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Differences in prey availability across space and time lead to interaction rewiring and reshape a predator–prey metaweb

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Abstract

Space and time promote variation in network structure by affecting the likelihood of potential interactions. However, little is known about the relative roles of ecological and biogeographical processes in determining how species interactions vary across space and time. Here we study the spatiotemporal variation in predator–prey interaction networks formed by anurans and arthropods and test for the effects of prey availability in determining interaction patterns, information that is often absent and limits the understanding of the determinants of network structure. We found that network dissimilarity between ecoregions and seasons was high and primarily driven by interaction rewiring. We also found that species turnover was positively related to geographical distance. Using a null model approach to disentangle the effect of prey availability on the spatial and temporal variation, we show that differences in prey availability were important in determining the variation in network structure between seasons and among areas. Our study reveals that fluctuations in prey abundance, alongside the limited dispersal abilities of anurans and their prey, may be responsible for the spatial patterns that emerged in our predator–prey metaweb. These findings contribute to our understanding of the assembly rules that maintain biotic processes in metacommunities and highlight the importance of prey availability to the structure of these systems.

KEYWORDS
beta diversity, community assembly, ecological networks, food web, interaction turnover, metacommunities

INTRODUCTION

Communities vary in composition over time and space. Whenever species compositions differ between places or over time, species interactions will also vary, forming interaction networks that may be structurally different even under similar environmental contexts (Guimarães, 2020). Multiple mechanisms can produce spatial and temporal turnover in species composition (Leibold & Chase, 2017; Jabot et al., 2020). Ecological filtering imposed by local

environmental features can limit the set of species that occur in a given site, and environmental heterogeneity may lead to increased turnover depending on species niches (Belmaker & Jetz, 2012; Jabot et al., 2020; Leibold & Chase, 2017). Species dispersal abilities will further determine local and regional species turnover, which also affects how similar interaction networks can be across a heterogeneous landscape (Nuvoloni et al., 2016; Shmida & Wilson, 1985). Thus, sites that have similar environmental conditions and are closer to each other should have a more similar species composition and similar interaction networks (Carstensen et al., 2014).

Yet, even when the same species are present in different locations or composition is consistent over time, interactions and interaction strengths may vary across space and time. Variation in species abundances, for instance, may make certain prey more profitable in certain localities, leading to prey switching across the consumer distribution or even across seasons (Boyd et al., 2017; Coblentz, 2020). Likewise, spatial asynchrony in phenologies can create divergent interaction patterns in space and time (McKinney & Goodell, 2011). Fluctuating environmental conditions and diseases can also favor the consumption of certain prey that may become easier to catch under specific conditions (Lopez et al., 2017; Moleón et al., 2012), which may generate dynamic scenarios that favor a high frequency of transient links in networks (Ings et al., 2009; Lopez et al., 2017).

Because ecological interactions among species may increase or decrease the odds that species from the regional pool can establish and persist in a local community, investigating the variation in species interaction networks over time, space, or environments can offer insights into the underlying processes of community assembly dynamics, that is, how species composition changes over time and space (Poisot et al., 2012). The dissimilarity between interaction networks, herein network dissimilarity, 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 (Poisot et al., 2012). Interaction rewiring refers to how networks are reassembled over space or time because of changes in pairwise interactions within the same set of co-occurring species (Poisot et al., 2012). The gain or loss of interactions will depend on which species co-occur spatially or temporally (reviewed in CaraDonna et al. 2020). There is evidence that species turnover may be the main driver of plant–pollinator network dissimilarity across space (Carstensen et al., 2014; Simanonok & Burkle, 2014) and in a plant–herbivore system over time and space (Kemp et al., 2017). In a study carried out in the Brazilian Pantanal with plant–pollinator networks, species turnover

explained most of the network β-diversity (Souza et al., 2021). Additionally, plant-centered networks resulted in higher network dissimilarity in space than animal-centered networks, suggesting that spatial differences in networks were mainly driven by plant distribution. In contrast, interaction rewiring was the major component of the week-to-week turnover in plant–pollinator interactions (CaraDonna et al., 2017). On a macroecological scale, Dáttilo and Vasconcelos (2019) found that interaction rewiring was the main contributor to the total network dissimilarity in ant–tree networks in neotropical savannas, suggesting that networks are maintained by species' ability to switch interaction partners across their distribution. In another example, the network dissimilarity over time 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). These examples illustrate how partitioning the dissimilarity of interaction networks and investigating their ecological drivers can shed light on processes organizing network assembly.

Seasonal environments allow us to study the assembly and disassembly of ecological systems over time and test how space and time reshape ecological networks. Within the neotropics, different ecoregions undergo varying levels of seasonal changes, especially in terms of the rainfall regime, which can cause temporal changes in species composition (Grimm, 2011). The Brazilian Central-West comprises the ecoregions of Atlantic Forest, Cerrado, Chaco, and Pantanal, each one having unique environmental characteristics. The Atlantic Forest and Cerrado ecoregions support the highest species richness and rates of endemism and are biodiversity hotspots because of their high rates of habitat loss (Myers et al., 2000; Ribeiro et al., 2009). Yet, whereas dense humid forests predominate in the Atlantic Forest ecoregion, the Cerrado constitutes a mosaic with varying levels of vegetation openness and is subject to a marked dry season. The Chaco is one of the most threatened subtropical woodland savannas in the world and is also subject to varying rainfall levels (Nori et al., 2016; Zak et al., 2004), whereas the Pantanal is one of the largest wetlands on the planet, notable for its abundance of wildlife (Harris et al., 2005; Pott & Pott, 2004).

