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Meta analysis

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

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Karoline Ceron, Luiz Gustavo R. Oliveira-Santos, Camila S. Souza, Daniel O. Mesquita, Francis L. S. Caldas, Andréa C. Araujo and Diego J. Santana

K. Ceron (https://orcid.org/0000-0003-2354-3756) (adenomera@gmail.com) and C. S. Souza (https://orcid.org/0000-0003-0856-9392), Programa de Pós Graduação em Ecologia e Conservação, Inst. de Biociências, Univ. Federal de Mato Grosso do Sul, Cidade Universitária, CEP 79002-970, Campo Grande, Mato Grosso do Sul, Brazil. CSS also at: Campus Centro Politécnico, Depto de Botânica, Univ. Federal do Paraná, Curitiba, Paraná, Brazil. – L. G. R. Oliveira-Santos (https://orcid.org/0000-0001-9632-5173), A. C. Araujo (https://orcid.org/0000-0003-0394-2012) and D. J. Santana (https://orcid.org/0000-0002-8789-3061), Inst. de Biociências, Univ. Federal de Mato Grosso do Sul, Cidade Universitária, Campo Grande, Mato Grosso do Sul, Brazil. – D. O. Mesquita (https://orcid.org/0000-0002-8174-6837), Depto de Sistemática e Ecologia, Univ. Federal da Paraíba, Cidade Universitária, João Pessoa, Paraíba, Brazil. – F. L. S. Caldas (https://orcid.org/0000-0003-1987-4560), Depto de Biologia, Univ. Federal de Sergipe, São Cristóvão - SE, Brazil.

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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,

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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

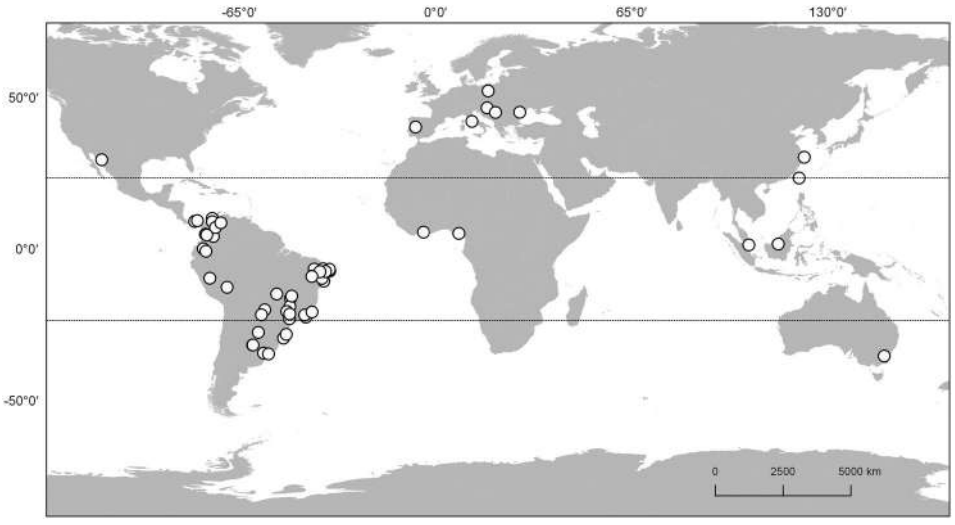

Figure 1. Distribution of 55 anuran–prey interaction networks included in the analysis of this study.

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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

