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Temporal variation in plant–pollinator networks from seasonal tropical environments: Higher specialization when resources are scarce

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Abstract

1. The temporal dynamics of plant phenology and pollinator abundance across seasons should influence the structure of plant–pollinator interaction networks. Nevertheless, such dynamics are seldom considered, especially for diverse tropical networks.

2. Here, we evaluated the temporal variation of four plant–pollinator networks in two seasonal ecosystems in Central Brazil (Cerrado and Pantanal). Data were gathered on a monthly basis over 1 year for each network. We characterized seasonal and temporal shifts in plant–pollinator interactions, using temporally discrete networks. We predicted that the greater floral availability in the rainy season would allow for finer partitioning of the floral niche by the pollinators, i.e. higher specialization patterns as previously described across large spatial gradients. Finally, we also evaluated how sampling restricted to peak flowering period may affect the characterization of the networks.

3. Contrary to our expectations, we found that dry season networks, although characterized by lower floral resource richness and abundance, showed higher levels of network-wide interaction partitioning (complementary specialization and modularity). For nestedness, though, this between-seasons difference was not consistent. Reduced resource availability in the dry season may promote higher interspecific competition among pollinators leading to reduced niche overlap, thus explaining the increase in specialization.

4. There were no consistent differences between seasons in species-level indices, indicating that higher network level specialization is an emergent property only seen when considering the entire network. However, bees presented higher values of specialization and species strength in relation to other groups such as flies and wasps, suggesting that some plant species frequently associated with bees are used only by this group.

5. Our study also indicates that targeted data collection during peak flowering generates higher estimates of network specialization, possibly because species activity spans longer periods than the targeted time frame. Hence, depending on the period of data collection, different structural values for the networks of interactions may be found.

6. *Synthesis.* Plant–pollinator networks from tropical environments have structural properties that vary according to seasons, which should be taken into account in the description of the complex systems of interactions between plants and their pollinators in these areas.

1 | INTRODUCTION

Ecological communities are complex and dynamic, comprised of temporally variable populations that interact in distinct ways. Species activities follow variations in the environment, associated with resource constraints and changes in species interactions (Rosenzweig et al., 2008; Stiles, 1977; Wright, 2002). Such temporal dynamics affect the local occurrence of species, and their role within communities through effects on development, life cycle and behaviour (Trøjelsgaard & Olesen, 2016). The diversity of plant phenological patterns, in this sense, is one of the main mechanisms responsible for the maintenance of biodiversity (Morellato et al., 2016). Because most plants are associated with animals for pollination—especially in the tropics (Ollerton, Winfree, & Tarrant, 2011), the temporal dynamics of plants and animals at different scales, including those associated with seasons, should translate to important changes on the structure of plant–pollinator interaction networks (Dupont, Padrón, Olesen, & Petanidou, 2009; Martín González, Allesina, Rodrigo, & Bosch, 2012; Olesen, Bascompte, Elberling, & Jordano, 2008; Trøjelsgaard & Olesen, 2016). Despite a clear appreciation of the temporally dynamic nature of populations and communities (e.g. Chesson & Huntly, 1989; Clements, 1936; Cowles, 1899), interaction networks are often treated as temporally static entities (Poisot, Stouffer, & Gravel, 2015).

Previous studies, mostly conducted in temperate regions, have indeed demonstrated that plant–pollinator networks show considerable variability through time at different temporal scales, from within day variation to over a time span of centuries (Baldock, Memmott, Ruiz-Guajardo, Roze, & Stone, 2011; Burkle, Marlin, & Knight, 2013; Dupont et al., 2009; Petanidou, Kallimanis, Tzanopoulos, Sgardelis, & Pantis, 2008). Temporal variation may be caused by fluctuations in the number of species and interactions, as well as by changes on the identity of species and interactions performed by them, which affect the entire structure of networks (Burkle & Alarcón, 2011; Morellato et al., 2016; Olesen et al., 2008; Petanidou et al., 2008). However, studies on temporal interaction networks are still scarce in tropical

environments where species diversity is higher and plant–animal activity is not restricted to favourable seasons (Bender et al., 2017; Vizentin-Bugoni et al., 2018; Wright, 2002). Studies on such environments may offer new perspectives on how interactions between plants and their mutualistic partners are temporally structured (Bender et al., 2017; Weinstein & Graham, 2017; Wright, 2002).