The high rainfall seasonality can be particularly challenging to frogs inhabiting these regions, which depend on water bodies for reproduction (Wells, 2007). Anurans and their prey (mainly arthropods) are well known for their limited dispersal abilities (Semlitsch, 2008; Smith & Green, 2005; Winterbourn et al., 2007), so both predator and prey composition can change throughout the seasons and across ecoregions in response to climatic variations, differences in species requirements, and life-history

stages (Janzen, 1973; Kikuchi & Ueida, 1998; Michelin et al., 2020). Surprisingly, anuran species composition in western Brazil changes little between seasons and is similar among ecoregions (Ceron et al., 2020). The unique features of those disparate ecoregions in western Brazil, together with anuran sensitivity to climate, offer a good scenario to test hypotheses about the drivers of temporal and spatial variations in the structure of networks formed by predators and their prey.

Two issues often limit understanding of the assembly processes underlying network structure: the difficulty in delimiting the system and sample assemblages comprehensively and the lack of information about resource availability. We circumvented these two problems by sampling all anurans within well-delimited ponds and by independently sampling the available prey around each pond. We examined the spatial and temporal variations in predator–prey interaction networks formed by anurans and arthropods and tested for the effects of prey availability in determining interaction patterns. Specifically, we quantified the species turnover and interaction rewiring components of the network dissimilarity of predator–prey interaction networks 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 the dissimilarity of anuran–prey networks would be driven by the rewiring of interactions between seasons (i.e., temporal variation) and determined by differences in prey availability and species turnover among ecoregions (i.e., spatial variation). We expected changes in species composition among ecoregions would be responsible for network dissimilarity because frogs have narrow physiological requirements (e.g., reproductive modes and thermal tolerance), and both anurans and their prey have low dispersal abilities. 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 arthropods in 19 ponds distributed in four ecoregions, among which three were in the Chaco, five in the Cerrado, five in the Atlantic Forest, and six in the Pantanal of Mato Grosso do Sul, central Brazil. All ponds had similar surface areas and were sampled from August 2017 to November 2018. Each pond was surveyed

for frogs using standard protocols (Crump & Scott Jr., 1994) for 1 day in the dry and 1 day in the rainy season, totaling 6 h of sampling effort per pond per season. We collected all individuals found during surveys for posterior stomach content analysis. Because all adult individuals found within ponds were collected, we could not perform multiple surveys in the same pond in short time intervals, opting to perform a single exhaustive search in each pond per season.

To estimate the availability of potential prey in the environment, we installed 20 pitfall traps around each sampled pond, which consisted of 1-L plastic flasks filled with 70% ethanol that remained open for 12 h (from 6:00 PM to 6:00 AM) during the nights we collected frogs. We also sampled arthropods in the herbaceous and shrubby vegetation around ponds using a beating sheet for 30 min before we start collecting frogs. By limiting the arthropod sampling to the same day anurans had been collected, our objective was to characterize the arthropod assemblage available as prey at the same moment of the frog survey. Thus, although the predators and prey sampled represent a snapshot of the local communities, they provide a comprehensive characterization of the interactions taking place at a given point in time. For further details on sampling and a map of sampling locations, see Ceron et al. (2020).

We analyzed the stomach contents of collected anurans under a stereomicroscope and identified each item to operational taxonomic units (OTUs). This classification was employed because arthropods were usually partially digested. The taxonomic unity was usually Order, except for the families Formicidae (Hymenoptera) and Ixodidae (Ixodida). Larvae were included as separate OTUs (e.g., Lepidoptera, Lepidoptera larvae).

Beta diversity of predator–prey interactions

For each study site, we built weighted matrices of interactions containing predator species in columns and the abundance of prey categories (OTU) in rows. For each area, we constructed one matrix including all recorded interactions and separated matrices for each season (wet and dry). We calculated the dissimilarity in predator–prey networks using the framework proposed by Poisot et al. (2012). The overall dissimilarity of interactions (β_{WN}) varies from 0 (meaning complete similarity) to 1 (complete dissimilarity) and can be additively partitioned into dissimilarity of interactions due to species turnover (β_{ST}, the overall dissimilarity including nonshared species) and the spatial or temporal rewiring of interactions (β_{OS}, the interaction dissimilarity between shared species) (CaraDonna et al.,

2017; Poisot et al., 2012). This partitioning allows us to determine whether the variation in structure among interaction networks is mostly affected by (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). We used weighted matrices and the Bray–Curtis dissimilarity index to calculate beta diversity as implemented in the bipartite package (Dormann et al., 2008) in R 3.4.0 (R Core Team, 2020).

Recently, Fründ (2021) proposed an alternative normalization of dissimilarities to the partition proposed by Poisot et al. (2012) to downweigh the importance of interaction rewiring in relation to species turnover. However, Poisot (2021) makes a strong case that this normalization is inadequate for use in network-diversity measurements because it uses components of the network in the denominator of the equation that are not part of the networks being compared. To make sure that our main conclusions are not due to different methodological choices, we show the results of the original framework along with those of the alternative normalization of dissimilarities proposed by Fründ (2021).

Comparison of interaction beta diversity among ecoregions and seasons

To understand how networks varied across space and time, we examined network dissimilarity across ecoregions 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 species turnover (β_{ST}) and interaction rewiring (β_{OS}) within ecoregions to the temporal beta diversity 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 from both seasons. We calculated mean beta diversity by averaging the pairwise beta diversity between the 19 sites. We also computed species turnover for predator species alone ($\beta_{predator}$), prey species alone (β_{prey}), and predators and preys together (β_{shared}) to better understand the drivers of interaction beta diversity. Relationships between the network dissimilarity components and β_{shared}, $\beta_{predator}$, β_{prey}, and geographic distance were tested using linear regression in the R package ecodist (Goslee & Urban, 2007).