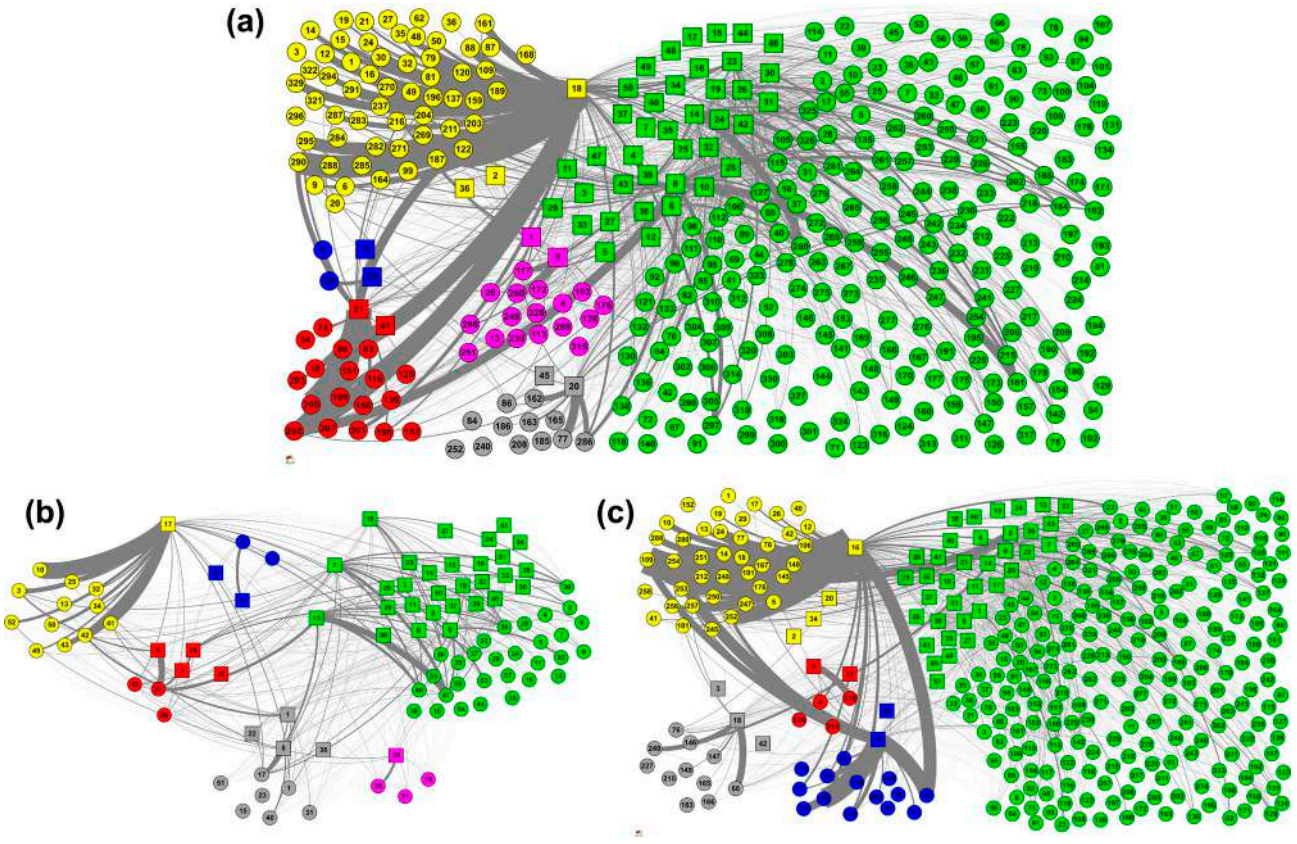

Figure 2. (a) Graphs showing modules in the compiled anuran–prey meta-network including 55 networks worldwide, (b) the meta-network combining 16 temperate sites and (c) the meta-network combining 39 tropical sites. Boxes represent prey categories and circles denote anuran species. Widths of connecting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

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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,

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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