For instance, the inclusion of pollinator groups not commonly encountered in networks from temperate areas, such as vertebrates (Vizentin-Bugoni et al., 2018), could reveal distinct dynamics within the whole network (Bergamo et al., 2017; Watts, Dormann, González, & Ollerton, 2016). At the same time, climatic seasonality acts as the main factor determining plant phenological patterns even in the tropics (Frankie, Baker, & Opler, 1974; Morellato et al., 2016). Thus, seasonality of floral availability might be an important driver affecting network structure. Especially in seasonal tropical environments, such as the savannas and dry forests, the community-wide peak flowering times occur during the most favourable season, when highest floral diversity and associated pollination modes are observed (Ramirez, 2006). Previous studies indicated greater availability of floral resources is associated to a higher diversity of pollinators, leading them to specialize on certain floral traits (Fontaine, Dajoz, Meriguet, & Loreau, 2006; Ghazoul, 2006) and to show higher floral constancy (Brosi, 2016). Thus, higher specialization may be expected during the most favourable season (Bender et al., 2017; Magrach, González-Varo, Boiffier, Vilà, & Bartomeus, 2017). From the pollinator's perspective, using a plant with a well-matched trait also increases its ability to efficiently extract resources (Maglianesi, Blüthgen, Böhning-Gaese, & Schleuning, 2014), and such specialization may be especially favoured when resource availability increases, according to predictions of optimal foraging theory (Robinson & Wilson, 1998). Conversely, lower availability of resources was previously associated with higher generalization of pollinators (Fontaine, Collin, & Dajoz, 2008; Schoener, 1971). Therefore, pollinator diet breadth is a flexible trait resulting from behavioural responses to resource availability (Fontaine et al., 2008). How such intrinsic dynamics of plant–pollinator interactions may lead to temporal variation in

the network structure in tropical areas, with year-round flowering activity of plants and including different pollinator groups, however, have not yet been investigated.

Here, we evaluated the temporal variation of four plant–pollinator networks from two seasonal ecosystems in Central Brazil (Cerrado and Pantanal), comprised of four distinct vegetation types: Cerrado woody grassland (*Campo sujo*), Chaco, Palm swamp (*Vereda*) and Pantanal wetland. We characterized the seasonal dynamics of plant–pollinator interactions using temporally discrete networks. For this purpose, we first analysed several network indices that characterize their overall structure. Then, we investigated how the metrics in these networks change across the seasons, including for periods of higher availability of flowers within seasons when data collection is often concentrated (hereafter referred as "peak season networks"). Finally, we asked which community variables may explain changes in the structure of these networks over time. We predicted that greater floral resource availability and higher functional diversity (FD) values expected for the rainy season would allow for finer partitioning of the floral niche by the pollinators, i.e. higher specialization and modularity, accompanied by lower overlap on the interaction between species, i.e. lower nestedness.

2 | MATERIALS AND METHODS

2.1 | Study site and periods

We collected data on plants and potential pollinators in four communities with distinct vegetation types located in the Central region of Brazil, being all characterized by a marked seasonality (Figure S1). Data were collected using similar sampling procedures, according to characteristics of the study site. These study sites have a warm and rainy season from October to March and a relatively colder and dry period from April to September. All study sites are characterized by high and threatened biodiversity (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Ramsar and MMA, 2010), and are located within geographical gaps of plant–pollinator network studies (Vizentin-Bugoni et al., 2018). Below, we describe each of the study sites and periods of data collection.

2.1.1 | Cerrado woody grassland (*Campo sujo*)

Vegetation consists of an herbaceous/low, xerophyllous shrub layer dominated by grasses and a few scattered shrubs (Munhoz & Felfili, 2006). Data were collected from October 2008 to September 2009 at Chapadão do Céu municipality, Emas National Park–PNE (104.359 ha of total area, state of Goiás: 52°02′53″W, 18°16′50″S). Fieldwork was conducted in 37 plots of 15 × 25 m, at least 50 m away from each other, totalizing 560 hr and 13,875 m^2 of sampling.