To test for differences in prey availability between seasons and ecoregions, we used a model-based approach. This method allows us to identify multivariate patterns in species abundances by fitting separate generalized linear models (GLM) using a common set of explanatory variables (Wang et al., 2012). We fit a Poisson GLM with season (factor with two levels), ecoregion (factor with four

levels), and their interaction as predictors and the availability of potential prey found in each environment (counts) as the response. We checked model assumptions using Dunn–Smyth residuals versus fitted plots (Appendix S1: Figure S2). We detected no strong departure from homogeneity of variance. Analyses were conducted in the R package mvabund (Wang et al., 2012).

To test whether the variation in interaction beta diversity among areas and between seasons could result solely from differences in prey availability, we used a null model approach. We built a null model based on prey availability per season in each area and calculated interaction beta diversity. For this purpose, we simulated random networks sampling the same number of observed interactions per predator, according to the proportions in which each prey was detected in a given area in a given season. These model networks thus represent the expected networks if all anurans consumed prey according to their local availability. We generated 100 model networks per observed network and then computed the pairwise interaction beta diversity across all these model networks to obtain a distribution of interaction beta diversity values under the hypothesis that they were fully determined by differences in prey availability (see data on Zenodo). Afterward, we compared the interaction beta diversity of the null model against our real interaction beta diversity
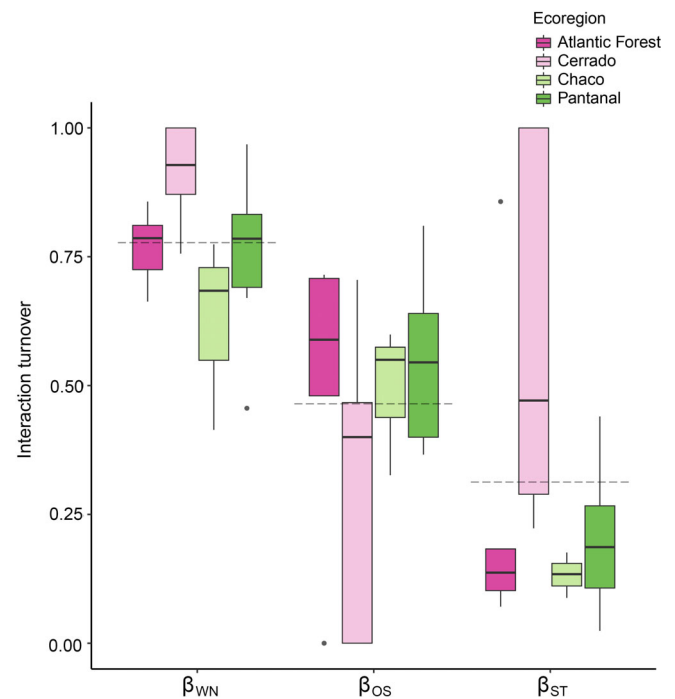

FIGURE 1 Comparison of components of predator–prey network dissimilarity between seasons: total network dissimilarity (β_{WN}), interaction rewiring (β_{OS}), and turnover in species composition (β_{ST}) between seasons. Data points represent raw values of interaction beta diversity and its components. No significant differences were detected between β_{ST} and β_{OS} via a two-tailed t-test. Dashed lines are the mean per group

among ecoregions and between seasons using a *Z*-test. The R script to reproduce the analyses and the functions used to run the null model are available in Zenodo: https://doi.org/10.5281/zenodo.6122474.

RESULTS

We sampled 1488 frogs belonging to 43 species and 14 genera, which consumed 42 prey categories. The dissimilarity between networks from different seasons was consistently high and driven by both rewiring of interactions and species turnover (Figure 1; Appendix S1: Table S1). The network dissimilarity between seasons was high for all ecoregions (mean 0.77, SD $\pm$ 0.15), with Cerrado having the highest values (0.91) and the Chaco the lowest (0.62) (Figure 1). The contribution of rewiring to total network dissimilarity was higher than that of species turnover in 14 sites (73.68% of sites; mean 0.41, SD $\pm$ 0.23), but species turnover was consistently high for sites in the Cerrado. Using an alternative partitioning method, we still found that rewiring was higher than species turnover for the Atlantic Forest and Chaco regions, while species turnover was higher than rewiring in the Cerrado (Appendix S1: Figure S1). The only difference between the two methods

was for the Pantanal, which had a large variance in species turnover (Appendix S1: Figure S1).

Network dissimilarity (β_{WN}) was also high among ecoregions (mean 0.77, SD $\pm$ 0.15) and primarily driven by interaction rewiring (β_{OS}; Figure 2; $t_{9.81} = 5.32$, $p < 0.0001$). The only exception was the interaction beta diversity between the Atlantic Forest and Pantanal, which was dominated by species turnover ($\beta_{ST} = 0.37$). The pairwise comparison between Cerrado and Chaco had the highest values of rewiring ($\beta_{OS} = 0.88$), whereas Cerrado and Atlantic Forest had the lowest ($\beta_{OS} = 0.67$). In the cross-comparisons between ecoregions using an alternative partitioning method, we found that rewiring was as important as species turnover and was greater than the species turnover component for the comparison between Chaco and Pantanal (Appendix S1: Figure S2).

