	CE4_wet	0.706	0.749	0.193
PA4_wet	CE4_dry	0.829	1.000	0.000
PA4_wet	CE5_wet	1.000	0.700	0.142
PA4_wet	CE5_dry	0.852	1.000	0.000
PA4_wet	AF1_wet	1.000	1.000	0.000
PA4_wet	AF1_dry	1.000	0.565	0.105
PA4_wet	AF2_wet	0.652	0.629	0.065
PA4_wet	AF2_dry	0.667	0.664	0.081
PA4_dry	CE2_wet	0.583	0.497	0.116

Site1/season	**Site2/season**	**Interaction beta-diversity**		
		Real	**Null-model (mean)**	**SD (±)**
PA4_dry	CE2_dry	0.784	0.773	0.063
PA4_dry	CH1_wet	1.000	0.410	0.083
PA4_dry	CH1_dry	0.800	0.575	0.106
PA4_dry	CH2_wet	0.833	0.395	0.053
PA4_dry	CH2_dry	0.677	0.540	0.079
PA4_dry	CH3_wet	0.829	0.381	0.070
PA4_dry	CH3_dry	0.785	0.577	0.078
PA4_dry	PA5_wet	0.652	0.610	0.103
PA4_dry	PA5_dry	0.762	0.342	0.066
PA4_dry	PA6_wet	0.625	0.828	0.177
PA4_dry	PA6_dry	0.950	0.402	0.064
PA4_dry	AF3_wet	0.789	0.618	0.082
PA4_dry	AF3_dry	0.544	0.638	0.070
PA4_dry	AF4_wet	0.917	0.326	0.085
PA4_dry	AF4_dry	0.813	0.762	0.075
PA4_dry	AF5_wet	0.900	0.489	0.070
PA4_dry	AF5_dry	0.607	0.411	0.076
PA4_dry	CE3_wet	0.725	0.394	0.102
PA4_dry	CE3_dry	0.929	0.475	0.110
PA4_dry	CE4_wet	0.756	0.654	0.154
PA4_dry	CE4_dry	0.952	1.000	0.000
PA4_dry	CE5_wet	1.000	0.653	0.081
PA4_dry	CE5_dry	0.941	1.000	0.000
PA4_dry	AF1_wet	1.000	1.000	0.000
PA4_dry	AF1_dry	1.000	0.578	0.083
PA4_dry	AF2_wet	0.733	0.504	0.077
PA4_dry	AF2_dry	0.622	0.440	0.062
CE2_wet	CE2_dry	0.714	0.456	0.187
CE2_wet	CH1_wet	0.929	0.409	0.081
CE2_wet	CH1_dry	0.690	0.604	0.138
CE2_wet	CH2_wet	0.826	0.481	0.089
CE2_wet	CH2_dry	0.633	0.527	0.107
CE2_wet	CH3_wet	0.794	0.615	0.108
CE2_wet	CH3_dry	0.810	0.551	0.120
CE2_wet	PA5_wet	0.761	0.526	0.117
CE2_wet	PA5_dry	0.650	0.405	0.085
CE2_wet	PA6_wet	0.452	0.729	0.219
CE2_wet	PA6_dry	0.947	0.440	0.120
CE2_wet	AF3_wet	0.673	0.552	0.168
CE2_wet	AF3_dry	0.782	0.811	0.142
CE2_wet	AF4_wet	0.826	0.479	0.122
CE2_wet	AF4_dry	0.774	0.822	0.145
CE2_wet	AF5_wet	0.895	0.595	0.144
CE2_wet	AF5_dry	0.667	0.609	0.127

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
CE2_wet	CE3_wet	0.510	0.336	0.160
CE2_wet	CE3_dry	0.630	0.474	0.175
CE2_wet	CE4_wet	0.641	0.417	0.167
CE2_wet	CE4_dry	0.900	1.000	0.000
CE2_wet	CE5_wet	1.000	0.572	0.138
CE2_wet	CE5_dry	0.813	1.000	0.000
CE2_wet	AF1_wet	1.000	1.000	0.000
CE2_wet	AF1_dry	1.000	0.546	0.198
CE2_wet	AF2_wet	0.643	0.513	0.138
CE2_wet	AF2_dry	0.543	0.521	0.100
CE2_dry	CH1_wet	0.765	0.000	0.000
CE2_dry	CH1_dry	0.745	0.000	0.000
CE2_dry	CH2_wet	0.886	0.719	0.263
CE2_dry	CH2_dry	0.796	0.867	0.268
CE2_dry	CH3_wet	0.860	0.000	0.000
CE2_dry	CH3_dry	0.885	0.855	0.171
CE2_dry	PA5_wet	0.893	0.000	0.000
CE2_dry	PA5_dry	0.724	0.775	0.053
CE2_dry	PA6_wet	0.765	0.000	0.000
CE2_dry	PA6_dry	0.926	0.788	0.050
CE2_dry	AF3_wet	0.864	0.840	0.368
CE2_dry	AF3_dry	0.818	0.751	0.144
CE2_dry	AF4_wet	1.000	0.000	0.000
CE2_dry	AF4_dry	0.804	0.000	0.000
CE2_dry	AF5_wet	0.926	0.754	0.210
CE2_dry	AF5_dry	0.907	0.773	0.138
CE2_dry	CE3_wet	0.789	0.750	0.121
CE2_dry	CE3_dry	0.860	0.695	0.270
CE2_dry	CE4_wet	0.786	0.000	0.000
CE2_dry	CE4_dry	0.862	0.000	0.000
CE2_dry	CE5_wet	1.000	0.888	0.133
CE2_dry	CE5_dry	0.524	1.000	0.000
CE2_dry	AF1_wet	1.000	1.000	0.000
CE2_dry	AF1_dry	1.000	0.810	0.394
CE2_dry	AF2_wet	0.882	0.763	0.257
CE2_dry	AF2_dry	0.833	0.765	0.034
CH1_wet	CH1_dry	1.000	0.664	0.083
CH1_wet	CH2_wet	1.000	0.349	0.061
CH1_wet	CH2_dry	1.000	0.550	0.074
CH1_wet	CH3_wet	1.000	0.467	0.058
CH1_wet	CH3_dry	1.000	0.647	0.076
CH1_wet	PA5_wet	0.959	0.628	0.077
CH1_wet	PA5_dry	1.000	0.523	0.045
CH1_wet	PA6_wet	1.000	0.721	0.085

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
CH1_wet	PA6_dry	1.000	0.567	0.058
CH1_wet	AF3_wet	0.946	0.557	0.094
CH1_wet	AF3_dry	1.000	0.843	0.086
CH1_wet	AF4_wet	0.929	0.445	0.076
CH1_wet	AF4_dry	1.000	0.764	0.081
CH1_wet	AF5_wet	1.000	0.573	0.099
CH1_wet	AF5_dry	1.000	0.496	0.090
CH1_wet	CE3_wet	0.935	0.432	0.086
CH1_wet	CE3_dry	0.944	0.542	0.097
CH1_wet	CE4_wet	0.905	0.518	0.129
CH1_wet	CE4_dry	1.000	1.000	0.000
CH1_wet	CE5_wet	1.000	0.402	0.137
CH1_wet	CE5_dry	1.000	1.000	0.000
CH1_wet	AF1_wet	1.000	1.000	0.000
CH1_wet	AF1_dry	1.000	0.415	0.109
CH1_wet	AF2_wet	1.000	0.501	0.090
CH1_wet	AF2_dry	1.000	0.448	0.075
CH1_dry	CH2_wet	0.724	0.625	0.097
CH1_dry	CH2_dry	0.528	0.274	0.073
CH1_dry	CH3_wet	0.625	0.630	0.080
CH1_dry	CH3_dry	0.680	0.377	0.074
CH1_dry	PA5_wet	0.772	0.715	0.107
CH1_dry	PA5_dry	0.654	0.673	0.087
CH1_dry	PA6_wet	0.703	0.787	0.188
CH1_dry	PA6_dry	0.920	0.752	0.129
CH1_dry	AF3_wet	0.791	0.617	0.173
CH1_dry	AF3_dry	0.821	0.794	0.131
CH1_dry	AF4_wet	0.966	0.600	0.113
CH1_dry	AF4_dry	0.730	0.770	0.169
CH1_dry	AF5_wet	0.920	0.692	0.123
CH1_dry	AF5_dry	0.818	0.370	0.135
CH1_dry	CE3_wet	0.770	0.892	0.174
CH1_dry	CE3_dry	0.848	0.616	0.113
CH1_dry	CE4_wet	0.882	0.842	0.160
CH1_dry	CE4_dry	0.885	1.000	0.000
CH1_dry	CE5_wet	1.000	0.906	0.168
CH1_dry	CE5_dry	0.864	1.000	0.000
CH1_dry	AF1_wet	1.000	1.000	0.000
CH1_dry	AF1_dry	1.000	0.429	0.201
CH1_dry	AF2_wet	0.850	0.598	0.119
CH1_dry	AF2_dry	0.830	0.650	0.117
CH2_wet	CH2_dry	0.733	0.447	0.046
CH2_wet	CH3_wet	0.676	0.318	0.065
CH2_wet	CH3_dry	0.683	0.519	0.043

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
CH2_wet	PA5_wet	0.701	0.646	0.070
CH2_wet	PA5_dry	0.750	0.477	0.050
CH2_wet	PA6_wet	0.806	0.615	0.089
CH2_wet	PA6_dry	1.000	0.499	0.060
CH2_wet	AF3_wet	0.927	0.604	0.089
CH2_wet	AF3_dry	0.891	0.735	0.088
CH2_wet	AF4_wet	1.000	0.424	0.086
CH2_wet	AF4_dry	0.774	0.792	0.085
CH2_wet	AF5_wet	0.947	0.583	0.086
CH2_wet	AF5_dry	0.889	0.502	0.074
CH2_wet	CE3_wet	0.796	0.440	0.090
CH2_wet	CE3_dry	1.000	0.490	0.099
CH2_wet	CE4_wet	0.795	0.394	0.167
CH2_wet	CE4_dry	0.950	1.000	0.000
CH2_wet	CE5_wet	1.000	0.567	0.109
CH2_wet	CE5_dry	1.000	1.000	0.000
CH2_wet	AF1_wet	1.000	1.000	0.000
CH2_wet	AF1_dry	1.000	0.535	0.109
CH2_wet	AF2_wet	0.857	0.541	0.102
CH2_wet	AF2_dry	0.943	0.502	0.065
CH2_dry	CH3_wet	0.463	0.388	0.052
CH2_dry	CH3_dry	0.481	0.238	0.047
CH2_dry	PA5_wet	0.580	0.694	0.082
CH2_dry	PA5_dry	0.667	0.563	0.049
CH2_dry	PA6_wet	0.605	0.536	0.105
CH2_dry	PA6_dry	0.808	0.627	0.064
CH2_dry	AF3_wet	0.739	0.618	0.110
CH2_dry	AF3_dry	0.797	0.688	0.082
CH2_dry	AF4_wet	0.833	0.445	0.087
CH2_dry	AF4_dry	0.763	0.675	0.104
CH2_dry	AF5_wet	0.923	0.670	0.098
CH2_dry	AF5_dry	0.676	0.394	0.089
CH2_dry	CE3_wet	0.683	0.690	0.098
CH2_dry	CE3_dry	0.853	0.618	0.087
CH2_dry	CE4_wet	0.774	0.768	0.174
CH2_dry	CE4_dry	0.889	1.000	0.000
CH2_dry	CE5_wet	1.000	0.747	0.164
CH2_dry	CE5_dry	0.870	1.000	0.000
CH2_dry	AF1_wet	1.000	1.000	0.000
CH2_dry	AF1_dry	1.000	0.445	0.145
CH2_dry	AF2_wet	0.762	0.611	0.098
CH2_dry	AF2_dry	0.714	0.588	0.081
CH3_wet	CH3_dry	0.482	0.507	0.051
CH3_wet	PA5_wet	0.506	0.702	0.079

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
CH3_wet	PA5_dry	0.839	0.566	0.050
CH3_wet	PA6_wet	0.762	0.530	0.092
CH3_wet	PA6_dry	0.833	0.629	0.062
CH3_wet	AF3_wet	0.792	0.650	0.082
CH3_wet	AF3_dry	0.922	0.914	0.091
CH3_wet	AF4_wet	0.941	0.420	0.095
CH3_wet	AF4_dry	0.833	0.698	0.113
CH3_wet	AF5_wet	0.933	0.653	0.113
CH3_wet	AF5_dry	0.816	0.366	0.082
CH3_wet	CE3_wet	0.831	1.000	0.000
CH3_wet	CE3_dry	0.974	0.563	0.088
CH3_wet	CE4_wet	0.902	0.851	0.161
CH3_wet	CE4_dry	0.935	1.000	0.000
CH3_wet	CE5_wet	1.000	0.764	0.137
CH3_wet	CE5_dry	0.963	1.000	0.000
CH3_wet	AF1_wet	1.000	1.000	0.000
CH3_wet	AF1_dry	1.000	0.444	0.097
CH3_wet	AF2_wet	0.880	0.564	0.096
CH3_wet	AF2_dry	0.895	0.777	0.062
CH3_dry	PA5_wet	0.500	0.695	0.100
CH3_dry	PA5_dry	0.754	0.520	0.053
CH3_dry	PA6_wet	0.772	0.527	0.121
CH3_dry	PA6_dry	0.855	0.694	0.078
CH3_dry	AF3_wet	0.806	0.482	0.087
CH3_dry	AF3_dry	0.889	0.571	0.091
CH3_dry	AF4_wet	1.000	0.579	0.075
CH3_dry	AF4_dry	0.797	0.788	0.145
CH3_dry	AF5_wet	0.927	0.542	0.094
CH3_dry	AF5_dry	0.887	0.387	0.080
CH3_dry	CE3_wet	0.788	0.680	0.098
CH3_dry	CE3_dry	1.000	0.654	0.094
CH3_dry	CE4_wet	0.821	0.810	0.145
CH3_dry	CE4_dry	0.965	1.000	0.000
CH3_dry	CE5_wet	1.000	0.804	0.142
CH3_dry	CE5_dry	1.000	1.000	0.000
CH3_dry	AF1_wet	1.000	1.000	0.000
CH3_dry	AF1_dry	1.000	0.530	0.171
CH3_dry	AF2_wet	0.822	0.597	0.086
CH3_dry	AF2_dry	0.885	0.559	0.072
PA5_wet	PA5_dry	0.902	0.497	0.097
PA5_wet	PA6_wet	0.759	0.748	0.118
PA5_wet	PA6_dry	0.831	0.544	0.098
PA5_wet	AF3_wet	0.868	0.582	0.158
PA5_wet	AF3_dry	0.737	0.872	0.121