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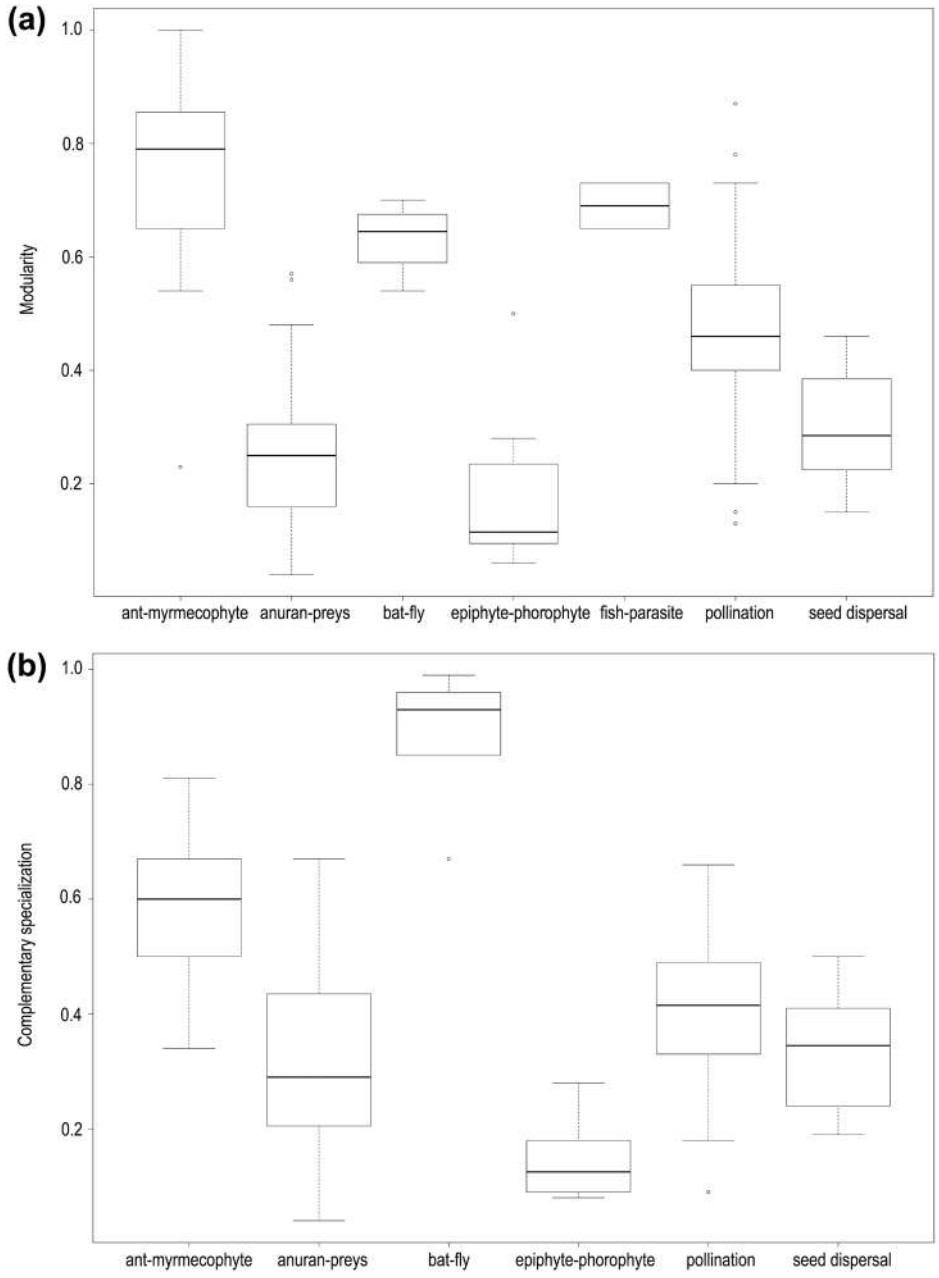

Figure 3. Variation in network metrics across network interaction types: anuran–prey, commensalistic epiphyte–phorophyte, bat–fly, fish–parasite, seed dispersal, pollination, ant–myrmecophyte, networks. (a) Modularity, (b) complementary specialization.

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

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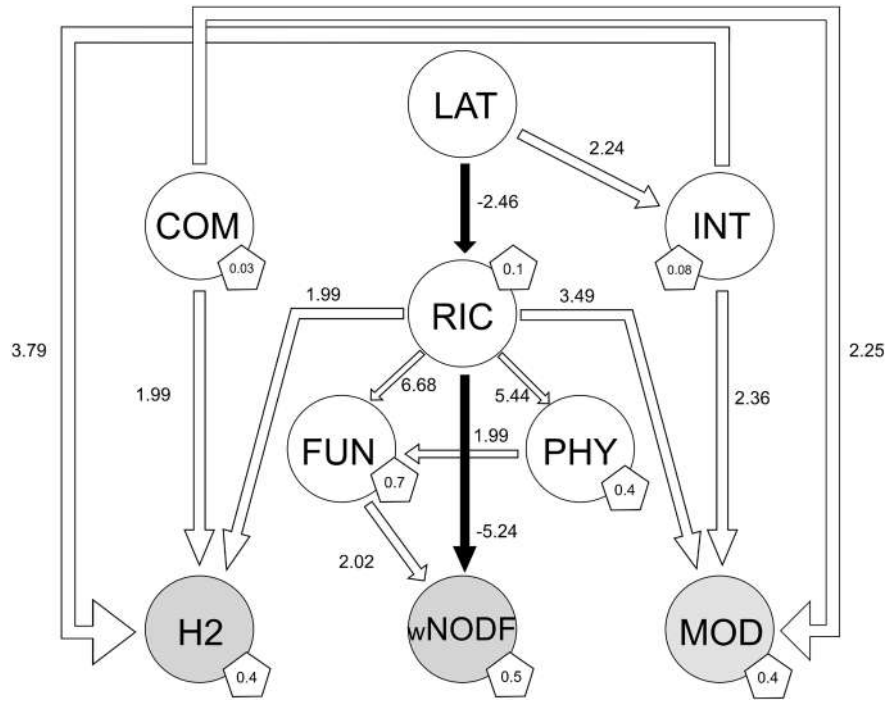