2.1.2 | Chaco

Vegetation is characterized by a discontinuous canopy and predominance of spiny and microphyllous species (Souza et al., 2017). Data were collected from November 2009 to October 2010 within the Porto Murtinho municipality, at the Retiro Conceição farm (10 ha, state of Mato Grosso do Sul: 57°53′06″W, 21°42′04″S). Fieldwork was conducted in five plots of 200 × 3 m, at least 50 m away from each other, totalizing an area of 3,000 m^2 and 384 hr of sampling.

2.1.3 | Palm swamp (*Vereda*)

This type of vegetation is usually associated with water springs, which allows for some soil humidity even during the dry season. It is characterized by the dominance of *Mauritia flexuosa* palms (Moreira, Eisenlohr, Pott, Pott, & Oliveira-Filho, 2015; Souza, Aoki, Ribas, Pott, & Sigrist, 2016), which represent the upper layer of vegetation; understorey includes some herbs and shrubs. Data were collected from September 2012 to August 2013 at Campo Grande municipality, in the private natural reserve "Guariroba" (5 ha, state of Mato Grosso do Sul: 54°23′54″W, 20°32′39″S). Fieldwork was conducted in eight plots of 50 m × 3 m, at least 10 m away from each other, totalizing an area of 1,200 m^2 and 288 hr of sampling.

2.1.4 | Pantanal wetland

Studied plots included areas of flooded savanna dominated by *Tabebuia aurea* and *Byrsonima cydoniifolia* (mono-dominant stands) and areas of riparian forest (Nunes da Cunha & Junk, 2009), which are representative habitat types in the region. Data were collected from October 2014 to September 2015, close to the Pantanal Field Station of Federal University of Mato Grosso do Sul (100 ha, state of Mato Grosso do Sul: 57°02′22.80″W; 19°34′52.24″S), in the Miranda subregion of South Pantanal. For each sampling, we established 60 plots of 10 × 10 m, at least 50 m away from each other, totalizing an area of 6,000 m^2 and 576 hr of sampling.

2.2 | Plant–pollinator interactions sampling

In all communities, except for the Cerrado, a monthly sampling of pollinators was performed between 07:00 and 17:00 hr for all flowering plants. For the Cerrado, the sampling was done every 30 days, and some months were not sampled. Ten (Chaco, Vereda, Pantanal) or five (Cerrado) minutes of focal observations were performed per individual plant, in all periods of the day (usually four/five days of data collection per month). Sampling of pollinators was conducted in all flowering individuals inside the plots. Thus, the sampling effort depended on the species occurrence and abundance, resulting in a variable observation time for each species (range, $M \pm SD$): Chaco: 10–4,500 minutes, $\bar{x} = 247 \pm 600$ minutes per plant species; Cerrado: 10–990 minutes, $\bar{x} = 55 \pm 85$ minutes per plant species; Palm swamp: 10–9,900 minutes, $\bar{x} = 565 \pm 846$ minutes per plant species; Pantanal: 10–1,780 minutes, $\bar{x} = 177 \pm 293$ minutes per plant species. In order to include time-dependent variations on plant–pollinator interactions, all plots were recorded at different periods of the day. Also, focal observations on a given plant species were performed both in the morning and in the afternoon. We

recorded the number of flowers visited by each floral visitor, which were identified in the field or collected for posterior identification in the laboratory with the help of experts. Collected samples were later deposited at the Zoological Collection of Federal University of Mato Grosso do Sul (UFMS). We only included in the analysis legitimate interactions, when the floral visitor contacted the reproductive structures of the flowers, indicating potential for pollination. Hereafter, these legitimate visitors are referred as "pollinators," although we did not evaluate their role in the subsequent production of fruits to visited plant species. Vouchers for all plant species were collected, identified and deposited in the CGMS Herbarium. The family names followed the Angiosperm Phylogeny Group (APG IV, 2016), and species names were confirmed in the Plant list database (http://www.theplantlist.org/) and updated/corrected whenever necessary.