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
PA5_wet	AF4_wet	0.881	0.561	0.105
PA5_wet	AF4_dry	0.831	0.902	0.113
PA5_wet	AF5_wet	0.966	0.600	0.150
PA5_wet	AF5_dry	0.707	0.690	0.129
PA5_wet	CE3_wet	0.743	0.398	0.160
PA5_wet	CE3_dry	0.920	0.487	0.132
PA5_wet	CE4_wet	0.800	0.446	0.147
PA5_wet	CE4_dry	1.000	1.000	0.000
PA5_wet	CE5_wet	1.000	0.480	0.137
PA5_wet	CE5_dry	0.962	1.000	0.000
PA5_wet	AF1_wet	1.000	1.000	0.000
PA5_wet	AF1_dry	1.000	0.625	0.208
PA5_wet	AF2_wet	0.837	0.526	0.139
PA5_wet	AF2_dry	0.786	0.603	0.110
PA5_dry	PA6_wet	0.679	0.841	0.061
PA5_dry	PA6_dry	0.875	0.349	0.060
PA5_dry	AF3_wet	0.755	0.470	0.061
PA5_dry	AF3_dry	0.755	0.631	0.059
PA5_dry	AF4_wet	1.000	0.378	0.073
PA5_dry	AF4_dry	0.714	0.837	0.087
PA5_dry	AF5_wet	0.875	0.409	0.058
PA5_dry	AF5_dry	0.792	0.476	0.066
PA5_dry	CE3_wet	0.767	0.285	0.070
PA5_dry	CE3_dry	0.833	0.464	0.142
PA5_dry	CE4_wet	0.818	0.410	0.138
PA5_dry	CE4_dry	0.765	1.000	0.000
PA5_dry	CE5_wet	1.000	0.555	0.060
PA5_dry	CE5_dry	0.692	1.000	0.000
PA5_dry	AF1_wet	1.000	1.000	0.000
PA5_dry	AF1_dry	1.000	0.612	0.095
PA5_dry	AF2_wet	0.636	0.501	0.053
PA5_dry	AF2_dry	0.724	0.364	0.064
PA6_wet	PA6_dry	0.963	0.701	0.092
PA6_wet	AF3_wet	0.521	0.745	0.172
PA6_wet	AF3_dry	0.662	0.910	0.288
PA6_wet	AF4_wet	0.903	0.678	0.123
PA6_wet	AF4_dry	0.795	1.000	0.000
PA6_wet	AF5_wet	0.926	0.656	0.279
PA6_wet	AF5_dry	0.657	0.743	0.213
PA6_wet	CE3_wet	0.662	0.796	0.116
PA6_wet	CE3_dry	0.771	0.000	0.000
PA6_wet	CE4_wet	0.782	0.623	0.113
PA6_wet	CE4_dry	0.893	1.000	0.000
PA6_wet	CE5_wet	1.000	0.714	0.172

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
PA6_wet	CE5_dry	0.833	1.000	0.000
PA6_wet	AF1_wet	1.000	1.000	0.000
PA6_wet	AF1_dry	1.000	0.000	0.000
PA6_wet	AF2_wet	0.773	0.702	0.329
PA6_wet	AF2_dry	0.647	0.823	0.140
PA6_dry	AF3_wet	0.957	0.681	0.070
PA6_dry	AF3_dry	1.000	0.607	0.064
PA6_dry	AF4_wet	1.000	0.552	0.086
PA6_dry	AF4_dry	0.926	0.908	0.110
PA6_dry	AF5_wet	1.000	0.519	0.069
PA6_dry	AF5_dry	0.957	0.590	0.075
PA6_dry	CE3_wet	0.951	0.313	0.065
PA6_dry	CE3_dry	0.957	0.530	0.148
PA6_dry	CE4_wet	1.000	0.386	0.142
PA6_dry	CE4_dry	0.813	1.000	0.000
PA6_dry	CE5_wet	1.000	0.575	0.074
PA6_dry	CE5_dry	0.917	1.000	0.000
PA6_dry	AF1_wet	1.000	1.000	0.000
PA6_dry	AF1_dry	1.000	0.751	0.101
PA6_dry	AF2_wet	1.000	0.553	0.079
PA6_dry	AF2_dry	1.000	0.358	0.064
AF3_wet	AF3_dry	0.813	0.537	0.063
AF3_wet	AF4_wet	0.891	0.490	0.058
AF3_wet	AF4_dry	0.915	0.496	0.073
AF3_wet	AF5_wet	1.000	0.555	0.062
AF3_wet	AF5_dry	0.778	0.551	0.068
AF3_wet	CE3_wet	0.793	0.762	0.094
AF3_wet	CE3_dry	0.778	0.654	0.180
AF3_wet	CE4_wet	0.875	0.631	0.153
AF3_wet	CE4_dry	0.837	1.000	0.000
AF3_wet	CE5_wet	1.000	0.628	0.174
AF3_wet	CE5_dry	0.805	0.666	0.157
AF3_wet	AF1_wet	1.000	1.000	0.000
AF3_wet	AF1_dry	1.000	0.608	0.185
AF3_wet	AF2_wet	0.892	0.592	0.109
AF3_wet	AF2_dry	0.818	0.690	0.089
AF3_dry	AF4_wet	0.600	0.602	0.067
AF3_dry	AF4_dry	0.606	0.408	0.070
AF3_dry	AF5_wet	0.574	0.679	0.072
AF3_dry	AF5_dry	0.619	0.364	0.054
AF3_dry	CE3_wet	0.552	0.531	0.117
AF3_dry	CE3_dry	0.905	0.691	0.095
AF3_dry	CE4_wet	0.833	0.878	0.144
AF3_dry	CE4_dry	0.959	1.000	0.000

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
AF3_dry	CE5_wet	1.000	0.772	0.130
AF3_dry	CE5_dry	0.902	0.668	0.140
AF3_dry	AF1_wet	0.889	1.000	0.000
AF3_dry	AF1_dry	1.000	0.772	0.103
AF3_dry	AF2_wet	0.838	0.705	0.111
AF3_dry	AF2_dry	0.682	0.501	0.089
AF4_wet	AF4_dry	0.742	0.506	0.057
AF4_wet	AF5_wet	0.526	0.618	0.067
AF4_wet	AF5_dry	0.741	0.412	0.050
AF4_wet	CE3_wet	0.592	0.581	0.080
AF4_wet	CE3_dry	0.852	0.506	0.082
AF4_wet	CE4_wet	0.846	0.619	0.108
AF4_wet	CE4_dry	1.000	1.000	0.000
AF4_wet	CE5_wet	1.000	0.545	0.186
AF4_wet	CE5_dry	0.938	1.000	0.000
AF4_wet	AF1_wet	0.852	1.000	0.000
AF4_wet	AF1_dry	1.000	0.400	0.100
AF4_wet	AF2_wet	0.929	0.481	0.105
AF4_wet	AF2_dry	0.829	0.630	0.081
AF4_dry	AF5_wet	0.630	0.828	0.074
AF4_dry	AF5_dry	0.829	0.344	0.062
AF4_dry	CE3_wet	0.477	0.856	0.147
AF4_dry	CE3_dry	0.829	0.743	0.205
AF4_dry	CE4_wet	0.782	1.000	0.000
AF4_dry	CE4_dry	0.786	0.000	0.000
AF4_dry	CE5_wet	1.000	1.000	0.000
AF4_dry	CE5_dry	0.917	0.838	0.271
AF4_dry	AF1_wet	1.000	1.000	0.000
AF4_dry	AF1_dry	1.000	0.651	0.197
AF4_dry	AF2_wet	0.818	0.809	0.170
AF4_dry	AF2_dry	0.804	0.874	0.110
AF5_wet	AF5_dry	0.870	0.667	0.062
AF5_wet	CE3_wet	0.561	0.500	0.080
AF5_wet	CE3_dry	0.957	0.549	0.141
AF5_wet	CE4_wet	0.871	0.618	0.169
AF5_wet	CE4_dry	1.000	1.000	0.000
AF5_wet	CE5_wet	1.000	0.591	0.122
AF5_wet	CE5_dry	1.000	0.787	0.175
AF5_wet	AF1_wet	1.000	1.000	0.000
AF5_wet	AF1_dry	1.000	0.698	0.148
AF5_wet	AF2_wet	0.800	0.497	0.087
AF5_wet	AF2_dry	0.852	0.529	0.080
AF5_dry	CE3_wet	0.649	0.642	0.098
AF5_dry	CE3_dry	0.742	0.492	0.114

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
AF5_dry	CE4_wet	0.787	0.780	0.159
AF5_dry	CE4_dry	0.750	1.000	0.000
AF5_dry	CE5_wet	1.000	0.834	0.103
AF5_dry	CE5_dry	0.900	1.000	0.000
AF5_dry	AF1_wet	0.943	1.000	0.000
AF5_dry	AF1_dry	1.000	0.484	0.114
AF5_dry	AF2_wet	0.778	0.542	0.089
AF5_dry	AF2_dry	0.628	0.444	0.064
CE3_wet	CE3_dry	0.754	0.530	0.136
CE3_wet	CE4_wet	0.667	0.561	0.115
CE3_wet	CE4_dry	0.907	1.000	0.000
CE3_wet	CE5_wet	1.000	0.526	0.088
CE3_wet	CE5_dry	0.886	1.000	0.000
CE3_wet	AF1_wet	1.000	1.000	0.000
CE3_wet	AF1_dry	1.000	0.793	0.147
CE3_wet	AF2_wet	0.677	0.515	0.117
CE3_wet	AF2_dry	0.579	0.338	0.096
CE3_dry	CE4_wet	0.787	0.529	0.110
CE3_dry	CE4_dry	0.792	1.000	0.000
CE3_dry	CE5_wet	1.000	0.589	0.259
CE3_dry	CE5_dry	0.800	1.000	0.000
CE3_dry	AF1_wet	1.000	1.000	0.000
CE3_dry	AF1_dry	1.000	0.606	0.131
CE3_dry	AF2_wet	0.944	0.493	0.177
CE3_dry	AF2_dry	0.767	0.591	0.102
CE4_wet	CE4_dry	0.818	1.000	0.000
CE4_wet	CE5_wet	1.000	0.422	0.164
CE4_wet	CE5_dry	0.920	1.000	0.000
CE4_wet	AF1_wet	1.000	1.000	0.000
CE4_wet	AF1_dry	1.000	0.000	0.000
CE4_wet	AF2_wet	0.714	0.536	0.194
CE4_wet	AF2_dry	0.714	0.520	0.154
CE4_dry	CE5_wet	1.000	1.000	0.000
CE4_dry	CE5_dry	0.846	0.000	0.000
CE4_dry	AF1_wet	1.000	0.000	0.000
CE4_dry	AF1_dry	1.000	0.000	0.000
CE4_dry	AF2_wet	1.000	1.000	0.000
CE4_dry	AF2_dry	1.000	1.000	0.000
CE5_wet	CE5_dry	1.000	1.000	0.000
CE5_wet	AF1_wet	1.000	1.000	0.000
CE5_wet	AF1_dry	0.000	0.910	0.288
CE5_wet	AF2_wet	1.000	0.620	0.193
CE5_wet	AF2_dry	1.000	0.615	0.081
CE5_dry	AF1_wet	1.000	0.000	0.000

Site1/season	Site2/season	Interaction beta-diversity		
		Real	Null-model (mean)	SD (±)
CE5_dry	AF1_dry	1.000	0.000	0.000
CE5_dry	AF2_wet	0.857	1.000	0.000
CE5_dry	AF2_dry	0.810	1.000	0.000
AF1_wet	AF1_dry	1.000	1.000	0.000
AF1_wet	AF2_wet	1.000	1.000	0.000
AF1_wet	AF2_dry	1.000	1.000	0.000
AF1_dry	AF2_wet	1.000	0.613	0.134
AF1_dry	AF2_dry	1.000	0.679	0.104
AF2_wet	AF2_dry	0.529	0.550	0.078

Table S2. Within-season interaction turnover (dry to wet season) for all turnover metrics for each sampling site (CE = Cerrado, CH = Chaco, AF = Atlantic Forest, PA = Pantanal), where βs= dissimilarity on species composition, βwn= Beta diversity of interactions, βos= Temporal rewiring of species, and βst= Changes in species composition.

Network	βs	βint	βrw	βst
CE1	0.606	0.756	0.467	0.289
CE2	0.647	0.871	0.400	0.471
CE3	0.640	0.928	0.705	0.223
CE4	0.894	1.000	0.000	1.000
CE5	0.810	1.000	0.000	1.000
CH1	0.564	0.774	0.599	0.176
CH2	0.317	0.414	0.326	0.088
CH3	0.545	0.684	0.550	0.134
AF1	0.571	0.857	0.000	0.857
AF2	0.544	0.786	0.715	0.071
AF3	0.473	0.663	0.480	0.183
AF4	0.484	0.725	0.589	0.137
AF5	0.527	0.811	0.708	0.102
PA1	0.284	0.456	0.366	0.090
PA2	0.532	0.670	0.646	0.024
PA3	0.598	0.837	0.622	0.215
PA4	0.658	0.752	0.468	0.284
PA5	0.656	0.818	0.377	0.440
PA6	0.715	0.968	0.810	0.158

Final Considerations

Anuran-prey networks have high connectance and low complementary specialization and modularity in relation to other network types, and they are shaped by latitude, anuran richness, functional and phylogenetic richness.