Figure 4. Path diagram showing statistically significant positive (white arrow) and negative (black arrow) influences of variables on network metrics (grey circles), where: LAT (latitude), RIC (anuran richness), FUN (functional richness), PHY (phylogenetic richness), INT (sampling intensity), COM (sampling 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,

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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

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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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References

Almeida–Neto, M. and Ulrich, W. 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. – Environ. Model. Softw. 26: 173–178.
Araujo, A. C. et al. 2018. Spatial distance and climate determine modularity in a cross-biomes plant–hummingbird interaction network in Brazil. – J. Biogeogr. 45: 1846–1858.
de Araújo, W. S. 2016. Global patterns in the structure and robustness of plant–herbivore networks. – Front. Biogeogr. 8: e31053.
Banašek–Richter, C. et al. 2004. Sampling effects and the robustness of quantitative and qualitative food-web descriptors. – J. Theor. Biol. 226: 23–32.
Banašek–Richter, C. et al. 2009. Complexity in quantitative food webs. – Ecology 90: 1470–1477.
Bascompte, J. and Jordano, P. 2007. Plant–animal mutualistic networks: the architecture of biodiversity. – Annu. Rev. Ecol. Evol. Syst. 38: 567–593.
Bascompte, J. et al. 2003. The nested assembly of plant–animal mutualistic networks. – Proc. Natl. Acad. Sci. 100: 9383–9387.
Bascompte, J. et al. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. – Science 312: 431–433.
Bastazini, V. A. et al. 2017. Untangling the tangled bank: a novel method for partitioning the effects of phylogenies and traits on ecological networks. – Evol. Biol. 44: 312–324.
Bates, D. et al. 2015. Package 'lme4'. – R package ver. 1.1-21. <http://cran. r-project.org>.
Beckett, S. J. 2016. Improved community detection in weighted bipartite networks. – R. Soc. Open Sci. 3: 140536.
Belgrano, A. 2005. Aquatic food webs: an ecosystem approach. – Oxford Univ. Press.
Bellay, S. et al. 2015. The patterns of organisation and structure of interactions in a fish–parasite network of a neotropical river. – Int. J. Parasitol. 45: 549–557.
Blüthgen, N. 2010. Why network analysis is often disconnected from community ecology: a critique and an ecologist's guide. – Basic Appl. Ecol. 11: 185–195.
Blüthgen, N. et al. 2006. Measuring specialization in species interaction networks. – BMC Ecol. 6: 9.
Brito, S. V. et al. 2014. Phylogeny and micro-habitats utilized by lizards determine the composition of their endoparasites in the semiarid Caatinga of northeast Brazil. – Parasitol. Res. 113: 3963–3972.
Brown, J. H. 2014. Why are there so many species in the tropics? – J. Biogeogr. 41: 8–22.
Campião, K. et al. 2015. Diversity and patterns of interaction of an anuran–parasite network in a neotropical wetland. – Parasitology 142: 1751–1757.
Cantor, M. et al. 2017. Nestedness across biological scales. – PLoS One 12: e0171691.
Cattin, M. F. et al. 2004. Phylogenetic constraints and adaptation explain food-web structure. – Nature 427: 835.
Ceron, K. et al. 2018. Diet and first report of batracophagy in *Leptodactylus podicipinus* (Anura: Leptodactylidae). – Neotrop. Biodivers. 4: 69–73.
Chacoff, N. P. et al. 2012. Evaluating sampling completeness in a desert plant–pollinator network. – J. Anim. Ecol. 81: 190–200.
Crump, M. L. 2015. Anuran reproductive modes: evolving perspectives. – J. Herpetol. 49: 1–16.
Dalsgaard, B. et al. 2011. Specialization in plant-hummingbird networks is associated with species richness, contemporary precipitation and quaternary climate-change velocity. – PLoS One 6: e25891.
Dalsgaard, B. et al. 2013. Historical climate–change influences modularity and nestedness of pollination networks. – Ecography 36: 1331–1340.
Dalsgaard, B. et al. 2017. Opposed latitudinal patterns of network-derived and dietary specialization in avian plant–frugivore interaction systems. – Ecography 40: 1395–1401.