2.3 | Plant–pollinator interaction networks

For each of the study sites, we built quantitative interactions matrices using the number of flowers visited by a pollinator as the frequency for the links among pairs of plants and pollinators. For each community, we constructed a summarized network considering the entire period of sampling (complete networks) and two seasonal networks considering the dry and rainy season separately. We also estimated the sampling completeness for each constructed network, following Chacoff et al. (2012), but considering each combination of a pollinator and plant species as equivalent of "species" and the frequency of each pairwise interaction as their "abundances" (Ramírez-Burbano et al., 2017; Vizentin-Bugoni et al., 2016). Using these data, we computed the Chao 1 estimator of species richness using the iNEXT package (Hsieh, Ma, & Chao, 2014) in R (R Development Core Team, 2016). With the same package, we also plotted individual-based rarefaction and extrapolation curves with Hill numbers for each network (Chao et al., 2014; Hsieh et al., 2014).

We additionally constructed peak season networks, considering distinct time intervals during the peak flowering period in the studied habitats to illustrate how temporally targeted sampling of plant–pollinator networks influences the characterization of communities. We separated rainy season into two periods according to the months of highest flowering availability (beginning of rainy season: November and December) and end of the rainy season (January and February). For Cerrado, as the data collection was separated in thirty days, only one peak flowering network was elaborated. We calculated metrics illustrating distinct structural properties of the network, focusing on quantitative network indices, which were previously shown to be less sensitive to sampling effort (Fründ, McCann, & Williams, 2016; Vizentin-Bugoni et al., 2016). Nestedness quantifies the degree to which interactions of specialized species are subsets of interactions of the more generalist species in the network, and was quantified by the wNODF index (Almeida-Neto & Ulrich, 2011) which illustrates whether the core of the network also contains the highest frequencies of interactions (Almeida-Neto & Ulrich, 2011). Network-wide specialization was estimated by the H_2' index, which describes if species restrict their interactions from

those randomly expected based on a partner's availability (Blüthgen, Menzel, & Blüthgen, 2006). Modularity indices quantify the prevalence of interactions within subsets of species in the community. We calculated weighted modularity using the QuanBiMo algorithm (Dormann & Strauss, 2014). The modularity algorithms used here are built on optimization procedures that iteratively maximize the modularity of the final solution, meaning that the algorithm is stochastic and module arrangement as well as the value of Q might vary slightly between runs (Dormann & Strauss, 2014). We repeated the analysis ten times for each network and kept the module conformation that yielded the highest Q-value. All network metrics were calculated using the package "bipartite" in R (Dormann, Gruber, & Fründ, 2008).

Network metrics can be affected by intrinsic characteristics such as the number of interacting species and sampling effort (Blüthgen et al., 2006; Fründ et al., 2016; Vizentin-Bugoni et al., 2016), hence the significance of metrics is assessed by comparison with null model networks. Here, we used the Patefield null model, which fixes the network size and the marginal totals, i.e. species richness and species' total number of interactions, while shuffling interactions randomly (Patefield, 1981). We estimated the 95% confidence interval for each metric from the 10,000 simulated values, and a metric value was considered significant if it did not overlap with the confidence interval. We additionally used another null model, proposed by Vázquez, Morris, and Jordano (2005), which constrains the connectance, network size and total number of interactions. Moreover, besides comparing the "raw" network metrics, we also compared Δ-transformed metrics between seasons. Δ transformation is done by subtracting the mean value of a metric obtained by multiple randomizations from the observed value and has been shown to minimize differences owed to sampling in network metrics used here (Dalsgaard et al., 2017).

2.4 | Availability and diversity of floral resources

To evaluate the potential factors determining the structure of plant–pollinator networks across seasons, we quantified the availability and diversity of floral resources. We considered the richness of blooming species as well as floral abundance as the simplest indicators of resource availability. In addition, we also recorded floral traits for each of the plant species observed to quantify further floral trait diversity across time. Traits evaluated were type of flower (inconspicuous, tube, gullet, flag, brush, chamber; sensu Machado & Lopes, 2004), flower width and length, and reward offered to pollinators (pollen, nectar, oil, floral tissue). We used colour as seen by humans, using colour classes similar to those used by previous related studies (e.g. Carvalheiro et al., 2014). We defined four classes of flower colour: white (includes all white and very pale flowers); yellow; warm colours (includes all orange, red and pink/"salmon" flowers); cold colours (includes all blue and purple flowers). Flowers with more than one colour were classified according to the predominant colour.