In regard to anurans metacommunities, they show LCBD patterns similar between seasons, i.e., sites tended to contribute in the same way for community composition uniqueness during the dry and rainy seasons. Among studied ecoregions, Cerrado showed higher LCBD values in both seasons, despite lower values during the rainy season. Also, LCBD variation was explained by pure environmental variables (ecoregion) in the dry season, but models were non-significant during the rainy season.

The variation in interaction beta diversity between seasons and among areas were mainly generated by differences in prey availability. Interaction turnover between both ecoregions and seasons were high and driven primarily by interaction rewiring. In addition, beta diversity of species was positively related to geographic distance but not interaction beta diversity, suggesting that species interactions vary less, across space, than do species identity.

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Supplementary Material

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OIKOS

Meta analysis

Global patterns in anuran–prey networks: structure mediated by latitude

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Life on Earth is supported by an infinite number of interactions among organisms. Species interactions in these networks are influenced by latitude, evolutionary history and species traits. We performed a global-scale literature analysis to build up a database of interactions between anuran communities and their preys, from a wide range of geographical areas, using a network approach. For this purpose, we compiled a total of 55 weighted anuran–prey interaction networks, 39 located in the tropics and 16 in temperate areas. We tested the influence of latitude, as well as anuran taxonomic, functional and phylogenetic richness on network metrics. We found that anuran–prey networks are not nested, exhibit low complementary specialization and modularity and high connectance when compared to other types of networks. The main effects on network metrics were related to latitude, followed by anuran taxonomic, functional and phylogenetic richness, a pattern similar to the emerging in mutualistic networks. Our study is the first integrated analysis of the structural patterns in anuran–prey antagonistic interaction networks in different parts of the world. We suggest that different processes, mediated mainly by latitude, are modeling the architecture of anuran–prey networks across the globe.

Keywords: amphibia, ecological networks, food webs, macroecology

Synthesis

We compiled studies on anuran diet around the globe and analyzed these communities under the approach of networks. We found that anuran–prey networks are not nested, exhibit low specialization and modularity and high connectance when compared to other types of networks. The pattern emerged in anuran–preys networks metrics reflect the generalist and opportunistic habits of anurans diet. We also intended to split the effects of different factors on the network metrics based on a priori causal assumptions. The main effects on network metrics were related to latitude, followed by anuran taxonomic, functional and phylogenetic richness, a pattern similar to the emerging in mutualistic networks. Our study is the first integrated analysis of the structural patterns in anuran–prey antagonistic interaction networks in different parts of the world.

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Introduction

Maintenance of life on Earth is supported by an infinity of interactions among organisms (Jordano 2016), which also play an important role in the origin and evolution of species diversity (Bascompte et al. 2006, Schemske et al. 2009). Such interactions among organisms are not evenly distributed throughout the globe (Olesen et al. 2007). Some recent studies have made substantial efforts to describe the structure and to understand the ecological communities assembling (Pires and Guimarães 2013). The complex web of interactions that structures biotic communities is the study focus of ecological networks. This science aims to describe and evaluate patterns of species interactions and their effects on ecological processes (Dáttilo and Rico-Gray 2018). The most commonly studied networks are unipartite food webs (i.e. those where species are not divided into groups such as plants and pollinators) and bipartite networks of two interacting guilds (Dáttilo and Rico-Gray 2018). However, in nature, interactions gather multiple interaction types, which vary in space and time and are interconnected such as networks of networks, which are represented by multilayer networks (Pilosof et al. 2017). Interaction networks can be mutualistic, if they involve species that have mutual benefits, as in pollination and seed-dispersal networks (Bascompte and Jordano 2007); or antagonistic, when one member in the pair of interacting species can be negatively affected while the other benefits, such as in predation, parasitism and competition (Morris et al. 2014, Kéfi et al. 2015). Food webs are antagonistic networks which represent the trophic connections among species, a central role in the study of biological communities (McClanahan and Branch 2008, Kéfi et al. 2015).

Different aspects of network structure are measured by specific metrics like network size, connectance, nestedness and modularity (Dormann et al. 2009, Zanata et al. 2017). Patterns on these metrics usually differ between antagonistic and mutualistic networks (Morris et al. 2014, Estes et al. 2016), and they tend to change along biogeographical scales, such as latitudinal and climatic gradients (Schleuning et al. 2012, Zanata et al. 2017). The gradient of latitudinal diversity is a prominent pattern on Earth (Fischer 1960) and, in accordance, the majority of taxonomic groups, including anurans and invertebrates, exhibits richer communities in the tropics decreasing towards the poles (Hillebrand 2004, Wiens 2007). Species richness has been shown to affect networks metrics, as detected, for example, in plant–hummingbird networks, which are more specialized in richer communities (Dalsgaard et al. 2011). Accordingly, species richness strongly influences network architecture, reducing nestedness and increasing modularity in plant–pollinator networks (Spiesman and Inouye 2013). These findings support the idea that network metrics also vary in response to latitude. For example, in plant–pollinator networks specialization increases towards the tropics (Zanata et al. 2017), whereas in plant–frugivore networks the opposite occurs (Schleuning et al. 2012). On the other hand, antagonistic networks, as plant–herbivore and host–parasitoid networks, seem to be structured independently of latitude (Morris et al. 2014, de Araújo 2016). These contrasting results suggest that biotic interactions respond differently to latitude (Schemske et al. 2009), according to the taxonomic group or type of interaction.

Environmental conditions vary according to latitude and these abiotic conditions can act for molding morphologies (Schöb et al. 2012). Ecological processes mediated by species interactions are suitable systems to investigate whether species' traits affect their functional roles (Dáttilo and Rico-Gray 2018). The use of trait-based and phylogenetic tree-based proxies lies in the idea of niche complementarity, whereby species with similar functional traits and thus partially overlapping niches are expected to perform similar and, to a certain degree, redundant, ecological roles (Pigot et al. 2016). Frugivores with distinct traits tend to be more functionally specialized, interacting with plants that are less frequently visited by other members of the community, thus increasing specialization (Junker et al. 2012, Maglianesi et al. 2015, Watts et al. 2016, Tinoco et al. 2017) and modularity (Maruyama et al. 2014, Morente-López et al. 2018) of networks. On the other hand, it was not detected an effect of species' traits on metrics of host–parasitoid networks (Morris et al. 2014). Regarding food-webs, it was demonstrated that species traits affect their trophic structure (Petchey et al. 2008), although there is no study testing their influence on network metrics. The architecture of an interaction network can also be influenced by the phylogeny of the component species (Cattin et al. 2004, Brito et al. 2014). Species that are phylogenetically closely related may have more similar dietary preferences or parasite communities than unrelated species (Krasnov et al. 2012, Fontaine and Thébault 2015). In addition, if interspecific differences in species traits is a result of differences on phylogenetic histories, it may also affect network metrics (Minoarivelo et al. 2014, Schleuning et al. 2014). Indeed, it was demonstrated that phylogenetic distance among species affects nestedness and modularity in mutualistic networks (Rezende et al. 2007, Schleuning et al. 2014, but see Ponisio and M'Gonigle 2017), as well as in antagonistic plant–herbivore networks (Fontaine and Thébault 2015) and in host–parasitoid networks (Krasnov et al. 2012, Brito et al. 2014, but see Campião et al. 2015). In spite of the possible relation between phylogeny and species traits, these drivers can influence network metrics in different ways (Ponisio and M'Gonigle 2017), according to the network type and location.

Regardless of the growing number of network studies in the last decade, few evaluated the structure of antagonistic networks in large spatial scales (Morris et al. 2014). And those which did it focused mainly on marine and freshwater food-webs involving fishes (Belgrano 2005, McClanahan and Branch 2008, Kéfi et al. 2015), evidencing the need for further studies for terrestrial organisms (Dobson 2009). Anurans play an important role in the food webs as they represent a link between terrestrial and aquatic environments (Duré et al. 2009). Despite the fact that there are several studies of anuran diets, mainly in the tropics (Duellman 1978, Toft 1980, Vignoli et al. 2009, Menin et al. 2015), most of these studies are locally constrained in space and time and aimed to describe the food repertoire of a small subset of anurans. Therefore, this abundance of scattered empirical evidence asks for broader approaches that unravel the structure of anurans–prey networks in a wider context, indicating the main forces that determine their structure on a global scale.

Herein, we describe the structure of antagonistic anuran–prey interactions from a wide range of geographical areas, using a network approach. We expect that anuran–prey networks will present high connectance and low values of nestedness, modularity and complementary specialization in relation to other types of interaction networks. Connectance would be elevated because anuran's diet is usually highly generalized (Vignoli and Luiselli 2012). Anurans usually eat what is available in the environment with no preference for any type of prey. The only constraint is the relationship prey/mouth-size, because mouth dimensions tend to restrict the upper limit of prey size they can consume (Duellman and Trueb 1986). Thus, the number of links between anurans and preys would be high, increasing connectance. In addition, network metrics can be driven by different ecological factors (Dáttilo and Rico-Gray 2018). Here we tested the influence of latitude, and of anuran taxonomic, functional and phylogenetic richness on networks metrics. We expect: 1) a latitudinal effect on networks metrics, because there are more species of anurans (Wiens 2007), prey availability (Novotny et al. 2006, Roslin et al. 2017), and biotic interactions (Schemske et al. 2009) in the tropics, which would lead to lower values of nestedness, complementary specialization and modularity in networks of high latitudes when compared to their low latitudes counterparts. This expected pattern agrees to the recorded for mutualistic networks and other food-web systems (Schleuning et al. 2012, Saporiti et al. 2015). 2) As in the tropical region communities richness, as well as functional and phylogenetic diversity are higher (Petchey and Gaston 2002) than in the temperate region, we expect that the abundance of specialists' would be higher in tropical region, leading these networks to be more nested than in the temperate region. Nestedness indicates that specialists' diet would be a subset of the generalists' diets. On the other hand, this higher abundance of specialists in the tropics would result in higher values of complementary specialization and modularity in relation to temperate region.

Material and methods

We compiled interactions using a globally distributed database of anurans and their preys, after a comprehensive review of the literature (Supplementary material Appendix 1 Table A1). We searched for studies in the Web of Science (<https://webofknowledge.com/>) and Scopus (<https://www.scopus.com>) databases, using the keywords 'Trophic ecology OR Feed* OR Diet*' and 'assemblage structure' and 'trophic overlap OR trophic plasticity OR niche breadth OR Autoecol*' up to 2017. In addition, we gather all data from direct searches of references in Google Scholar (<https://scholar.google.com.br/>), and got unpublished data by private correspondence with researchers active within the subject field. Among these compiled references, we selected only studies presenting data on diet and including at least three syntopic species of anurans. This minimum value was established because studies on anurans' diet are scarce in the temperate region, and species richness are characteristically low (Wiens 2007, Marin and Hedges 2016). From each of the selected studies data on taxonomic information on anurans (only species identified at least to genus level) and prey categories (usually to order, with exception of the family Formicidae and suborder Isoptera), prey abundance in stomachs as well as country and geographical coordinates of the study site were recorded. In studies of anurans diet, preys are usually identified only at the level of order (categories) because of their fragmentation

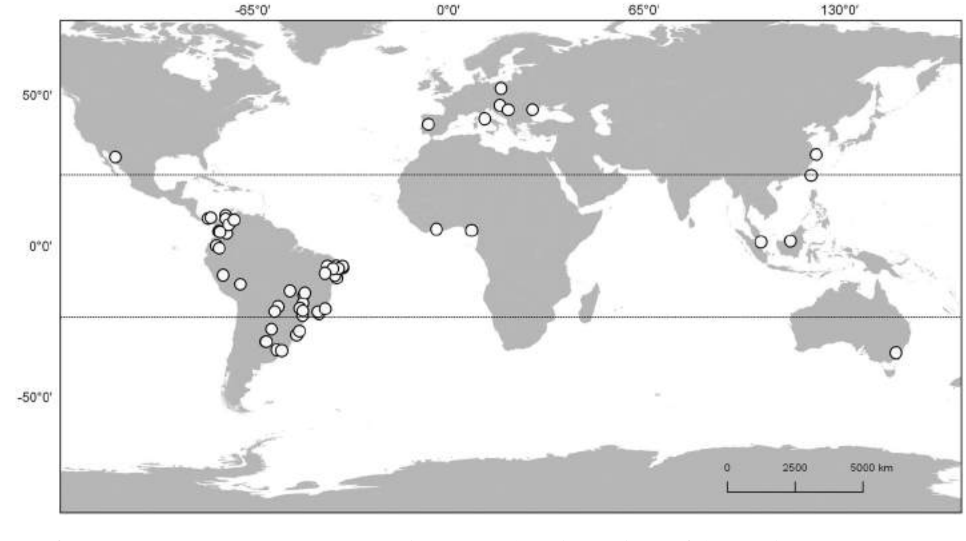

Figure 1. Distribution of 55 anuran–prey interaction networks included in the analysis of this study.

after consumption, being impossible to a finer identification (Duellman 1978, Toft 1980, Ceron et al. 2018).