Geographical distance was positively related to the beta diversity of predators ($\beta_{predator}$) (slope = 0.000385, $F_{1,148} = 44.68$, $R^2 = 0.22$, $p < 0.001$), prey (β_{prey}) (slope = 0.000236, $F_{1,148} = 23.44$, $R^2 = 0.13$, $p < 0.001$), and shared species (β_{shared}) (slope = 0.000236, $F_{1,148} = 9.618$, $R^2 = 0.05$, $p < 0.001$), but this latter component had a low coefficient of determination (R^2). However, the overall network dissimilarity (β_{WN}) did not vary with geographical distance (slope = 0.000098, $F_{1,148} = 2.61$, $R^2 = 0.01$, $p = 0.108$,
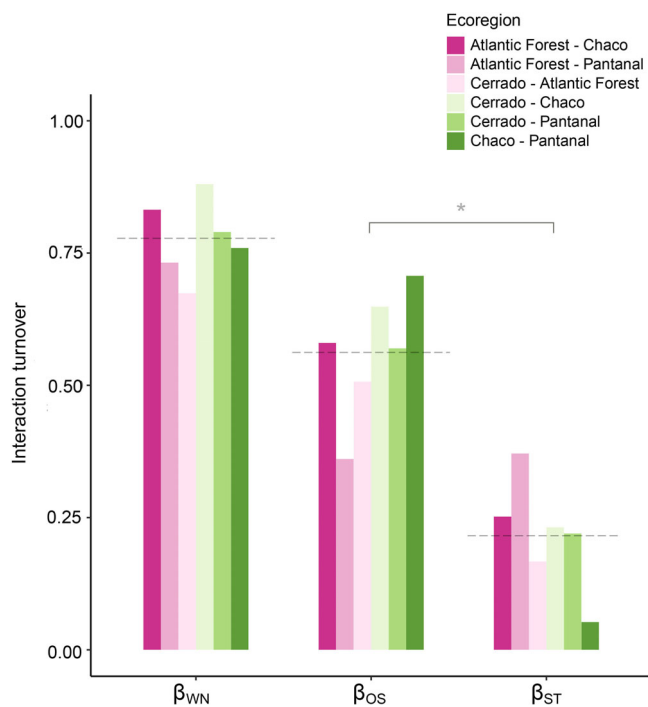

FIGURE 2 Comparison of the components of predator–prey interaction beta diversity among ecoregions: network dissimilarity (β_{WN}), interaction rewiring (β_{OS}), and turnover in species composition (β_{ST}) among ecoregions. Bars represent the network dissimilarity and its components. Asterisk indicates significant differences ($p < 0.05$) between β_{ST} and β_{OS} via a two-tailed *t*-test. Dashed lines are the mean per group
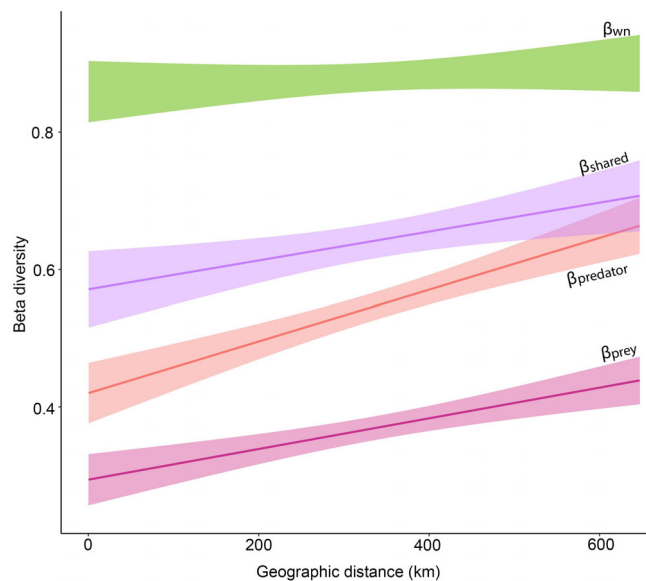