These traits were combined into two measures of FD, based on the computation of pairwise Gower distance between species projected into a functional trait space with a Principal Coordinate

Analysis (Villéger, Mason, & Mouillot, 2008). We used two measures to quantify distinct facets of FD in the flowering plant communities: functional evenness and dispersion (FEve and FDis; Villéger et al., 2008; Laliberté & Legendre, 2010). FEve quantifies the regular distribution of individual species abundances in the trait space, and ranges between 0 and 1. Higher values indicate a more equally spaced distance among species (Villéger et al., 2008). FDis is computed by projecting a community centroid in the trait space and calculating the mean distance of species in the community to the centroid, with high values indicating the presence of functionally distinct species (Laliberté & Legendre, 2010). Both FEve and FDis accounts for differences in species frequencies in the community by weighting their calculations by species relative abundances, here represented by flower abundance.

2.5 | Species roles in networks

To assess the role of species within networks and how it varies between the seasons, we calculated three species-level indices that capture distinct topological properties of a species: (1) species strength, which is the sum of the proportions of interactions performed by a given species across all its interaction partners. Higher values indicate that more plants depend on a specific pollinator species, and vice versa (Bascompte, Jordano, & Olesen, 2006) and (2) species-level specialization index d', which quantifies how interaction frequencies of a given species deviate in relation to the availability of interaction partners in the network, with higher values indicating higher specialization (Blüthgen et al., 2006). The availability of plants was represented by their floral abundance, while for pollinators it was represented by the sum of all interactions recorded (Blüthgen et al., 2006). Calculations of all network-related indices were conducted with the "bipartite" package version 2.05 (Dormann et al., 2008) in R (R Development Core Team, 2016).

2.6 | Statistical analysis

We first contrasted plant–pollinator network indices according to the seasons within habitats with linear mixed-effects models with "lme4" package in R (Bates, Mächler, Bolker, & Walker, 2015). We considered network indices as response variables, with season as fixed- and habitats as random-factors in the models. Whether season had significant effects on network indices was tested using a likelihood ratio test comparing the model with and without the fixed factor using the R package "car" (Fox & Weisberg, 2011). Similar models were constructed considering sampling completeness, plant richness, floral abundance ($\log_{10}$ transformed) and functional diversity (FDis and FEve) of flowering plants as distinct measures of floral resource availability. Finally, in order to compare the differences in pollinator diversity between seasons, we used the Shannon diversity index (H') as a response variable in a similar model, with pollinator visitation frequency as an estimate of their abundances.

We also evaluated whether seasons, for plants and pollinators, and functional/taxonomic groups of pollinators were important

determinants for species-level indices. Pollinators were classified as bees, flies, wasps, beetles, birds or butterflies. Ants, crickets and flower bugs were grouped into a unique category named "others," as these were less diverse (eleven, two and nine species, respectively) and performed few interactions (fifteen, two and eleven interactions, respectively). We applied linear mixed effect models in the species-level data, including seasons (dry or rainy) and functional groups in the pollinator model as fixed effects and the species identity nested within vegetation type as random effects with "lme4" (Bates et al., 2015). For species strength, we $\log_{10}$ transformed the data to improve the distribution of the residuals. After detecting that pollinator group was a significant factor, we conducted multiple comparisons (post hoc Tukey test) using the function glht in the package "multcomp" (Hothorn, Bretz, & Westfall, 2008). We also repeated the species-level analysis considering only the species which occurred both in the dry and rainy seasons, with the seasons as fixed and species identity nested within the vegetation type as random effects. All analyses were conducted in R (R Development Core Team, 2016).

3 | RESULTS

A total of 29,077 flower visits from 349 animal species (or morphospecies) to 278 plant species, distributed in 73 families, were recorded across all sites sampled. The Cerrado network presented a greater number of plant and pollinator species (104 plant and 131 pollinator species), followed by the Pantanal (103 plants and 70 pollinators), Chaco (62 plants and 89 pollinators) and Vereda (25 plants and 109 pollinators) networks (Table S1 and Figure 1). Regarding the plant families recorded, the Asteraceae (43 species) was the most frequently visited, receiving 16% from the total of visits, followed by plants in the Rubiaceae (9%) and the Euphorbiaceae (9%). The most frequent pollinators were bees (34%) and flies (25%), followed by wasps (15%), beetles (10%) and butterflies/moths (8%). *Apis mellifera* was the most frequent bee pollinator (15% of all bee interactions) and also the most frequent among all recorded pollinators (9% of all interactions). Plant–pollinator network data were deposited in Dryad Digital Repository (Souza et al., 2018). Sampling completeness is equivalent between seasons across the studied networks ($\chi^2 = 1.32$, $p = .52$; Table S2 and Figure S2).