We compiled a total of 55 weighted anuran–prey interaction networks, with 39 located in tropical and 16 in temperate regions (Fig. 1, Supplementary material Appendix 1 Table A1). For each study site, we built up weighted matrices of interactions containing the anuran species as columns and their prey categories as rows. In these matrices, predation interaction was represented by their interaction abundance. Interaction abundance represents the number of each specific prey ingested by the anuran. We used weighted networks because they better reflect dependencies among species and the structure of interaction networks (Vázquez et al. 2005, Lewinsohn et al. 2006a). Additionally, metrics based on weighted networks have been shown to be less sensitive to sampling bias than those based on binary networks (Banašek-Richter et al. 2009, Dormann et al. 2009, Fründ et al. 2016, Vizentin-Bugoni et al. 2016). Additionally, for data visualization, we also built up a meta-network compiling all these 55 networks together, one meta-network combining the 39 tropical sites, and another one combining the 16 temperate sites (Fig. 2). For graphical representation of the networks, we used the PAJEK software (<http://pajek.imfm.si/doku.php?id=pajek>).

Measuring network metrics

We calculated six network metrics commonly used to describe distinct aspects of the network structure. These metrics were calculated separately for each of the 55 networks.

Network size refers to the total number of anurans and the prey categories they consumed. It can be calculated as species richness and indicates the maximum possible number of interactions (Olesen and Jordano 2002). We also measured the *Mean number of links per species*, which corresponds to the total number of links observed in the network divided by the total number of species (Dormann et al. 2008).

Connectance describes the ratio between the total number of realized 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 distributed within the community (Jordano 1987).

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 corresponds to a subset of the interaction partners of generalist species (Bascompte et al. 2003). We calculated the weighted nestedness (wNODF), which is based on the

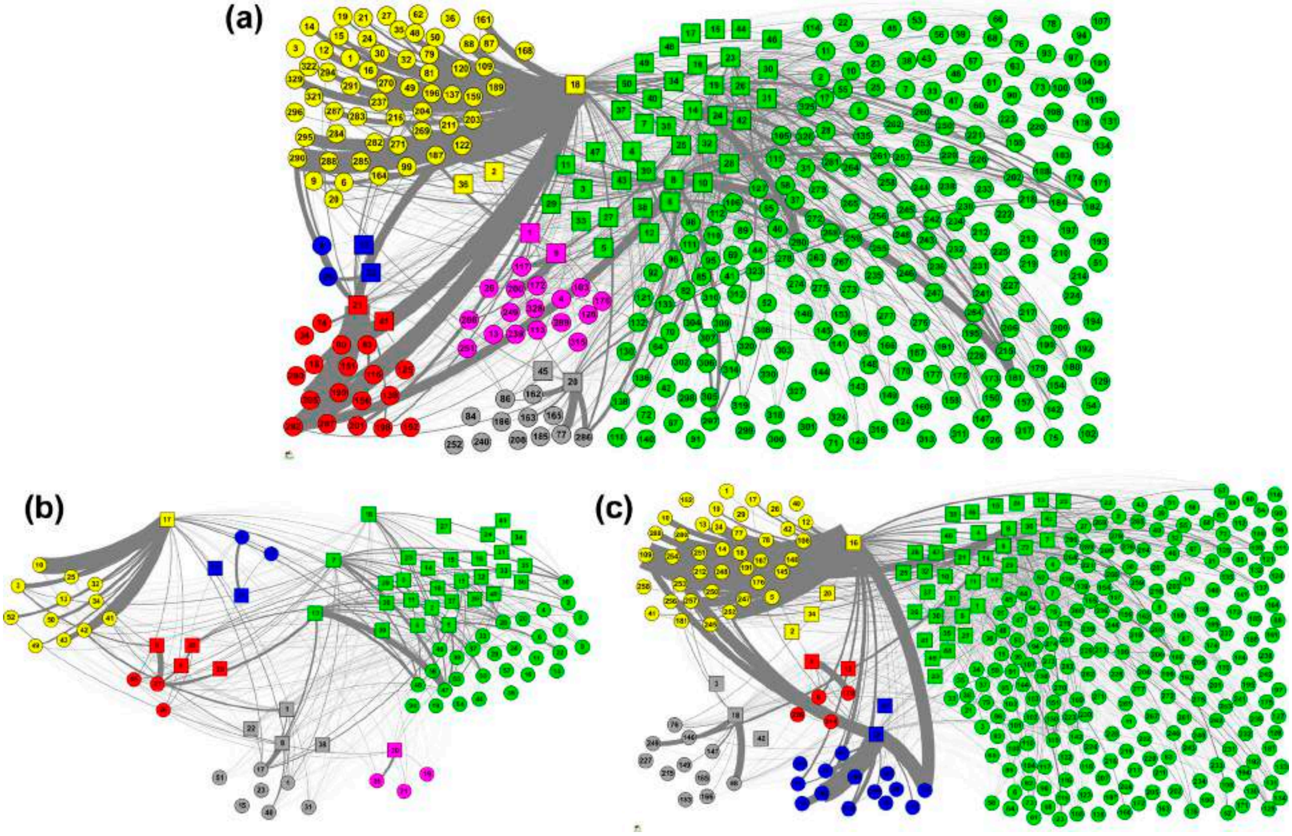

Figure 2. (a) Graphs showing modules in the compiled anuran–prey meta-network including 55 networks worldwide, (b) the meta-network combining 16 temperate sites and (c) the meta-network combining 39 tropical sites. Boxes represent prey categories and circles denote anuran species. Widths of connecting lines (grey) indicate the relative number of observed interactions (Supplementary material Appendix 1 Table A2 to numbers legend).

overlap and decreasing fill in the weighted matrix (Almeida-Neto and Ulrich 2011). Nestedness values ranges from 0 (non-nested network) to 100 (perfect nesting).

Modularity is a network property that emerges when groups of species are densely connected and have sparser connections to other groups of interacting species. The organization of interactions into modules may reflect similarity of traits, phylogeny, biogeography and climate among species, providing information on how the interactions are partitioned in the community (Maruyama et al. 2014, Araujo et al. 2018). We analyzed modularity using the recently implemented LPAwb + algorithm (Liu and Murata 2010, Beckett 2016). LPAwb+ algorithm uses label propagation and multi-step agglomeration to attempt to maximize modularity in networks (Beckett 2016). Also, it is currently the most used algorithm to calculate modularity in biological systems such as interactions between plants and pollinators and food webs. Besides that, the LPAwb+algotithm robustly identify partitions with high modularity scores, showing to be efficient for the detection of subgroups in ecological networks (Beckett 2016).

Complementary specialization (H_2') is derived from two-dimensional Shannon entropy, and quantifies the niche partitioning among species considering partner availability (Blüthgen et al. 2006, Zanata et al. 2017). Thus, it is interpreted as a measure of interactions´ 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.

In order to compare network metrics obtained for the anuran–prey networks with those recorded for other network types, we applied linear mixed models (LMMs) following the same procedures adopted by Naranjo et al. (2019). For this purpose we used data on epiphyte–phorophyte, as well as on mutualistic (seed dispersal, pollination, ant–myrmecophyte) and parasitic networks (bat–fly and fish–parasite), obtained in Naranjo et al. (2019) and specific literature (Lima et al. 2012, Bellay et al. 2015, Zarazúa-Carbajal et al. 2016, Durán et al. 2019, Vizentin-Bugoni et al. 2019). Linear mixed models were fitted using the 'lme4' package in R (Bates et al. 2015).

Null-model corrections of network metrics

To assess the significance of the network metrics wNODF, modularity and H_2', we compared the observed values to those generated by null models. We used the Patefield algorithm (Patefield 1981) to generate simulated matrices with the same marginal totals as the original network so that species interacting with highest or lowest frequencies in the observed matrices were the same in the simulated ones (Patefield 1981). We used the Patefield algorithm because it keeps the number of interactions constant (i.e. the same as in the original matrix) when simulating the null models. For each of the observed networks, we generated 1000 randomized matrices to estimate nestedness and complementary specialization and 100 to estimate the modularity. We used fewer randomizations for modularity because their calculation requires excessively time-consuming algorithms (Olesen et al. 2007, Zanata et al. 2017). For each of the randomized networks, we calculated the network metrics following the same procedure as adopted for the observed networks. To quantify the departure of the observed network values from the null expectation, we calculated null-model corrected values by subtracting the observed metric value from the mean value across all randomized networks (Δ – transformation). Then, the Δ – transformed value was divided by the standard deviation of values across all randomized networks (z – transformation; Dalsgaard et al. 2017, Zanata et al. 2017). All network metrics and null models were calculated with the 'bipartite' ver. 2.08 package (Dormann et al. 2008) in R ver. 3.4.0 (<www.r-project.org>).

Sampling completeness and intensity

Food web metrics are useful for comparisons to other food webs in order to detect regularities in respect to their structure (Banašek-Richter et al. 2004). Detected network patterns may be biased depending on the sampling effort employed and the metrics considered (Vizentin-Bugoni et al. 2016). To avoid such bias we estimated sampling intensity following Schleuning et al. (2012) and sampling completeness following Chacoff et al. (2012) and Vizentin-Bugoni et al. (2016). Sampling intensity was defined as the square-root of the number of interaction events in the network divided by the square-root of the product of the number of anuran and preys in the network (Schleuning et al. 2012). Using abundance data and the Chao 1 estimator of species richness (Magurran 2013), we estimated the total number of anurans–prey interactions in each community. After, we calculated sampling completeness dividing the observed by the estimated richness of interactions (Chacoff et al. 2012). The Chao 1 estimator was calculated with the 'iNEXT' ver. 2.0.12 package (Hsieh et al. 2016) in R ver. 3.4.0 (<www.r-project.org>).

Path analysis for the association between network metrics and their predictors

Given that networks are influenced by structural factors like latitude (Dalsgaard et al. 2017), richness (Jordano 1987), phylogeny (Schleuning et al. 2014), species traits (Bastazini et al. 2017) and sampling metrics (Vizentin-Bugoni et al. 2016), our main goal was to split the effects of different factors on the network metrics based on a priori causal assumptions (Table 1). In order to calculate the functional richness of sites, data on species traits such as habitat use (fossorial terrestrial, aquatic or arboreal), body size (snout-vent length, SVL), breeding strategy (development direct, larvae or viviparous) and reproductive modes (number of reproductive mode, see Crump 2015) from anurans were obtained from AmphiBIO_ver. 1. (Oliveira et al. 2017) and specific literature (Duellman and Trueb 1986,

Table 1. Overview of the path model components showing the influence of explicative variables (path from) on network metrics.

	Rationale	Reference
	Path from	
Anuran richness	The tropical region harbors a higher diversity of anurans than the temperate region. Besides that, adaptations to some combination of abiotic conditions and biotic interactions allow tropical species to be more specialized, dividing resources more finely among more species. This niche separation in tropics leads to different levels of complementary specialization, modularity and nestedness in the networks	Jordano 1987, Hillebrand 2004, Wiens 2007, Brown 2014
Latitude	Network metrics tend to be influenced by latitude in mutualistic systems and in food-webs, but not in bipartite antagonistic networks like host–parasitoid and plant–herbivore	Guilhaumon et al. 2012, Trøjelsgaard and Olesen 2013, Morris et al. 2014, Saporiti et al. 2015, de Araújo 2016
Functional richness	It is well established that species' traits influence networks metrics through complementary specialization in mutualistic networks. As anurans' functional traits influence their diet, we expect such traits to reflect in the network metrics such as complementary specialization	Bascompte et al. 2003, Petchey et al. 2008, Bastazini et al. 2017, Maruyama et al. 2018
Phylogenetic richness	Phylogenetic richness, the phylogenetic volume filled by the global pool of taxa calculated from the phylogenetic distance between species, may influence their position in networks. In mutualistic systems and in antagonistic plant–herbivore networks, the phylogenetic signal can affect network metrics	Schleuning et al. 2014, Fontaine and Thébault 2015
Control variable		
Sampling effort	Different sampling efforts bias network metrics. Given that our data fits such scenario with different sampling efforts, we have controlled this effect in the network metrics	Vizentin-Bugoni et al. 2016

Haddad et al. 2013, Crump 2015). Pairwise functional distances between all functional entities were computed using the Gower distance, which allows mixing different types of variables while giving them equal weight (Legendre and Legendre 2012). For evolutionary history, we use a phylogeny proposed by Jetz and Pyron (2018), which includes all 304 anuran species registered in our dataset. We calculated pairwise phylogenetic distances among all pairs of anurans using the cophenetic distance (PDist) based on branch lengths (Sneath and Sokal 1973, Parker et al. 2015). Then, principal coordinates analysis (PCoA) were performed using the functional distance and phylogenetic distance matrix separately. Functional and phylogenetic entities coordinates on the first three principal axes (PC) of this PCoA were kept to build a multidimensional functional and phylogenetic space (Villéger et al. 2011, Mouillot et al. 2014). After, we calculated the volume of the multidimensional functional and phylogenetic space using the package 'geometry' (Habel et al. 2015) in R ver. 3.4.0 (<www.r-project.org>). Similarly, functional and phylogenetic richness of each site were measured as the volume inside the convex hull shaping all of the functional and phylogenetic richness recorded worldwide. These raw volumes were then standardized by the volume filled by the global pool of taxa to obtain values constrained (Villéger et al. 2011). Thus, functional and phylogenetic richness represents the amount of functional or phylogenetic space filled by each network in relation to the total volume filled by the global pool of taxa (Villéger et al. 2008 for details on method). Therefore, we performed a path analysis using the sampling metrics as control variable to observe the raw effect of structural factors (latitude, species richness, functional and phylogenetic richness) on network metrics. The path analysis was performed using 'lava' package (Holst and Budtz-Jørgensen 2013) in R ver. 3.4.0 (<www.r-project.org>). In order to detect spatial autocorrelation in our data we checked the path analysis residuals using Moran's I with 'ape' package (Paradis et al. 2004) in R ver. 3.4.0 (<www.r-project.org>).