FIGURE 3 Beta diversity of species and interactions as a function of geographical distance between sites. Network dissimilarity (β_{WN}, green), predator beta diversity ($\beta_{predator}$, red), beta diversity of interactions between shared species (β_{shared}, light purple), and prey beta diversity (β_{prey}, dark purple). All components, except β_{WN}, relate positively to geographical distance (β_{shared}: slope = 0.000236, $F_{1,148} = 9.618$, $R^2 = 0.05$, $p < 0.001$; $\beta_{predator}$: slope = 0.000385, $F_{1,148} = 44.68$, $R^2 = 0.22$, $p < 0.001$; β_{prey}: slope = 0.000236, $F_{1,148} = 23.44$, $R^2 = 0.13$, $p < 0.001$). Shaded areas represent 95% confidence intervals
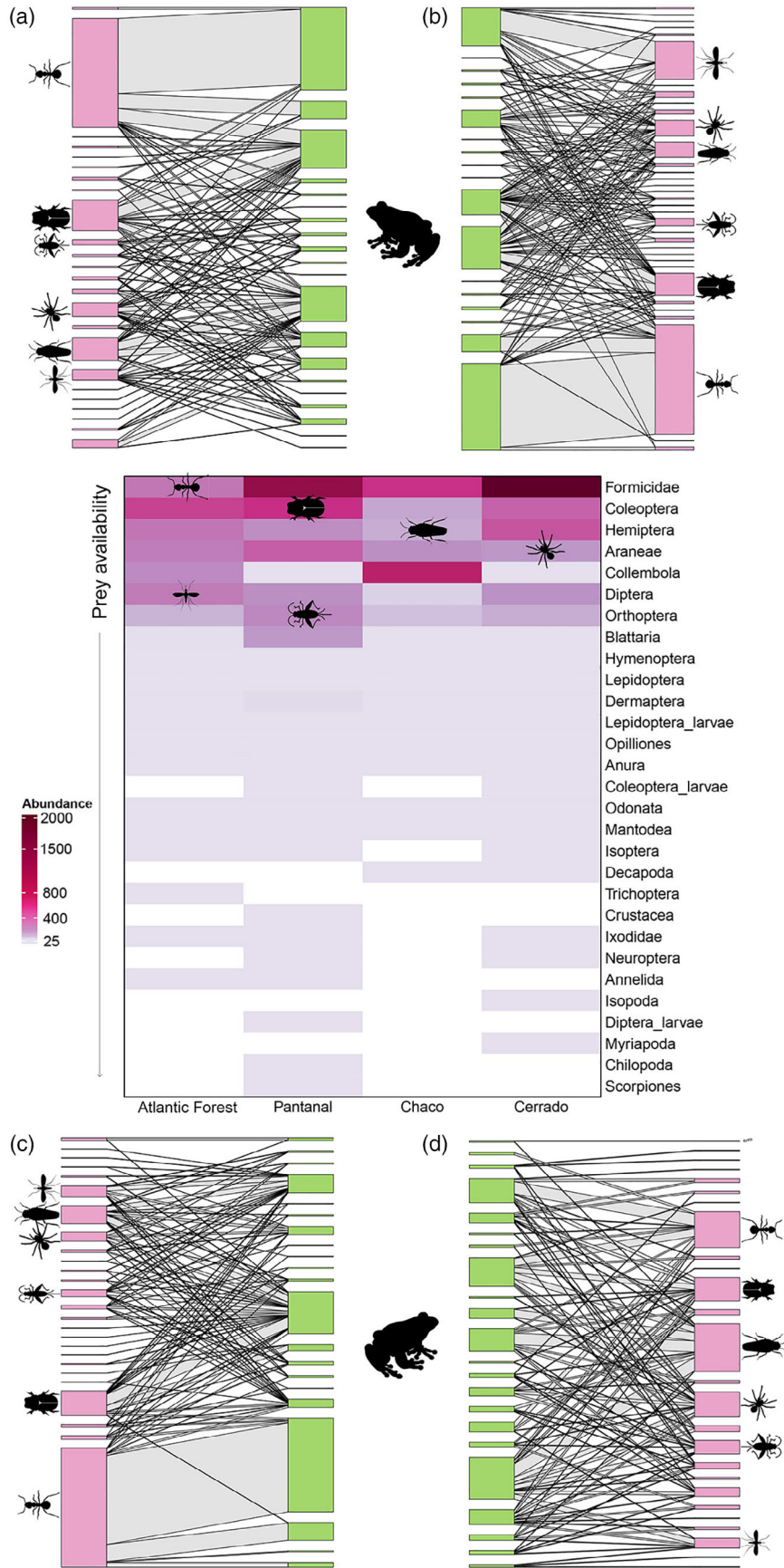
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Figure 3). Prey availability differed between seasons (Likelihood-ratio test [LRT] = 1707, df = 1, p = 0.001), among ecoregions (LRT = 4469, df = 3, p = 0.001), and the interaction between season and ecoregion was also significant (LRT = 822, df = 3, p = 0.001; Figure 4; Appendix S1: Figures S3 and S4). There was no significant difference between the observed network dissimilarities and the dissimilarity between model networks generated by the null model, that is, under the assumption that anurans consume prey according to their local availability (Z = −0.214, p = 0.83, Figure 4; Appendix S1: Figure S5). Taken together, these results mean that differences in network dissimilarity are driven by the variation in the composition of anuran assemblages across space and by the differences in prey availability among ecoregions and seasons.

DISCUSSION

We found that dissimilarity in anuran–prey networks, both among ecoregions and among seasons, was high and primarily driven by interaction rewiring. Whereas species turnover was positively related to geographic distance, interaction rewiring was high across seasons and ecoregions, suggesting different drivers for spatial and temporal variation in network structure.

For most comparisons of networks between seasons, the contribution of species turnover to network dissimilarity was low (or only about as high, when using an alternative partition method) compared to interaction rewiring. A previous work found that frog species composition did not change significantly between seasons in the same study area (Ceron et al., 2020). Yet, species turnover was particularly important for the network dissimilarity between seasons for ponds sampled in the Cerrado. The climate of the Cerrado is highly seasonal, and most ponds dry out in the dry season, forcing frogs to aestivate or seek shelter (Giaretta & Kokubum, 2004) in response to the decrease in the availability of prey and reproductive habitats. Species that require less water (e.g., viviparous species that do not depend on water for reproduction) tend to appear then, which increases the temporal species turnover.

When comparing the networks from different ecoregions, we found that species turnover was the most important component of network dissimilarity between Atlantic Forest and Pantanal, regardless of the method

used for partitioning, whereas the Chaco and the Pantanal had the smallest species turnover between ecoregions (Figure 2; Appendix S1: Figure S2). In the Pantanal, flood pulses are an important force, promoting the homogenization of communities (Junk et al., 2006). These pulses tend to connect ponds, favoring species dispersal among sites within each ecoregion (and among surrounding ecoregions, such as the Chaco, which has similar environmental features) (Ceron et al., 2020). Thus, the flood pulses could allow the colonization of widely distributed species coming from the surrounding regions, decreasing the turnover of species (Ceron et al., 2020). In contrast, the unique environmental features of the Atlantic Forest, besides the geographic distance from Pantanal and Chaco, result in a smaller number of shared species.

We also found that species turnover was positively related to geographical distance, which is likely related to the low dispersal abilities of anurans (Semlitsch, 2008; Smith & Green, 2005; Winterbourn et al., 2007). 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 (Soininen et al., 2007). Similar results were found in plant–pollinator and plant–insect networks (Carstensen et al., 2014; Novotny, 2009), in which geographically distant communities tended to be more dissimilar in species composition. However, network dissimilarity was not related to distance, suggesting that species interactions vary less, across space, than do species identity.