16000706, 2019, 11, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1111/oik.06621 by Diego Santana - UFMS - Fundacao Universidade Federal de Mato Grosso do Sul , Wiley Online Library on [01/03/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Dáttilo, W. and Rico–Gray, V. 2018. Ecological networks in the tropics: an integrative overview of species interactions from some of the most species–rich habitats on Earth. – Springer.
Davidson, D. W. et al. 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. – Science 300: 969–972.
Diamond, J. M. 1975. Assembly of species communities. – In: Cody, M. L. and Diamond, J. M. (eds), Ecology and evolution of communities. Harvard Univ. Press, pp. 342–444.
Dobson, A. 2009. Food-web structure and ecosystem services: insights from the Serengeti. – Phil. Trans. R. Soc. B 364: 1665–1682.
Dormann, C. F. et al. 2008. Introducing the bipartite package: analysing ecological networks. – R News 8: 8–11.
Dormann, C. F. et al. 2009. Indices, graphs and null models: analyzing bipartite ecological networks. – Open Ecol. J. 2: 7–24.
Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. – Misc. Pub. Univ. Kansas Mus. Nat. Hist. 65: 1–352.
Duellman, W. E. and Trueb, L. 1986. Biology of amphibians. – The Johns Hopkins Univ. Press.
Dunne, J. A. et al. 2004. Network structure and robustness of marine food webs. – Mar. Ecol. Prog. Ser. 273: 291–302.
Durán, A. A. et al. 2019. Specialization and modularity of a bat fly antagonistic ecological network in a dry tropical forest in northern Colombia. – Acta Chiropterol. 20: 503–510.
Duré, M. I. et al. 2009. Niche overlap and resource partitioning among five sympatric bufonids (Anura, Bufonidae) from northeastern Argentina. – Phyllomedusa J. Herpetol. 8: 27–39.
Estes, J. A. et al. 2016. Megafaunal impacts on structure and function of ocean ecosystems. – Annu. Rev. Environ. Resour. 41: 83–116.
Fischer, A. G. 1960. Latitudinal variations in organic diversity. – Evolution 14: 64–81.
Fontaine, C. and Thébault, E. 2015. Comparing the conservatism of ecological interactions in plant–pollinator and plant–herbivore networks. – Popul. Ecol. 57: 29–36.
Fortuna, M. A. et al. 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? – J. Anim. Ecol. 79: 811–817.
Fründ, J. et al. 2016. Sampling bias is a challenge for quantifying specialization and network structure: lessons from a quantitative niche model. – Oikos 125: 502–513.
Guilhaumon, F. et al. 2012. Latitudinal mismatches between the components of mammal–flea interaction networks. – Global Ecol. Biogeogr. 21: 725–731.
Habel, K. et al. 2015. Geometry: mesh generation and surface tesselation. – R package ver. 0.3–6. <https://CRAN.R-project.org/package=geometry>.
Haddad, C. F. B. et al. 2013. Guia dos Anfíbios da Mata Atlântica – Diversidade e Biologia. – Anolis Books.
Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. – Am. Nat. 163: 192–211.
Holst, K. K. and Budtz-Jørgensen, E. 2013. Linear latent variable models: the lava-package. – Comput. Stat. 28: 1385–1452.
Hsieh, T. C. et al. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). – Methods Ecol. Evol. 7: 1451–1456.
Jetz, W. and Pyron, R. A. 2018. The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. – Nat. Ecol. Evol. 2: 850–858.
Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries and coevolution. – Am. Nat. 129: 657–677.
Jordano, P. 2016. Chasing ecological interactions. – PLoS Biol. 14: e1002559.
Junker, R. R. et al. 2012. Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. – Funct. Ecol. 27: 329–341.
Kéfi, S. et al. 2015. Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. – Ecology 96: 291–303.
Krasnov, B. R. et al. 2012. Phylogenetic signal in module composition and species connectivity in compartmentalized host–parasite networks. – Am. Nat. 179: 501–511.
Legendre, P. and Legendre, L. F. 2012. Numerical ecology. – Elsevier.
Lewinsohn, T. M. et al. 2006a. Matrizes, redes e ordenações: a detecção de estrutura em comunidades interativas. – Oecol. Bras. 10: 90–104.
Lewinsohn, T. M. et al. 2006b. Structure in plant–animal interaction assemblages. – Oikos 113: 174–184.
Lima, D. P. et al. 2012. Patterns of interactions of a large fish–parasite network in a tropical floodplain. – J. Anim. Ecol. 81: 905–913.
Liu, X. and Murata, T. 2010. Advanced modularity–specialized label propagation algorithm for detecting communities in networks. – Physica A Stat. Mech. Appl. 389: 1493–1500.
Maglianesi, M. A. et al. 2015. Functional structure and specialization in three tropical plant–hummingbird interaction networks across an elevational gradient in Costa Rica. – Ecography 38: 1119–1128.
Magurran, A. E. 2013. Medindo a diversidade biológica. – Editora da UFPR.
Marin, J. and Hedges, S. B. 2016. Time best explains global variation in species richness of amphibians, birds and mammals. – J. Biogeogr. 43: 1069–1079.
Maruyama, P. K. et al. 2014. Morphological and spatio-temporal mismatches shape a neotropical savanna plant–hummingbird network. – Biotropica 46: 740–747.
Maruyama, P. K. et al. 2018. Functional diversity mediates macroecological variation in plant–hummingbird interaction networks. – Glob. Ecol. Biogeogr. 27: 1186–1199.
McClanahan, T. and Branch, G. 2008. Food webs and the dynamics of marine reefs. – Oxford Univ. Press.
Menin, M. et al. 2015. Notes on the diet of seven terrestrial frogs in three agroecosystems and forest remnants in northwestern São Paulo State, Brazil. – Herpetol. Notes 8: 401–405.
Minoarivelo, H. O. et al. 2014. Detecting phylogenetic signal in mutualistic interaction networks using a Markov process model. – Oikos 123: 1250–1260.
Morente-López, J. et al. 2018. Phenology drives species interactions and modularity in a plant–flower visitor network. – Sci. Rep. 8: 9386.
Morris, R. J. et al. 2014. Antagonistic interaction networks are structured independently of latitude and host guild. – Ecol. Lett. 17: 340–349.
Mouillot, D. et al. 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. – Proc. Natl Acad. Sci. USA 111: 13757.
Naisbit, R. E. et al. 2012. Phylogeny versus body size as determinants of food web structure. – Proc. R. Soc. B 279: 3291–3297.
Naranjo, C. et al. 2019. Evaluating the structure of commensalistic epiphyte–phorophyte networks: a comparative perspective of biotic interactions. – AoB Plants 11: plz011.