Results

Anuran richness for the 55 networks analyzed separately ranged from three to 64 species ($\bar{x} = 10.01 \pm 12.1$), and the prey richness ranged from four to 30 categories ($\bar{x} = 17.89 \pm 5.88$). Among the 50 prey categories registered, 42 are Arthropoda, six are Chordata, one is an Annelida and one a Mollusca. Coleoptera was the most frequent category (62.57%) and Hymenoptera (Formicidae) was the most abundant item (ca 56000 items), followed by termites (Isoptera) (ca. 20000 items). The size of networks varied from 27 to 1539 nodes ($\bar{x} = 196.7 \pm 286.3$). The number of links per anuran species varied from 1.36 to 4.94 ($\bar{x} = 2.42 \pm 0.16$).

Mean connectance for the 55 networks analyzed varied from 0.25 to 0.89 ($\bar{x} = 0.55 \pm 0.16$). Nestedness varied from 25.29 to 67.29 ($\bar{x} = 44.2 \pm 7.45$), but none of the communities were significantly nested. On the other hand, networks were significantly modular ($p < 0.05$) with values ranging between 0.04 to 0.56 ($\bar{x} = 0.24 \pm 0.12$). The number of modules varied from 2 to 6 ($\bar{x} = 3.1 \pm 0.83$). Complementary specialization ranged from 0.04 to 0.67 and was significant ($p < 0.05$) for most (96.36%) of the networks ($n = 53$). However, the mean specialization observed on networks were low ($\bar{x} = 0.32 \pm 0.15$). Sampling completeness of networks

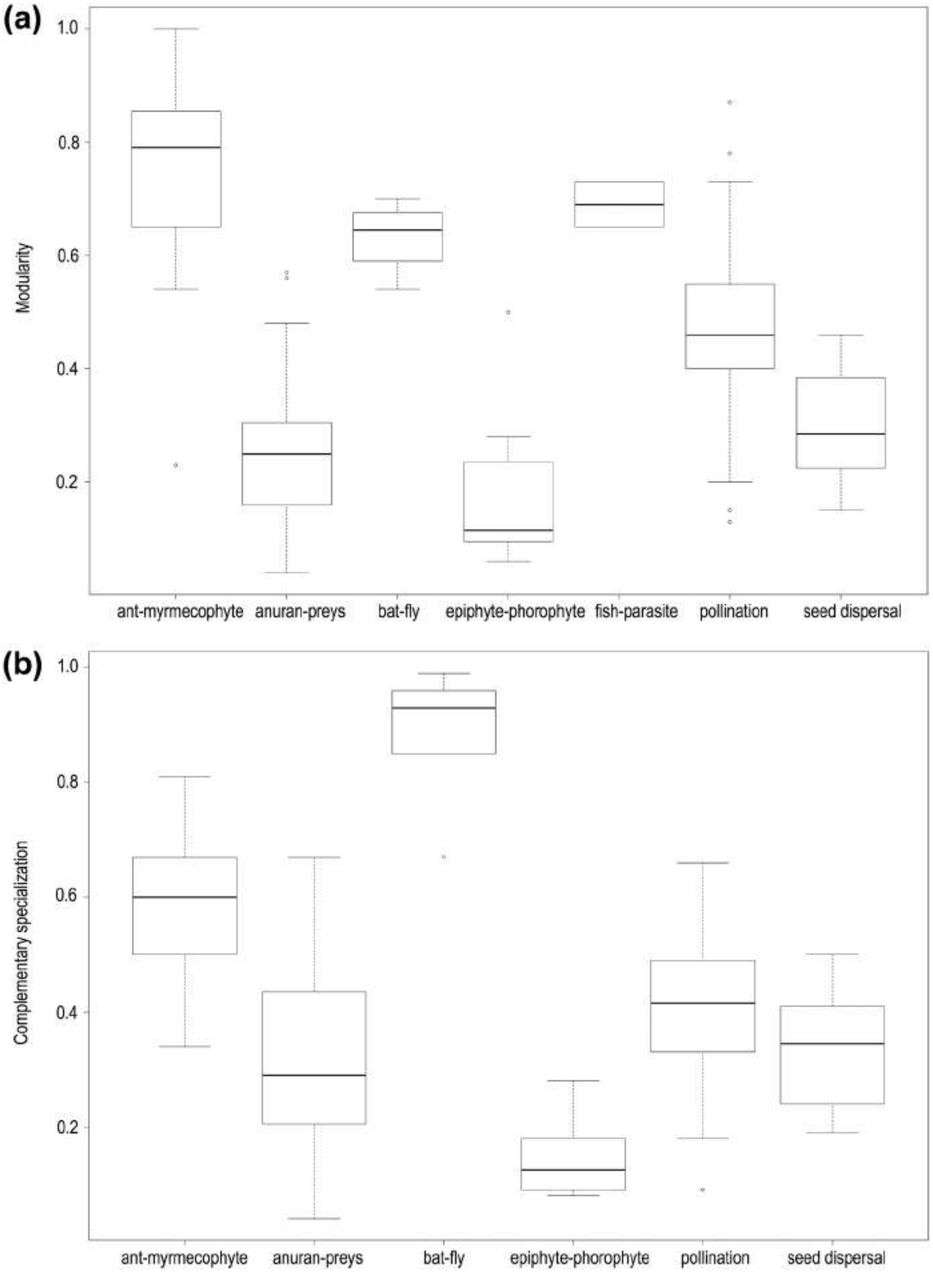

Figure 3. Variation in network metrics across network interaction types: anuran–prey, commensalistic epiphyte–phorophyte, bat–fly, fish–parasite, seed dispersal, pollination, ant–myrmecophyte, networks. (a) Modularity, (b) complementary specialization.

was high ($\bar{x} = 81.08 \pm 13.13\%$), ranging from 40.65 to 100%. Intensity varies from 0.7 to 5.96 ($\bar{x} = 2.49 \pm 1.37$).

Modularity and complementary specialization varied significantly among the different types of networks analyzed (all LMM tests; $p < 0.0001$; Fig. 3, see Supplementary material Appendix 1 Table A3). They were significantly lower in the anuran–prey networks than in the rest of the networks, with the exception of epiphyte–phorophyte networks (Fig. 3, all tests: $p < 0.01$). Network size influenced specialization values (LMM tests: $p = 0.09$; see Supplementary material Appendix 1 Table A3), but did not significantly affect modularity (LMM tests: all $p = 0.1$; see Supplementary material Appendix 1 Table A3). The variance explained by the entire model (Rc^2) ranged between 0.46 and 0.54 [Supplementary material Appendix 1 Table A3], with the variance explained by fixed factors (Rm^2) representing a large fraction in all cases (53–54%).

Path analysis showed that part of the effects of complementary specialization, nestedness and modularity are mediated by changes in latitude, sampling metrics, anuran richness, functional and phylogenetic richness (Fig. 4, Supplementary material Appendix 1 Table A3). We did not detect any spatial

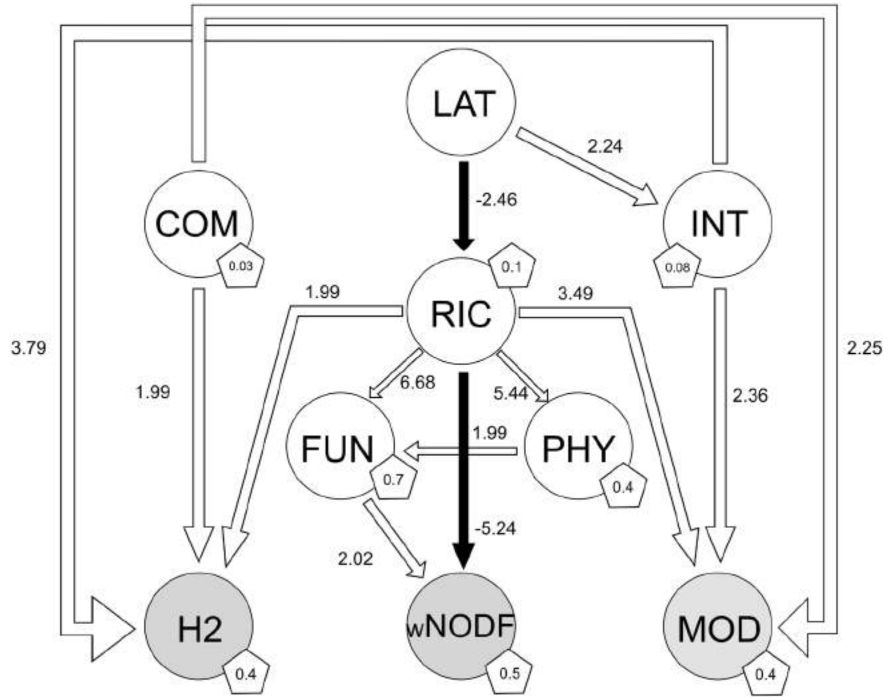

Figure 4. Path diagram showing statistically significant positive (white arrow) and negative (black arrow) influences of variables on network metrics (grey circles), where: LAT (latitude), RIC (anuran richness), FUN (functional richness), PHY (phylogenetic richness), INT (sampling intensity), COM (sampling completeness), H_2 (complementary specialization), wNODF (weighted nestedness) and MOD (modularity). Numbers in diamonds represent the r^2 values and numbers on arrows represent beta values.

structure for none of the response variables in our model ($p > 0.33$ for all variables). The fit index indicated a good fit between the model and the data ($RMSEA = 0.515$; $p < 0.05$). Sampling metrics (completeness and intensity, respectively) directly influenced complementary specialization ($\beta = 3.79$; $\beta = 1.99$) and modularity ($\beta = 2.36$; $\beta = 2.25$). Anuran richness was spatially structured, being higher towards the tropics ($\beta = -2.46$) and had effects on the functional and phylogenetic richness ($\beta = 6.68$; $\beta = 5.44$, respectively), with richer communities tending to be phylogenetic and functionally richer.

Latitude indirectly affected complementary specialization via richness ($\beta = -2.46 \times 1.99 = -4.89$), with tropical communities tending to be richer and to present greater specialization than the temperate ones. Likewise, latitude influenced complementary specialization mediated by sampling intensity ($\beta = 2.24 \times 3.79 = 8.48$), causing a total effect of 3.59 ($\beta = -4.89 + 8.48$), which indicates that temperate communities are better sampled, resulting in higher values of complementary specialization.

Nestedness was also indirectly affected by latitude, mediated by anuran richness ($\beta = -2.46 \times -5.24 = 12.89$). Temperate communities showed lower anuran richness, which resulted in higher values of nestedness. Similarly, latitude negatively influenced nestedness mediated by anuran richness and functional richness ($\beta = -2.46 \times 6.68 \times 2.02 = -33.19$), as well as by functional and phylogenetic richness, resulting in a total effect of – 53.79 ($\beta = -2.46 \times 5.44 \times 1.99 \times 2.02$). Richer communities tend to be phylogenetic and functionally more diverse, resulting in lower values of nestedness.

Modularity was indirectly affected by latitude, mediated by anuran richness ($\beta = -2.46 \times 3.49 = -8.58$). Poor communities tended to be less modular than richer communities. In addition, latitude indirectly affected modularity via sampling intensity ($\beta = 2.24 \times 2.36 = 5.28$), with temperate communities tending to be better sampled as denoted by their higher values of sampling intensity and completeness ($\beta = 2.25$). These resulted in higher values of modularity.

Discussion

We found that anuran–prey networks are not nested, exhibit high connectance and low complementary specialization and modularity when compared to other network types. The main effects on network metrics were mediated by changes in latitude, anuran richness, functional and phylogenetic richness.

The diet of anurans is generally based on arthropods (Duellman 1978). Among prey categories, Coleoptera was the most frequent and connected with a great number of anuran species, both in temperate and tropical networks. In addition, Formicidae and Isoptera were the most consumed prey categories. The worldwide elevated richness of Coleoptera, allied to the fact that ants and termites have eusocial habits and form big colonies, make these orders locally abundant, probably explaining their high abundance in the networks (Davidson et al. 2003, Rafael et al. 2012).

The pattern that emerged in the anuran–prey networks in a global scale is different from that reported for other antagonistic networks, such as host–parasitoid (Morris et al. 2014, Bellay et al. 2015) and marine food-webs (Dunne et al. 2004). The anuran–prey networks presented low complementary specialization and modularity in relation to other networks types, and high values of connectance, as we hypothesized. However, contrary to our expectations, our networks were not nested. These results can be attributed to the community structure of anurans resulting in effects on their diversity and local abundance (Jordano 1987, Lewinsohn et al. 2006b), as well as on their generalist and opportunistic food habits (Vignoli and Luiselli 2012). Community structure affects the connectance, as elevated values occur when the number of links in a network is close to the network size, indicating high generalization (Jordano 1987), as observed herein. Likewise, the generalist and opportunistic habits of anurans result in wide and non-restrictive diets and, consequently, in low values of complementary specialization (Blüthgen et al. 2006). In addition, the more specialized anurans did not feed exclusively on one item, but feed it more frequently than others, which lead to low values of complementary specialization and modularity (Toft 1980). This finding is similar to the recorded for epiphyte–phorophyte networks, which are modular, in spite of their low values of specialization (Naranjo et al. 2019). However, values of complementary specialization should be used for comparisons with care, because this metric is highly sensitive to sampling bias (Blüthgen 2010).

Anuran and insect richness are both affected by latitude (Hillebrand 2004, Wiens 2007). And we did detect a direct effect of latitude on anuran richness and sampling intensity. The latitudinal effect on richness is a well-known pattern, with the tropical region harboring higher diversity than temperate regions (Fischer 1960). In this sense, the number of anuran species and interactions are expected to be lower in temperate areas (Wiens 2007, Schemske et al. 2009). Consequently, sampling intensity tends to be higher in temperate than in tropical regions, where interactions tend to be more numerous due to higher species richness. Indeed, networks metrics have already been reported to be sensitive to sampling intensity (Fründ et al. 2016). In the same way, the influence of anuran richness on functional and phylogenetic richness was expected because richer communities tend to harbor higher phylogenetic and trait diversities (Diamond 1975).