Interaction rewiring was high among seasons and across ecoregions, suggesting that the same set of species vary in their interaction patterns over time and across space. Such differences seem to be mainly driven by variation in prey availability. 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 the United States (CaraDonna et al., 2017), where the turnover of pollinator species was low, but the variation in flowering phenology led to a high turnover in plant–pollinator associations across seasons (CaraDonna et al., 2017; Rabeling et al., 2019). Resource availability plays a central role in classical theories of species diversity and community assembly (Tilman, 1980). Although anurans are often viewed as opportunistic consumers (Wells, 2007),

FIGURE 4 Bipartite networks showing trophic interactions between frog species and their arthropod prey in four different ecoregions: (a) Atlantic Forest, (b) Pantanal, (c) Chaco, and (d) Cerrado. Each rectangle represents one species. Rectangle size represents the importance of each species in the network. The central panel shows the abundance of available prey found in the environment where frogs were collected in the four ecoregions. The color gradient indicates the abundance of each operational taxonomic unit, with white spaces denoting zero and dark red high abundance. Images of insects were obtained from PhyloPic in the public domain

which implies overlapping interaction patterns, we did not find totally connected networks between anurans and their prey, indicating that trophic niche partitioning may act to some extent locally. Besides differences in body size, which may generate differences in the consumed prey (Cohen et al., 1993), habitat use may also create heterogeneity in which prey is effectively available as the most abundant to different species (Inger & Marx, 1961). For instance, even within the same pond, species that forage in limnetic or littoral zones or species with arboreal or terrestrial habits have access to different sets of prey, which may lead to dietary differences. In this study, we saw that changes in prey availability also shape the variation in network structure over space and between seasons.

Climate seasonality influences arthropods' population dynamics depending on species-specific reproductive phenological patterns, so that different groups may peak in different seasons (Pinheiro et al., 2002). Optimal foraging theory predicts that dietary preferences and resource use patterns depend on many factors but are highly determined by the relative abundances of potential food items and the costs associated with consuming them (Emlen, 1966). For example, the relative abundance of a high-quality resource should determine whether or not an item of lower quality will be used (Pyke et al., 1977). This implies changes in the representativeness of prey in the diet, affecting the overall frequency of rewiring (CaraDonna et al., 2017). Because most anurans are generalist gape-limited predators, their diets are restricted mostly by their prey size and availability (Toft, 1980; Wilbur, 1980). We found that the same prey classes were present in most sites, but differences in their relative abundances within sites and among ecoregions may lead to considerable changes in interaction patterns, resulting in high interaction rewiring.

Our findings show how heterogeneous these different communities are, even within the same region. Variation across time and space shows how functionally complex interaction networks can be. Documenting and understanding the drivers of such variation is a much needed step toward a more comprehensive knowledge 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.

AUTHOR CONTRIBUTIONS

Karoline Ceron, Diogo B. Provete, Andréa C. Araujo, Nico Blüthgen, and Diego J. Santana conceived the research. Karoline Ceron and Diego J. Santana collected the data. Karoline Ceron and Mathias M. Pires analyzed the data. Karoline Ceron led the writing with contributions from all authors on interpretation and discussion of the results.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data, R script to reproduce the analyses, and functions used to run the null model (Ceron, 2022) are available in Zenodo: https://doi.org/10.5281/zenodo.6122474.

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REFERENCES

Belmaker, J., and W. Jetz. 2012. "Regional Pools and Environmental Controls of Vertebrate Richness." *The American Naturalist* 179(4): 512–23.

Boyd, C., D. Grünbaum, G. L. Hunt Jr, A. E. Punt, H. Weimerskirch, and S. Bertrand. 2017. "Effects of Variation in the Abundance and Distribution of Prey on the Foraging Success of Central Place Foragers." *Journal of Applied Ecology* 54(5): 1362–72. https://doi.org/10.1111/1365-2664.12832.

CaraDonna, P. J., L. A. Burkle, B. Schwarz, J. Resasco, T. M. Knight, G. Benadi, N. Blüthgen, et al. 2020. "Seeing through the Static: The Temporal Dimension of Plant–Animal Mutualistic Interactions." *Ecology Letters* 24(1): 149–61. https://doi.org/10.1111/ele.13623.

CaraDonna, P. J., W. K. Petry, R. M. Brennan, J. L. Cunningham, J. L. Bronstein, N. M. Waser, and N. J. Sanders. 2017. "Interaction Rewiring and the Rapid Turnover of Plant–Pollinator Networks." *Ecology Letters* 20(3): 385–94.

Carstensen, D. W., M. Sabatino, K. Trøjelsgaard, and L. P. C. Morellato. 2014. "Beta Diversity of Plant-Pollinator Networks and the Spatial Turnover of Pairwise Interactions." *PLoS One* 9(11): e112903.

Ceron, K. 2022. "karolceron/interactionbeta: v1.0 (v1.0)." Zenodo. https://doi.org/10.5281/zenodo.6122474.

Ceron, K., R. Luiz Gustavo, C. S. Oliveira-Santos, D. O. Souza, F. L. S. Mesquita, A. C. A. Caldas, and D. J. Santana. 2019. "Global Patterns in Anuran–Prey Networks: Structure Mediated by Latitude." *Oikos* 128(11): 1537–48.

Ceron, K., D. J. Santana, and F. Valente-Neto. 2020. "Seasonal Patterns of Ecological Uniqueness of Anuran Metacommunities along Different Ecoregions in Western Brazil." *PLoS One* 15(9): e0239874. https://doi.org/10.1371/journal.pone.0239874.

Coblentz, K. E. 2020. "Relative Prey Abundance and Predator Preference Predict Individual Diet Variation in Prey-Switching Experiments." *Ecology* 101(1): e02911. https://doi.org/10.1002/ecy.2911.

Cohen, J. E., S. L. Pimm, P. Yodzis, and J. Saldaña. 1993. "Body Sizes of Animal Predators and Animal Prey in Food Webs." *Journal of Animal Ecology* 62: 67–78.