16000706, 2019, 11, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1111/oik.06621 by Diego Santana - UFMS - Fundacao Universidade Federal de Mato Grosso do Sul , Wiley Online Library on [01/03/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Novotny, V. et al. 2006. Why are there so many species of herbivorous insects in tropical rainforests? – Science 313: 1115–1118.
Olesen, J. M. and Jordano, P. 2002. Geographic patterns in plant–pollinator mutualistic networks. – Ecology 83: 2416–2424.
Olesen, J. M. et al. 2007. The modularity of pollination networks. – Proc. Natl Acad. Sci. USA 104: 19891–19896.
Oliveira, B. F. et al. 2017. AmphiBIO, a global database for amphibian ecological traits. – Sci. Data 4: 170123.
Paradis, E. et al. 2004. APE: analyses of phylogenetics and evolution in R language. – Bioinformatics 20: 289–290.
Parker, I. M. et al. 2015. Phylogenetic structure and host abundance drive disease pressure in communities. – Nature 520: 542.
Patefield, W. M. 1981. Algorithm AS 159: an efficient method of generating random R×C tables with given row and column totals. – J. R. Stat. Soc. Ser. C Appl. Stat. 30: 91–97.
Petchey, O. L. and Gaston, K. J. 2002. Functional diversity (FD), species richness and community composition. – Ecol. Lett. 5: 402–411.
Petchey, O. L. et al. 2008. Size, foraging and food web structure. – Proc. Natl Acad. Sci. USA 105: 4191–4196.
Pigot, A. L. et al. 2016. Quantifying species contributions to ecosystem processes: a global assessment of functional trait and phylogenetic metrics across avian seed-dispersal networks. – Proc. R. Soc. B 283: 20161597.
Pilosof, S. et al. 2017. The multilayer nature of ecological networks. – Nat. Ecol. Evol. 1: 0101.
Pires, M. M. and Guimarães, P. R. 2013. Interaction intimacy organizes networks of antagonistic interactions in different ways. – J. R. Soc. Interface 10: 20120649.
Ponisio, L. C. and M'Gonigle, L. K. 2017. Coevolution leaves a weak signal on ecological networks. – Ecosphere 8: e01798.
Rafael, J. et al. 2012. Insetos do Brasil: diversidade e taxonomia. – Holos.
Rezende, E. L. et al. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. – Nature 448: 925.
Roslin, T. et al. 2017. Higher predation risk for insect prey at low latitudes and elevations. – Science 356: 742–744.
Saporiti, F. et al. 2015. Latitudinal changes in the structure of marine food webs in the southwestern Atlantic Ocean. – Mar. Ecol. Prog. Ser. 538: 23–34.
Schemske, D. W. et al. 2009. Is there a latitudinal gradient in the importance of biotic interactions? – Annu. Rev. Ecol. Evol. Syst. 40: 245–269.
Schleuning, M. et al. 2012. Specialization of mutualistic interaction networks decreases toward tropical latitudes. – Curr. Biol. 22: 1925–1931.
Schleuning, M. et al. 2014. Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. – Ecol. Lett. 17: 454–463.