The results of the latitudinal effect confirm our hypothesis, since we found indirect effects of latitude in all networks metrics. This result was similar to those that emerged in mutualistic networks, where some networks metrics tend to be influenced by latitude (Schleuning et al. 2012, 2014, Trøjelsgaard and Olesen 2013, Dalsgaard et al. 2017). Instead, in host–parasite networks, latitude did not influence network metrics (Guilhaumon et al. 2012, Morris et al. 2014). The indirect effect of latitude mediated by anuran richness on complementary specialization is explained because tropical communities tend to be richer than their temperate counterparts, resulting in higher specialization, because there are more chances of a species to be a specialist in a diverse community (Schemske et al. 2009), as indicated by path-analysis.

None of the communities were significantly nested. Nestedness occurs when interactions of less connected elements form proper subsets of the interactions of more connected elements. Thus, nestedness decrease when there is high connectance (Cantor et al. 2017), as observed in this study. The high generalization of anuran networks emerged from anurans generalist habits minimizing nestedness.

As predicted, we detected a positive effect of functional richness on nestedness, although values were not significant. We did not find any direct effect of phylogenetic richness on nestedness as hypothesized. However, phylogenetic richness indirectly influenced nestedness via functional richness. This effect starts with latitude, passing by anuran richness and phylogenetic richness. The relation and effects of phylogenetic similarity and species traits are a recurrent pattern in food webs (Cattin et al. 2004, Naisbit et al. 2012). In fact, in a study performed with 13 food-webs, it was demonstrated that body size and phylogenetic similarity are correlated and determine the trophic structure of those webs (Naisbit et al. 2012). Moreover, phylogenetic constraints can explain some empirical food web patterns as intervality, and species abundance mediated by body size (Cattin et al. 2004). Thus, these evidences suggest that the combined effects of phylogenetic and functional richness on nestedness are stronger than the effect of functional richness alone.

Modularity is an emerged pattern in pollination and seed-dispersal networks (Olesen et al. 2007, Schleuning et al. 2014). One of the possible explanations for creating modules in these networks is that modules are composed by groups of species with convergent traits and with the functional interdependence (Schleuning et al. 2014). The detected effect of richness on modularity can be explained because greater species richness can be associated with a high range of anuran sizes and habits. These differences may lead to the formation of modules, assembling some species (e.g. specialists, small sized and terrestrial species) with different characteristics from that in other modules (e.g. generalists, big-sized and arboreal species; Woodward and Hildrew 2002, Woodward et al. 2005, Olesen et al. 2007). A possible explanation for the detected modularity in the anuran–prey networks is that small-sized species may behave like specialists, preying only small insects, because of the relationship among frog body/mouth size and prey volume and size (Toft 1980). And big-sized anurans act as generalist species, preying insects of a different size range, causing modularity. Similarly, terrestrial species will prey different categories compared to arboreal species, being these groups assigned to different modules. Besides, communities most highly connected tend to exhibit nestedness or modularity properties (Fortuna et al. 2010), a pattern confirmed here, where anuran–prey communities exhibited high connectance and a modular pattern (even if lower than the detected in other types of interaction networks) with no nestedness. Despite this, the detected influence of latitude in modularity for our anuran–prey networks, is similar to the recorded in pollination and frugivore networks, where modularity increases with latitude (Dalsgaard et al. 2013, Schleuning et al. 2014). This is also related to the greater species richness in low latitudes (Hillebrand 2004, Wiens 2007).

Our study is the first integrated analysis of structural patterns among networks of antagonistic interactions between anuran and their preys, including information from different parts of the world. In conclusion, our results show that anuran–prey networks have high connectance and low complementary specialization and modularity in relation to other network types, and that they are shaped by latitude, anuran richness, functional and phylogenetic richness. Altogether, our results indicate that there is a latitudinal pattern in anuran–prey networks metrics, as previous mutualistic macroecological studies have shown. Latitude indirectly influenced network metrics via anuran richness and functional and/or phylogenetic richness. Furthermore, the pattern emerged in anuran–prey networks metrics reflect the generalist and opportunistic habits of anurans diet. We provide novel information on predator–prey interaction networks in a global scale, concluding that different processes are modeling the architecture of anuran–prey networks, mainly mediated by latitude.

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RESEARCH ARTICLE

Seasonal patterns of ecological uniqueness of anuran metacommunities along different ecoregions in Western Brazil

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Abstract

Beta diversity can be portioned into local contributions to beta diversity (LCBD), which represents the degree of community composition uniqueness of a site compared to regionally sampled sites. LCBD can fluctuate among seasons and ecoregions according to site characteristics, species dispersal abilities, and biotic interactions. In this context, we examined anuran seasonal patterns of LCBD in different ecoregions of Western Brazil, and assessed their correlation with species richness and if environmental (climatic variables, pond area and ecoregions) and/or spatial predictors (spatial configuration of sampling sites captured by distance-based Moran's Eigenvector Maps) would drive patterns of LCBD. We sampled anurans in 19 ponds in different ecoregions in the Mato Grosso do Sul state, Western Brazil, during one dry and one rainy season. We found that LCBD patterns were similar between seasons with sites tending to contribute in the same way for community composition uniqueness during the dry and rainy season. Among studied ecoregions, Cerrado showed higher LCBD values in both seasons. In addition, LCBD was negatively correlated with species richness in the dry season. We also found that LCBD variation was explained by ecoregion in the dry season, but in the rainy season both environmental and spatial global models were non-significant. Our results reinforce the compositional uniqueness of the Cerrado ecoregion when compared to the other ecoregions in both seasons, which may be caused by the presence of species with different requirements that tolerate different conditions caused by seasonality.

Introduction

Understanding the organization of species diversity through space and time is one of the main scopes of community ecology [1]. Species diversity can be divided into gamma (regional diversity), alpha (local diversity), and beta components [2]. The latter (beta diversity) is the variation in species composition among sites within a region, first described by Whittaker [2, 3].

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Such variation can be related to ecological processes, so analyzing beta diversity patterns can shed light on the comprehension of mechanisms underlying biodiversity patterns [4]. Beta diversity can be measured in different ways, including additive and multiplicative indices, dissimilarity measures, and beta diversity as variation in community structure among sampling units [4]. These methods include the partition of the variance of community data into species contributions to beta diversity (SCBD) and into local contributions to beta diversity (LCBD) [5]. LCBDs represent the degree of community composition uniqueness of a site compared to regionally sampled sites [5] and constitute an important tool to detect more unique sites in terms of community composition that can be used to guide conservation strategies and to detect keystone communities [6–8]. Keystone community is defined as communities with a disproportional positive impact relative to their weight in the metacommunity. One simple way to detect keystone communities is through the correlation between LCBD (a measure of the relative site impact in the metacommunity) and species richness (a measure of weight or size of local communities) [7–9]. Keystone communities would be those communities with high impact on metacommunity (high value of LCBD) and low value of species richness [8].

Local contributions to beta diversity can also be used to test if selection and/or dispersal-related processes explain biodiversity patterns [10–12]. Selection by both site characteristics and biotic interactions filters species from the regional species pool to occur in local communities. For example, in a study performed in Brazilian Atlantic Forest, Almeida-Gomes [13] found that larger forest patch sizes are important for amphibian persistence in fragmented landscapes. Dispersal also affects local community dynamics [9, 14]. High dispersal can reduce beta diversity among sites, homogenizing the metacommunity [9]. In contrast, low dispersion or dispersal limitation may increase beta diversity, because organisms cannot reach suitable sites and may increase the role of drift [15], as observed in the Brazilian Atlantic Forest [16, 17].

An increasing number of studies used the partitioning of beta diversity into LCBD and SCBD in a variety of plant and animal taxa to better understand biodiversity patterns [12, 18–22]. However, this method is still poorly explored among ecoregions, which are large units of land containing a distinct assemblage of natural communities and species [23, 24]. Typically, a given ecoregion is similar in structure along its extent, but shares few species with other ecoregions due to biogeographic barriers, species turnover caused by geographical distance, or by environmental and biotic selection [25, 26]. On a global scale, the relationship between dissimilarity in species composition and productivity varied according to ecoregion [27], but information on a finer scale is still scarce. The dissimilarity in species composition in a given region composed of different ecoregions can vary according to climate, vegetation type, disturbance regimes (e.g., fires), and migrations [23].

Besides the spatial variation in community composition, beta diversity can fluctuate over time in the same site, known as temporal beta diversity [28]. Understanding the temporal dynamics of communities can solve fundamental ecological processes, including effects of individual life histories on ecosystem change, the relative importance of biotic and abiotic factors in determining community structure, or how taxa and the networks in which they are embedded respond to environmental change [29]. Community composition changes through time occur due to gains and losses of species, as well as changes in species abundance, resulting from different ecological processes, including environmental seasonality [28, 30]. As consequence, LCDB value also fluctuate among seasons and its association with environmental and spatial factors can change among periods [31]. For example, Tolonen [31] found that drivers of compositional uniqueness of aquatic macroinvertebrates change between spring and autumn, which was mainly related to species life cycle events. The explained variation of compositional uniqueness by environmental variables (e.g., pH, particle size and stream width) decreased from spring to autumn, while the explained variation by the spatial variables increased notably [31]. Similarly, Kong [32] shown that compositional uniqueness of fish changes between the dry and rainy seasons because of the presence of particular species moving back and forth from floodplain habitats. Thus, seasonal variation in compositional uniqueness depend on the life history of organism model and physical characteristics of the study area.

Understanding compositional uniqueness variation between seasons and its drivers may help to identify sites and species with high conservation values or sites that need to be restored [5]. Indeed, assessing variation in composition uniqueness among sites and seasons can improve our understanding on processes that generate and maintain biodiversity. The mid-western Brazil location has a highly seasonal variation in environmental conditions in the Atlantic Forest, Cerrado, Chaco and, Pantanal ecoregions. This region allows us to explore seasonal patterns of compositional uniqueness and compare the relative importance of the potential mechanisms explaining those patterns.

Neotropical anurans are considered excellent ecological models because they are locally abundant and their sampling is relatively easy [33]. Anurans are particularly susceptible to environmental and spatial factors because they have permeable skin, a biphasic life cycle, unshelled eggs and limited dispersal [34]. Most of them are dependent on ponds or water bodies for tadpoles development and adults reproduction. Considering that anuran biodiversity is highly threatened, suffering a severe global decline by virtue of diseases, climate change, and habitat loss [17, 35, 36], understanding spatial and temporal patterns may be highly useful for biodiversity conservation and for detecting sites that disproportionally contribute to regional species pool relative to species richness [5, 7, 8].

We examined anuran seasonal patterns (dry and rainy seasons) of compositional uniqueness (LCBD) in different ecoregions of Western Brazil and their correlation with species richness, thus elucidating possible keystone communities. We also assessed if environmental (climatic variables, pond area and ecoregions) and/or spatial predictors (spatial configuration of sampling sites captured by distance-based Moran's Eigenvector Maps) would drive patterns of LCBD. We expected that LCBD would differ among ecoregions for the dry season, and no difference would be found in LCBD for the rainy season. This expectation is based on the low water availability in dry season compared to the rainy season, when all ecoregions tended to be equal in terms of water availability. This water restriction in the dry season would filter species in naturally seasonally dry ecoregions, such as the Cerrado and Chaco [37], where water availability is a constraint for many species in the dry season [37], leading to more unique communities. We also expected that this filter would be more intensive in the Cerrado because this ecoregion is not close to floodplains that may maintain water availability during the dry season. The Chaco region is close to the Pantanal and both occupy the area under influence of Paraguay Basin flood pulses, which would provide water to anuran reproduction throughout the year. In this way, we expected that the Cerrado ecoregion would have higher values of LCBD compared to other ecoregions in the dry season. We also hypothesized that LCBD variation would be driven by environmental variables in the dry and rainy seasons, but the total amount of variation would be higher in the dry season.