3.1 | Network metrics and resource availability across seasons

All networks were more specialized and modular than expected by the null models (see Table S1). Moreover, dry season networks had higher specialization than those from the rainy season across all communities (Table 1 and Figure 2a). Dry season networks were also generally more modular than rainy season ones (Table 1 and Figure 2b). For nestedness, no consistent differences among seasons were found (Table 1 and Figure 2c).
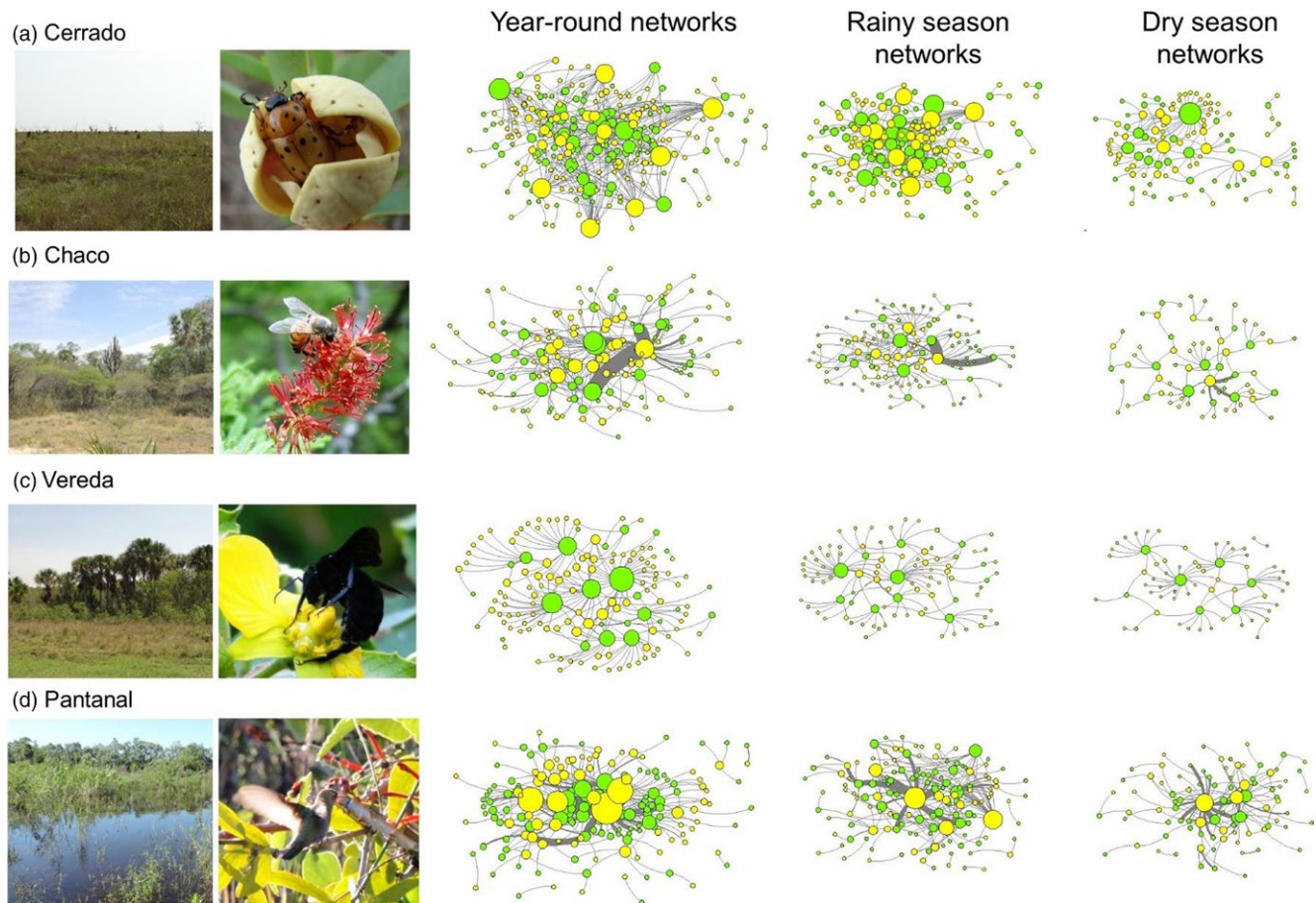
FIGURE 1 Left: views of studied formations and representative interactions. (a) In Cerrado, *Cyclocephala quatuordecimpunctata* visiting *Annona glaucophylla*, (b) In Brazilian Chaco, *Prosopis rubriflora* being visited by the exotic bee *Apis mellifera*; (c) in Vereda, the bee *Bombus morio* visiting a flower of *Ludwigia octovalvis* and (d) in Pantanal, the hummingbird *Hylocharis chrysura* visiting a flower of *Psittacanthus cordatus*. Right: Year-round, rainy and dry season networks of interactions for each studied formation (kamada-kawai graph in Pajek Program). Pollinator and plant species are represented by yellow and green circles, respectively. The thickness of lines and size of circles represent the number of flowers visited by each pollinator, and the abundance of each species, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