Crump, M. L., and N. J. Scott, Jr. 1994. "Standard Techniques for Inventory and Monitoring - Visual Encounter Surveys." In *Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians*, edited by W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, 84–92. Washington, DC: Smithsonian Institution Press.

Dáttilo, W., and H. L. Vasconcelos. 2019. "Macroecological Patterns and Correlates of Ant–Tree Interaction Networks in Neotropical Savannas." *Global Ecology and Biogeography* 28(9): 1283–94. https://doi.org/10.1111/geb.12932.

Dormann, C. F., B. Gruber, and J. Fründ. 2008. "Introducing the Bipartite Package: Analysing Ecological Networks." Interactions. 1: 0.2413793. http://portal.uni-freiburg.de/biometrie/mitarbeiter/dormann/publications-dormann/Dormann2008Rnews.pdf.

Emlen, J. M. 1966. "The Role of Time and Energy in Food Preference." *The American Naturalist* 100(916): 611–7.

Fründ, J. 2021. "Dissimilarity of Species Interaction Networks: How to Partition Rewiring and Species Turnover Components." *Ecosphere* 12(7): e03653.

Giaretta, A. A., and M. d. C. Kokubum. 2004. "Reproductive Ecology of *Leptodactylus furnarius* Sazima & Bokermann, 1978, a Frog that Lays Eggs in Underground Chambers." *Herpetozoa* 16: 115–26.

Goslee, S. C., and D. L. Urban. 2007. "The Ecodist Package for Dissimilarity-Based Analysis of Ecological Data." *Journal of Statistical Software* 22(7): 1–19.

Grimm, A. M. 2011. "Interannual Climate Variability in South America: Impacts on Seasonal Precipitation, Extreme Events, and Possible Effects of Climate Change." *Stochastic Environmental Research and Risk Assessment* 25(4): 537–54.

Guimarães, P. R. 2020. "The Structure of Ecological Networks across Levels of Organization." *Annual Review of Ecology, Evolution, and Systematics* 51: 433–60. https://doi.org/10.1146/annurev-ecolsys-012220-120819.

Harris, M. B., W. Tomas, G. Mourao, C. J. Da Silva, E. Guimaraes, F. Sonoda, and E. Fachim. 2005. "Safeguarding the Pantanal Wetlands: Threats and Conservation Initiatives." *Conservation Biology* 19(3): 714–20.

Inger, R. F., and H. Marx. 1961. "The Food of Amphibians." In *Exploration Du Parc National de l' Upemba 64*, Vol 86, edited by M. G. F. De Witte, R. F. Inger, and H. Marx. Bruxelles: Institut des Parcs Nationaux du Congo et du Ruanda-Urundi.

Ings, T. C., J. M. Montoya, J. Bascompte, N. Blüthgen, L. Brown, C. F. Dormann, F. Edwards, et al. 2009. "Ecological Networks–Beyond Food Webs." *Journal of Animal Ecology* 78(1): 253–69.

Jabot, F., F. Laroche, F. Massol, F. Arthaud, J. Crabot, M. Dubart, S. Blanchet, F. Munoz, P. David, and T. Datry. 2020. "Assessing Metacommunity Processes through Signatures in Spatiotemporal Turnover of Community Composition." *Ecology Letters* 23(9): 1330–9. https://doi.org/10.1111/ele.13523.

Janzen, D. H. 1973. "Sweep Samples of Tropical Foliage Insects: Description of Study Sites, with Data on Species Abundances and Size Distributions." *Ecology* 54(3): 659–86.

Junk, W. J., C. N. Da Cunha, K. M. Wantzen, P. Petermann, C. Strüssmann, M. I. Marques, and J. Adis. 2006. "Biodiversity and its Conservation in the Pantanal of Mato Grosso, Brazil." *Aquatic Sciences* 68(3): 278–309.

Kemp, J. E., D. M. Evans, W. J. Augustyn, and A. G. Ellis. 2017. "Invariant Antagonistic Network Structure despite High Spatial and Temporal Turnover of Interactions." *Ecography* 40(11): 1315–24.

Kikuchi, R. M., and V. S. Ueida. 1998. "Composição Da Comunidade de Invertebrados de Um Ambiente Lótico Tropical e Sua Variação Espacial e Temporal." *Oecologia Brasiliensis* 5(1): 11.

Leibold, M. A., and J. M. Chase. 2017. *Metacommunity Ecology*, Vol 59. Princeton, NJ: Princeton University Press.

Lopez, D. N., P. A. Camus, N. Valdivia, and S. A. Estay. 2017. "High Temporal Variability in the Occurrence of Consumer–Resource Interactions in Ecological Networks." *Oikos* 126(12): 1699–707. https://doi.org/10.1111/oik.04285.

Luna, P., Y. Peñaloza-Arellanes, A. L. Castillo-Meza, J. H. García-Chávez, and W. Dáttilo. 2018. "Beta Diversity of Ant-Plant Interactions over Day-Night Periods and Plant Physiognomies in a Semiarid Environment." *Journal of Arid Environments* 156: 69–76.

McKinney, A. M., and K. Goodell. 2011. "Plant–Pollinator Interactions between an Invasive and Native Plant Vary between Sites with Different Flowering Phenology." *Plant Ecology* 212(6): 1025–35. https://doi.org/10.1007/s11258-010-9882-y.

Michelin, G., K. Ceron, and D. J. Santana. 2020. "Prey Availability Influences the Diet of *Scinax fuscomarginatus* in a Cerrado Area, Central Brazil." *Animal Biodiversity and Conservation* 43(2): 169–75.

Moleón, M., E. Sebastián-González, J. A. Sánchez-Zapata, J. Real, M. M. Pires, J. M. Gil-Sánchez, J. Bautista, et al. 2012. "Changes in Intrapopulation Resource Use Patterns of an Endangered Raptor in Response to a Disease-Mediated Crash in Prey Abundance." *Journal of Animal Ecology* 81(6): 1154–60. https://doi.org/10.1111/j.1365-2656.2012.02006.x.