Material and methods

Study area

We sampled anurans in 19 ponds located in Mato Grosso do Sul state, covering the Atlantic Forest, Chaco, Cerrado, and Pantanal ecoregions in Brazil (*sensu* Olson [23], Fig 1 and S1 Table). Typically, the dry season ranges from April to September, and the rainy season extends from October to March in the region. The Atlantic Forest and Cerrado ecoregions support the highest species richness and rates of endemism, and they have been undergoing huge forest

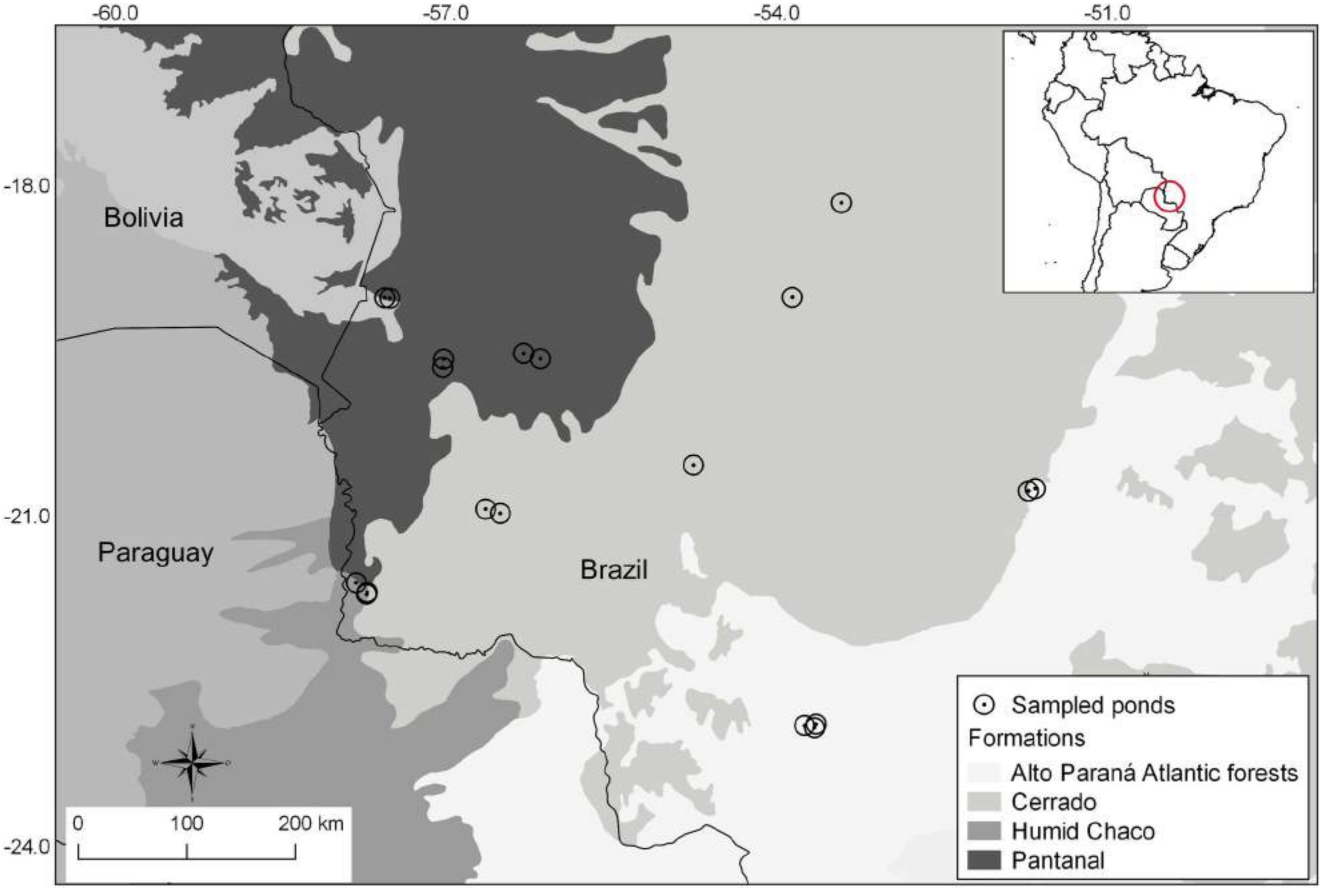

Fig 1. Location of the sampled ponds in West Brazil for each ecoregion (Atlantic Forest, Chaco, Cerrado, and Pantanal).

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loss, being classified as hotspots of biodiversity [38, 39]. Atlantic Forest is characterized by heterogeneous and highly diverse plant species, with lowland, montane, semideciduous, and deciduous forests, but most of them are represented by small fragments [39, 40]. Semideciduous parts of the domain shared many species with neighbouring ecoregions (e.g., Cerrado) [41] and receive in the study region around 1313 mm/year of rainfall [42].

The Cerrado ecoregion is characterized by an extremely variable physiognomy, ranging from open grassland to forest with a discontinuous grass layer [43]. The overall amount of rainfall in the study region of the Cerrado is 1,424 mm/year [42]. The Chaco ecoregion is one of the most threatened subtropical woodland savannas in the world [44, 45]. Vegetation comprises xerophytic forests, alternating with patches of secondary woodlands and scrubs, and in temporarily flooded areas; the vegetation is typically composed of sclerophyllous grasslands. The Chaco ecoregion receive in the study region around 1,161 mm per year of rainfall [42]. The Cerrado and Chaco ecoregions are considered 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 [37]. Pantanal is one of the largest wetlands in the world and is comprised of major vegetation formations: flood-free ridges (ancient levees) inhabited by trees, seasonally flooded plains with grasslands, and water bodies with aquatic macrophytes [46]. Although species diversity is not particularly high and endemism is practically absent, the region is notable for its abundance of wildlife [47]. Annual rainfall in the studied area of the Pantanal is around 1,177 mm [42]. Among the sampled sites, Cerrado is the only one that did not exhibit flood pulses during the rainy season. Cerrado and Pantanal ecoregion show the higher values of precipitation seasonality (55.54 and 59.01 coefficient of variation, respectively) in relation to Atlantic Forest (46.64 coefficient of variation) and Chaco (45.45 coefficient of variation) [42]."

We sampled three ponds in Chaco (CH), five each in Cerrado (CE) and Atlantic Forest (semideciduous forest) (AF), and six in Pantanal (PA), during 2017 and 2018 (Fig 2 and S1 Table). Each pond constituted a replicate. The minimum distance among ponds was 500 m between CE3 and CE4. The remaining ponds were far more than 1 km distance from each

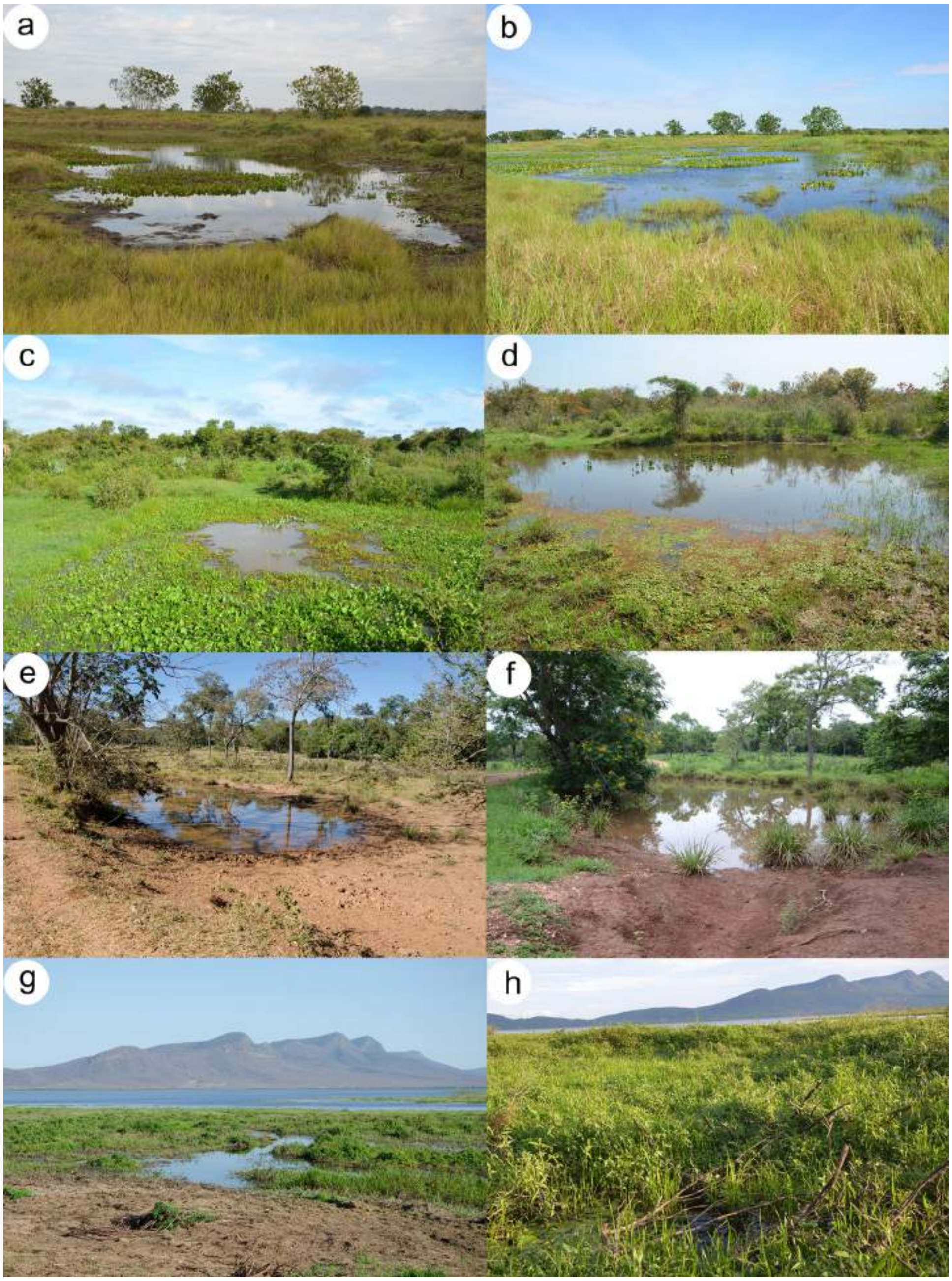

Fig 2. Some sampled sites during the dry and rainy season respectively in a–b) Atlantic Forest, c–d) Chaco, e–f) Cerrado, and g–h) Pantanal.

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other. Each area was surveyed for one day per season during one dry and one rainy season, totalizing six hours of sampled effort per pond per season. We sampled anurans by active search [48] and visual and acoustic encounters conducted during time limited transects [49]. Samplings started on sunset and extended through midnight.

Ethics statement

Anuran sampling was conducted under the permission of Brazilian wildlife regulatory service (SISBIO # 56729–1). The specimen manipulation was carried out following the recommendations of CEUA-UFMS protocol (# 838/2017). The collected individuals were sacrificed with the application of 5% lidocaine on the skin and fixed in 10% formalin, with later conservation in 70% alcohol.

Environmental predictors

We used the location of each pond to extract 19 climatic variables from the BioClim database [42]. These variables cover different aspects of the mean and seasonal variability of temperature and precipitation (for more details see S2 Table). Climate predictors were extracted from raster files with 30 arc-second resolution using 'raster' package [50] in R version 3.5.0 [51]. For each location, we averaged each climatic variable over a 2000 m buffer zone to reduce the effect of uncertainty in study location. In addition, we chose this radius because the home range size of anurans can reach up to 2000 m [52].

Climatic variables were summarized by local contribution to environmental heterogeneity (LCEH), method developed by Castro [53]. To estimate LCEH for each site, we used standardized Euclidean distance [54]. Similar to LCBD, sites with high LCEH have singular environmental conditions while sites with low values have common environmental conditions. In addition to LCEH, we also included three dummy variables representing ecoregion specificities other than climatic (e.g., vegetational structure) and pond area as environmental predictors.

Spatial predictors

We used distance-based Moran's eigenvector maps (dbMEM) on sampling sites' latitude and longitude [55, 56]. First, the minimum spanning tree distance that keeps all sites connected was calculated and used as a truncation threshold to construct the truncated matrix. This matrix was submitted to a Principal Coordinate Analysis (PCoA), and we selected the eigenvectors with significant patterns of spatial autocorrelation, i.e., with significant ($P < 0.05$) and positive Moran's I [57]. The eigenvectors represent spatial structures of relationships among the sampled sites, from broad to fine-scale patterns [57, 58]. We used the selected eigenvectors (MEMs) as spatial predictors in data analyses.

Data analysis

We used the method described by Legendre and De Cáceres [5] to estimate both total beta diversity (BDtotal) and local contribution to beta diversity (LCBD). A community composition matrix (abundance data) was Hellinger transformed and then used to estimate BDtotal as the unbiased total sum of square of the species composition data. The BDtotal will assess LCBD, which is the relative contribution of each sampling unit to beta diversity, i.e., the division of sum of squares corresponding to each sampling unit by the total sum of squares. LCBD was calculated for dry (LCBDdry) and rainy (LCBDrainy) seasons independently.

We used Pearson correlation to assess if LCBD patterns of dry and rainy seasons were correlated. We also used Pearson correlation to assess the relationship between LCBD and species richness. If a negative correlation between LCBD and richness is found, we may detect keystone communities as those that have high LCBD (impact) and low richness (weight) [6, 8].

We used forward selection as implemented by Blanchet *et al.* [59] for significant global models. To select variables from an explanatory matrix, forward selection requires significance ($p<0.05$) and R2adj have to be below the global R2adj [59]. In this way, the explained variance is not overestimated, preventing the inflation of Type I error [59]. For non-significant global, we did not proceed with forward selection and variation partitioning, reporting just significant global model after forward selection. If both global models were significant, we used variation partitioning to divide the LCBD variation of each season into four components: pure environmental component [a], the amount of variation shared by environmental component and spatial component [b], pure specific spatial component [c] and non-explained variation (residual) [d]. The significance [a] and [c] were tested via permutation-based (1000 permutations) tests of partial multiple regressions models.

To perform all analyses, we used R language and the packages 'vegan' [60] 'packfor' [61] and 'adespatial' [62].