Supplementary material (available online as Appendix oik-06621 at <www.oikosjournal.org/appendix/oik-06621>). Appendix 1.

Schöb, C. et al. 2012. Foundation species influence trait-based community assembly. – New Phytol. 196: 824–834.
Sneath, P. H. and Sokal, R. R. 1973. Numerical taxonomy. The principles and practice of numerical classification. – Freeman.
Spiesman, B. J. and Inouye, B. D. 2013. Habitat loss alters the architecture of plant–pollinator interaction networks. – Ecology 94: 2688–2696.
Tinoco, B. A. et al. 2017. Effects of hummingbird morphology on specialization in pollination networks vary with resource availability. – Oikos 126: 52–60.
Toft, C. A. 1980. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. – Oecologia 45: 131–141.
Trøjelsgaard, K. and Olesen, J. M. 2013. Macroecology of pollination networks. – Global Ecol. Biogeogr. 22: 149–162.
Vázquez, D. P. et al. 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. – Ecol. Lett. 8: 1088–1094.
Vignoli, L. and Luiselli, L. 2012. Dietary relationships among coexisting anuran amphibians: a worldwide quantitative review. – Oecologia 169: 499–509.
Vignoli, L. et al. 2009. Dietary patterns and overlap in an amphibian assemblage at a pond in Mediterranean central Italy. – Vie Milieu – Life Environ. 59: 54–57.
Villéger, S. et al. 2008. Stable trophic structure across coastal nekton assemblages despite high species turnover. – Mar. Ecol. Prog. Ser. 364: 135–146.
Villéger, S. et al. 2011. The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. – Ecol. Lett. 14: 561–568.
Vizentin-Bugoni, J. et al. 2016. Influences of sampling effort on detected patterns and structuring processes of a Neotropical plant–hummingbird network. – J. Anim. Ecol. 85: 262–272.
Vizentin-Bugoni, J. et al. 2019. Structure, spatial dynamics and stability of novel seed dispersal mutualistic networks in Hawaii. – Science 364: 78–82.
Watts, S. et al. 2016. The influence of floral traits on specialization and modularity of plant–pollinator networks in a biodiversity hotspot in the Peruvian Andes. – Ann. Bot. 118: 415–429.
Wiens, J. J. 2007. Global patterns of diversification and species richness in amphibians. – Am. Nat. 170: S86–S106.
Woodward, G. and Hildrew, A. G. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. – J. Anim. Ecol. 71: 1063–1074.
Woodward, G. et al. 2005. Body size in ecological networks. – Trends Ecol. Evol. 20: 402–409.
Zanata, T. B. et al. 2017. Global patterns of interaction specialization in bird–flower networks. – J. Biogeogr. 44: 1891–1910.
Zarazúa-Carbajal, M. et al. 2016. The specificity of host–bat fly interaction networks across vegetation and seasonal variation. – Parasitol. Res. 115: 4037–4044.

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