Mouquet, N., and M. Loreau. 2003. "Community Patterns in Source-Sink Metacommunities." *The American Naturalist* 162(5): 544–57.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Da Fonseca, and J. Kent. 2000. "Biodiversity Hotspots for Conservation Priorities." *Nature* 403(6772): 853.

Nori, J., R. Torres, J. N. Lescano, J. M. Cordier, M. E. Periago, and D. Baldo. 2016. "Protected Areas and Spatial Conservation Priorities for Endemic Vertebrates of the Gran Chaco, One of the Most Threatened Ecoregions of the World." *Diversity and Distributions* 22(12): 1212–9.

Novotny, V. 2009. "Beta Diversity of Plant–Insect Food Webs in Tropical Forests: A Conceptual Framework." *Insect Conservation and Diversity* 2(1): 5–9.

Nuvoloni, F. M., R. J. F. Feres, and B. Gilbert. 2016. "Species Turnover through Time: Colonization and Extinction Dynamics across Metacommunities." *The American Naturalist* 187(6): 786–96.

Pinheiro, F., I. R. Diniz, D. Coelho, and M. P. S. Bandeira. 2002. "Seasonal Pattern of Insect Abundance in the Brazilian Cerrado." *Austral Ecology* 27(2): 132–6.

Poisot, T. 2021. "Dissimilarity of Species Interaction Networks: Quantifying the Effect of Turnover and Rewiring." EcoEvoRxiv. https://doi.org/10.32942/osf.io/gxhu2.

Poisot, T., E. Canard, D. Mouillot, N. Mouquet, and D. Gravel. 2012. "The Dissimilarity of Species Interaction Networks." *Ecology Letters* 15(12): 1353–61.

Pott, A., and V. J. Pott. 2004. "Features and Conservation of the Brazilian Pantanal Wetland." *Wetlands Ecology and Management* 12(6): 547–52.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. "Optimal Foraging: A Selective Review of Theory and Tests." *The Quarterly Review of Biology* 52(2): 137–54.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing.

Rabeling, S. C., J. Le Lim, R. Tidon, J. L. Neff, B. B. Simpson, and S. Pawar. 2019. "Seasonal Variation of a Plant-Pollinator Network in the Brazilian Cerrado: Implications for Community Structure and Robustness." *PLoS One* 14(12): e0224997.

Ribeiro, M. C., J. P. Metzger, A. C. Martensen, F. J. Ponzoni, and M. M. Hirota. 2009. "The Brazilian Atlantic Forest: How Much Is Left, and how Is the Remaining Forest Distributed? Implications for Conservation." *Biological Conservation* 142: 1141–53. https://doi.org/10.1016/j.biocon.2009.02.021.

Semlitsch, R. D. 2008. "Differentiating Migration and Dispersal Processes for Pond-Breeding Amphibians." *The Journal of Wildlife Management* 72(1): 260–7. https://doi.org/10.2193/2007-082.

Shmida, A. V. I., and M. V. Wilson. 1985. "Biological Determinants of Species Diversity." *Journal of Biogeography* 12: 1–20.

Simanonok, M. P., and L. A. Burkle. 2014. "Partitioning Interaction Turnover among Alpine Pollination Networks: Spatial, Temporal, and Environmental Patterns." *Ecosphere* 5(11): 1–17.

Smith, A. J., and D. M. Green. 2005. "Dispersal and the Metapopulation Paradigm in Amphibian Ecology and Conservation: Are all Amphibian Populations Metapopulations?" *Ecography* 28(1): 110–28. https://doi.org/10.1111/j.0906-7590.2005.04042.x.

Soininen, J., J. J. Lennon, and H. Hillebrand. 2007. "A Multivariate Analysis of Beta Diversity across Organisms and Environments." *Ecology* 88(11): 2830–8.

Souza, C. S., P. K. Maruyama, K. C. B. S. Santos, I. G. Varassin, C. L. Gross, and A. C. Araujo. 2021. "Plant-Centred Sampling Estimates Higher Beta Diversity of Interactions than Pollinator-Based Sampling across Habitats." *New Phytologist* 230(6): 2501–12. https://doi.org/10.1111/nph.17334.

Tilman, D. 1980. "Resources: A Graphical-Mechanistic Approach to Competition and Predation." *The American Naturalist* 116(3): 362–93.

Toft, C. A. 1980. "Feeding Ecology of Thirteen Syntopic Species of Anurans in a Seasonal Tropical Environment." *Oecologia* 45: 131–41.

Wang, Y. I., U. Naumann, S. T. Wright, and D. I. Warton. 2012. "Mvabund–An R Package for Model-Based Analysis of Multivariate Abundance Data." *Methods in Ecology and Evolution* 3(3): 471–4.

Wells, K. D. 2007. *The Ecology and Behavior of Amphibians.* Chicago, IL: University of Chicago Press.

Wilbur, H. M. 1980. "Complex Life Cycles." *Annual Review of Ecology and Systematics* 11(1): 67–93.

Winterbourn, M. J., W. Lindsay Chadderton, S. A. Entrekin, J. L. Tank, and J. S. Harding. 2007. "Distribution and Dispersal of Adult Stream Insects in a Heterogeneous Montane Environment." *Fundamental and Applied Limnology/Archiv Für Hydrobiologie* 168(2): 127–35.

Zak, M. R., M. Cabido, and J. G. Hodgson. 2004. "Do Subtropical Seasonal Forests in the Gran Chaco, Argentina, Have a Future?" *Biological Conservation* 120(4): 589–98.

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