Furthermore, targeted sampling of interaction data during the peak flowering season usually returned more specialized networks than complete networks (Table 2 and Figure 2e). No such trend, however, was observed for modularity (Table 2 and Figure 2f). When considering nestedness, results were not consistent, but null model corrected values indicated a tendency of higher values for the complete networks in relation to peak networks (Table 2 and Figure 2g).

In contrast to network metrics, greater floral resource availability was found in the rainy season compared to the dry season networks (flowering plant richness: dry season = 9.7 ± 6.3 and rainy season = 16.2 ± 8.4; χ^2 = 77.23, p = .005; abundance of flowers: dry season = 11,816.73 ± 17,756.26 and rainy = 15,051.35 ± 20,806.84; χ^2 = 5.67, p = .017; Table 1). However, contrary to what we expected, FD of flowering plants did not differ between seasons (Table 1 and Figure 2d). Finally, the diversity of pollinators in the dry period (H' Chaco = 1.66; Cerrado = 2.58; Vereda = 2.11; Pantanal = 2.88) was lower than in the rainy season (H' Chaco = 3.71; Cerrado = 4.00; Vereda = 4.13; Pantanal = 3.36, χ^2 = 12.32, p < .001).

3.2 | Species roles and seasonality

In contrast to network level specialization and modularity, no species-level differences on specialization (χ^2 = 2.05, p = .15) or species strength (χ^2 = 2.16, p = .14) were detected for plants between dry and rainy seasons (Figures 3a,b). For the pollinators, likewise, species-level indices did not differ between seasons (specialization: χ^2 = 0.44, p = .50; species strength: χ^2 = 0.17, p = .68; Figures 3c,d). When we considered only species of pollinators and plants that occurred in both seasons (69 spp. of plants; 71 spp. of pollinators), plants were more specialized in the dry season (χ^2 = 6.19, p = .01) but no difference was detected for species strength (χ^2 = 2.16, p = .81; Tables S3–S5). For pollinators occurring in both seasons, species-level indices did not differ (specialization: χ^2 = 0.03, p = .85; species strength: χ^2 = 1.66, p = .19). In contrast, distinct groups of pollinators showed some differences on their roles within the networks. Notably, wasps showed lower specialization than other groups such as bees and butterflies, while flies were also less specialized than beetles

TABLE 1 Comparison of network metrics and floral resource availability between the dry and rainy season from seasonal tropical plant–pollinator networks. For network metrics, we report the uncorrected as well as network metrics corrected by two null models (Patefield and Vaznull). Comparisons were done with mixed effect models, using study sites as a random variable. Significance for the terms were obtained from a likelihood ratio test by comparing the models with and without the season variable and $p < .05$ are indicated in bold