Results

We sampled a total of 43 species and 1488 individuals distributed in Atlantic Forest (species = 20; individuals = 296), Cerrado (n = 25; 297), Chaco (n = 21; 289) and in Pantanal (n = 23; 606). On average, species richness tended to be higher in the Chaco ecoregion ($\bar{x}$= 10.3), followed by Atlantic Forest ($\bar{x}$= 8.8), Cerrado ($\bar{x}$= 7.4), and Pantanal ($\bar{x}$= 6.3) (S1 Table). *Dendropsophus nanus* was the most abundant species in Atlantic Forest (n = 64), Cerrado (n = 63), and in Pantanal (n = 138), and *Lysapsus limellum* was the most abundant species in Chaco (n = 62). Overall, species richness was higher during the wet season (n = 37) than the dry season (n = 32), as well as the total abundance (772 and 716, respectively). Atlantic Forest had 19 species in the wet season and 11 species in the dry season, while Cerrado had 21 and 14 species, in the wet season and dry seasons, respectively. Chaco had 18 and 14 species, and Pantanal 16 and 17 species, respectively for the rainy and the dry seasons. Of the sampled species, *Boana albopunctata*, *B. geographica*, *Leptodactylus furnarius*, *L. labyrinthicus*, *Phyllomedusa sauvagii*, *Pristimantis dundeei* were registered only in the Cerrado ecoregion, *Adenomera dyptix*, *L. latrans*, *L.* aff. *fuscus*, and *Scinax acuminatus* were registered only in the Pantanal, *Physalaemus biligonigerus*, *L. elenae*, *L. bufonius* and *Rhinella major* were registered only in the Chaco and *Dendropsophus sanborni*, *Elachistocleis bicolor* and *Scinax squalirostris* were registered only in the Atlantic Forest. The total beta diversity for the dry period was 0.60. The mean local contribution to beta diversity in this season was 0.052 (ranging from 0.024 to 0.097) (Fig 3A). Sites with the highest values (LCBD> = 0.080) had significant LCBDs (four sites, all in the Cerrado ecoregion), whereas sites with values lower than 0.080 had non-significant LCBDs. Cerrado sites had higher LCBD values than sites in other ecoregions. LCBD was negatively correlated with species richness in the dry season (Pearson correlation = -0.46, p = 0.04) (S2 Fig). In the rainy period, the total beta diversity was slightly lower compared to the dry season (BD total = 0.55). The mean local contribution to beta diversity in the rainy period was 0.052 (ranging from 0.030 to 0.100) (Fig 3B). Sites with the highest values in this period (LCBD> = 0.080) had significant LCBDs (two sites, one in the Cerrado and the other in the Pantanal ecoregions), whereas sites with values lower than 0.080 had no significant LCBDs. The pattern of higher LCBD in Cerrado sites was maintained in the rainy season (Fig 3). Contrary to the dry period, the relationship between LCBD and richness was not significantly correlated in the rainy season (Pearson correlation = 0.09, p = 0.69) (S2 Fig). LCBD values from dry period were significantly correlated with rainy season (Pearson correlation = 0.56, p = 0.01) (S1 Fig), demonstrating that similar sites contribute in the same way to compositional uniqueness (Fig 3).

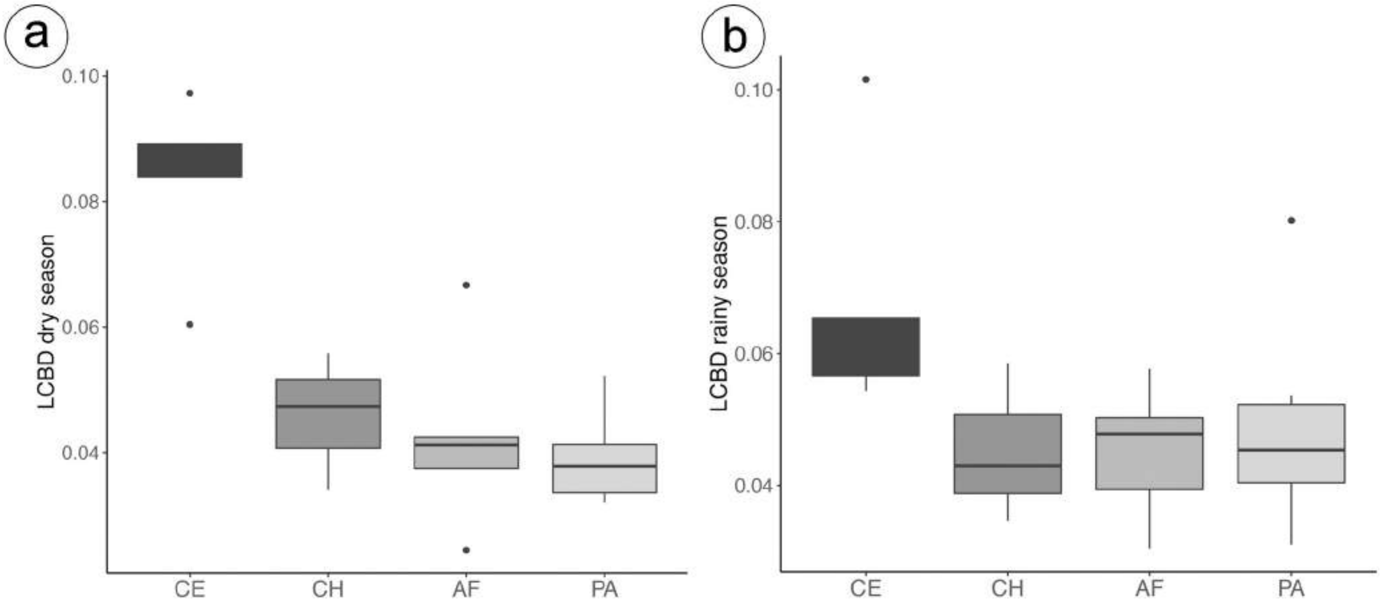

Fig 3. Local contributions to beta diversity (LCBD) values for the dry and rainy seasons from the four ecoregions sampled (AF = Atlantic Forest, CH = Chaco, CE = Cerrado, and PA = Pantanal).

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The environmental global model was significant for the dry period, ($p = 0.001$) and the Cerrado ecoregion was the variable selected. Distance-based Moran's eigenvector maps generated three eigenvectors, all of them with positive and significant spatial correlation. Spatial global model was also significant ($p = 0.008$) and MEM3 was selected to be included in the variation partitioning. Pure environmental component composed by Cerrado ecoregion [a] significantly explained variance in LCBD values ($p = 0.002$; adjusted $R^2 = 0.29$), whereas pure spatial component composed by MEM3 [c] was not significant to explain LCBD variation in the four ecoregions ($p = 0.20$; adjusted $R^2 = 0.01$). The shared component between environmental and spatial components explained 42% of variation in LCBD values and the unexplained variation in LCBD values corresponded to 27%. In the rainy season, both environmental and spatial global models were not significant (environmental: $F = 2.15$, $p = 0.22$; spatial: $F = 2.37$, $p = 0.11$), and, consequently, we did not proceed with variation partitioning (Table 1).

Discussion

In this study we found that LCBD patterns were similar between seasons, i.e., sites tended to contribute in the same way for community composition uniqueness during the dry and rainy season, contrary to our hypothesis. In addition, LCBD was negatively correlated with species

Table 1. Results of the partial redundancy analysis of site uniqueness for anurans during the dry season, where [a] pure environmental component, [b] the amount of variation shared by environmental component and spatial component, [c] pure specific spatial component and [d] non-explained variation (residual).

			[a]		[b]	[c]		[d]
	Env selected	**Spa selected**	**R2adj**	**F**	**R2adj**	**R2adj**	**F**	**R2adj**
LCBD Dry	Dummy_Cerrado	MEM3	**0.29**	**19.33****	0.42	0.01	1.80	0.27

[a] The explained variation for component b was -0.21 and for this reason the residual presented in the table is 0.50. According to Legendre & Legendre (2012) negative explained variance should be interpreted as 0.00. * $0.05<p<0.01$; * $0.01<p<0.001$.

Bold: represents significant fractions. Results for the rainy season were omitted because both environmental and spatial global models were non-significant.

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richness in the dry season. Among studied ecoregions, Cerrado showed higher LCBD values in both seasons, despite lower values during the rainy season. We also found that LCBD variation was explained by pure environmental variables (ecoregion) in the dry season, but models were non-significant during the rainy season.

For both seasons, local contributions to beta diversity were higher in Cerrado sites than in Atlantic Forest, Chaco and Pantanal, partially confirming our hypothesis. Cerrado is considered one of the world's 'hotspots' for biodiversity conservation because of its high endemism and its high rates of habitat conversion and biodiversity loss [38]. In relation to anurans, Cerrado has high species richness and endemism with assemblages from different lineages, which is likely a result of its contact with four South American ecoregions: Amazonia, Atlantic Forest, Caatinga, and Chaco [63, 64].

On the other hand, the similarity of LCBD values among Atlantic Forest, Chaco, and Pantanal might be related to their similarity in floodplain areas and by the elevated number of common and well-distributed species, such as *L. limellum*. In the study area, these ecoregions are strongly influenced by great rivers such as the Paraná and Paraguay, which flood seasonally and can act as migration routes for modern floras and faunas [65]. Moreover, sites of Atlantic Forest, Chaco, and Pantanal in this study can be considered transition zones because they are located at the boundaries between biogeographic regions and represent areas of biotic overlap, which are promoted by historical and ecological changes that allow the mixture of different biotic elements [66, 67]. Thus, each area could allow the entrance of well-distributed species coming from the surrounding ecoregions, in turn affecting the distribution of species and LCBD values in the core of the study sites.

We detected that sites tended to contribute in the same way to beta diversity in both seasons. Sampled sites in Atlantic Forest, Chaco, and Pantanal are composed of ponds that are more connected to adjacent ponds in the rainy season and isolated during the dry season. Conversely, in dry season Cerrado ponds experience the decreasing the amount of water available in ponds, forcing anurans to aestivate or seek shelter [68], and favour species that do not depend on water or are more adapted to desiccation (e.g., *P. dundeei* and *L. furnarius*) [69, 70], increasing LCBD values. In the rainy season, the greater water availability in Cerrado sites tends to decrease the difference between LCBD values from those values of other ecoregions. As a result, the seasonal LCBD patterns in the Cerrado ecoregion between seasons may be driven by drought periods and species requirements. Considering all these patterns, Cerrado sites may be keystone areas because of their disproportional contribution to regional species pool relative to their species richness in the dry season [7, 8].

Environmental heterogeneity is an important driver in metacommunity theory, with organisms tracking environmental variation over the region via dispersal [71]. In our study, sites tended to contribute in the same way for community composition uniqueness during the dry and rainy season, but the factors explaining each seasonal pattern differed. These results indicate that understanding the mechanisms responsible for beta diversity patterns is distant from to be cleared, as more unique habitats and marked seasons are not necessarily the ones harbouring more unique communities [53]. The different requirements among species can lead to some differences in community responses to environmental variables, when dispersal is limited or restrained by seasons [72]. In the dry season, our results indicated that LCBD variation was related to pure environmental variables (ecoregion characteristics) and by shared component (spatially structured environmental variables). The effect of environmental filters is stronger during the dry than the rainy season, filtering species that tolerate water restrictions [73]. Anurans can minimize energy use during dry periods and may aestivate or hibernate once the availability of resources and reproductive habitats decrease due to lower humidity or temperatures [74]. Also, species that require less water (e.g., viviparous species that do not depend on water for reproduction, *P. dundeei*) tend to appear in the dry season, mainly in Cerrado, increasing LCBD values in this ecoregion. Similar results were obtained for anurans from Amazonian sites, where the compositional uniqueness was more strongly associated with the environment [21], and for macrophytes in China when diversity patterns were driven mainly by spatially structured environmental determinism [75]. Therefore, pronounced seasonal environments may impose a fluctuating selection on life history traits, selecting species according to their requirements in the dry season due to desiccation.

During the rainy season, optimal conditions are experienced by the majority of anurans and environmental selection is less pronounced. The elevated rainfall triggers breeding in the majority of anurans [76], many of them widely distributed and habitat generalists, like *Dendropsophus nanus* and *D. minutus*. Anuran communities are more similar in this season, leading to similar LCBD values. For example, ponds in Pantanal and Chaco are more connected to adjacent sites in the rainy season, where flood pulses are more pronounced [77]. Flood pulses are also an important force for semideciduous areas of Atlantic forest near the Paraná River, promoting dispersion and the homogenization of communities. These pulses tend to connect ponds, favoring species dispersal among sites within each ecoregion (Pantanal, Chaco, and Atlantic Forest) [78, 79] and potentially between some of them, such as Pantanal and Chaco. This connection provides large areas available for breeding, which minimizes resource competition among individuals, favoring dispersion of species. These factors may be related to the non-significance of environmental and spatial models during this season. Besides to provide large areas for breeding the rainy season also provide a great amount of prey to anurans [80], because the composition of invertebrates in an environment change throughout a year in relation to climatic variations, different requirements among species, and life history stages [81]. Thus, the non-significance of environmental and spatial models can be related to the optimal conditions of species during this season, with species not being constrained by environmental or spatial filters.

Combining site-specific contributions to beta diversity in different seasons, we identified sites that consistently harbored unique communities, contributing to the maintenance of a regional species pool. Based on our analyses, Cerrado sites can be considered as keystone communities, because they have a disproportional contribution to the regional species pool in the dry season. The presence of a unique set of species composition, derived from its high endemism relative to the other ecoregions, increases the local contribution to beta diversity of Cerrado. Despite its enormous importance for species conservation and the provision of ecosystem services, only 19.8% of the native vegetation of Cerrado remains undisturbed [43]. The change in land uses as livestock and pastures is the main driver to deforestation of this hotspot and will drive ~480 endemic plant species to extinction [43, 82]. Thus, this elevated exploitation may reduce biodiversity in Cerrado sites, and consequently, would cause great effects in the anuran metacommunity. Therefore, to maintain the role of Cerrado as keystone areas, we suggest the identification and mapping more of these sites in order to preserve the regional biodiversity. In addition, through environmental education, owners of these areas should be made aware of the importance of these areas for regional diversity and should help maintain the ecological process associated with these species.

Supporting information

S1 Fig. Pearson correlation between LCBD values during dry and rainy seasons. Sites abbreviation can be seen in the S1 Table.
(JPG)

S2 Fig. Pearson correlation between richness and LCBD values during dry (a) and rainy seasons (b). To studied sites abbreviation see S1 Table.
(JPG)

S1 Table. Ponds sampled during the years of 2017 and 2018 in West Brazil.
(DOCX)

S2 Table. Raw climatic variables. All temperature and precipitation values were extracted from BioClim (http://worldclim.org/current) for each studied community. All values were averaged over the surrounding 2km to help buffer uncertainty in the reported locations. Variables indicates the name of the climatic variable in the respective date source.
(DOCX)

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