Response variable	Estimate	SE	Likelihood ratio test χ^2	p-value
Network metrics				
Specialization H_2'	0.64	0.08	48.33	**.027**
ΔVaznull H_2'	0.42	0.06	3.77	.052
Modularity Q	0.54	0.09	3.62	.056
ΔPatefield Q	0.36	0.05	6.87	**.008**
ΔVaznull Q	0.27	0.05	5.98	**.014**
Nestedness wNODF	7.01	2.00	0.01	.965
ΔPatefield wNODF	4.48	1.40	0.35	.553
ΔVaznull wNODF	4.16	1.85	0.60	.437
Floral availability				
Abundance	3.84	0.21	5.67	**.017**
Richness	34.50	12.34	77.23	**.005**
Functional dispersion	0.28	0.02	11.45	.284
Functional evenness	0.35	0.05	0.00	.975

(Figure 3c). Furthermore, bees were the most frequent pollinators, i.e. they presented higher species strength, than flies or wasps, with more plant species depending on them for pollination (Figure 3d).
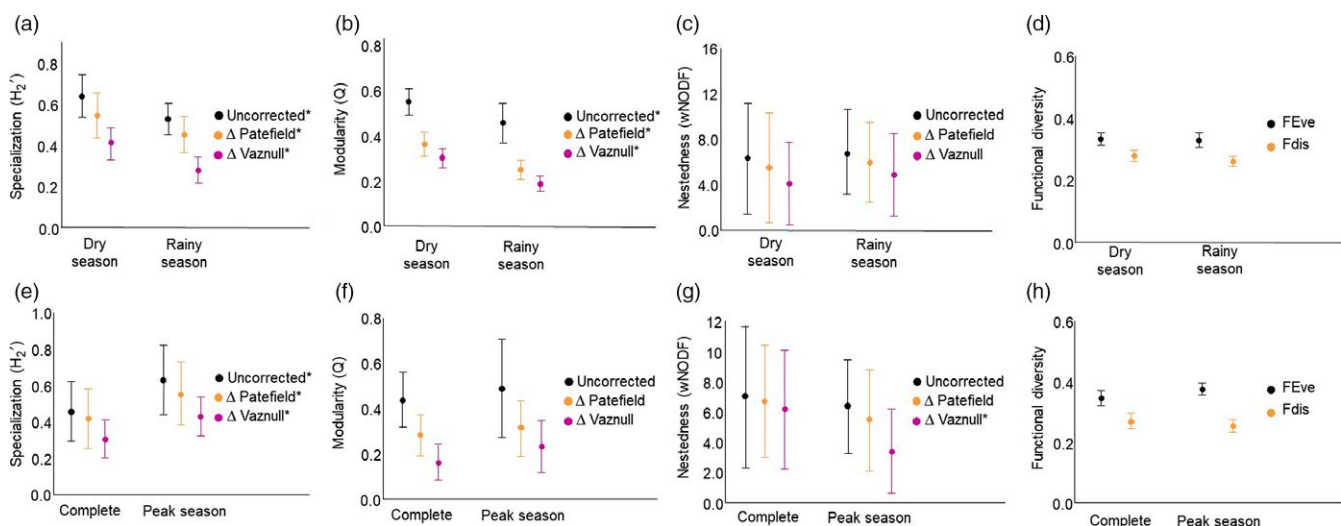
TABLE 2 Comparison of network metrics between the networks considering the entire sampling period and the ones considering only the peak flowering season. We report the uncorrected as well as network metrics corrected by two null models (Patefield and Vaznull). Comparisons were done with mixed effect models, using study sites as a random variable. Significance for the terms were obtained from a likelihood ratio test by comparing the models with and without the season variable and $p < .05$ are indicated in bold

| Response variable	Estimate	SE	Likelihood ratio test χ^2	p-value
Network metrics				
Specialization H_2'	0.49	0.11	4.85	**.027**
ΔPatefield H_2'	0.41	0.11	4.75	**.029**
ΔVaznull H_2'	0.30	0.07	4.47	**.034**
Modularity Q	0.43	0.10	1.25	.262
ΔPatefield Q	0.25	0.07	1.73	.187
ΔVaznull Q	0.18	0.07	1.04	.307
Nestedness wNODF	7.40	1.80	2.57	.109
ΔPatefield wNODF	5.80	1.57	3.38	.065
ΔVaznull wNODF	5.15	1.44	6.01	**.014**

4 | DISCUSSION

4.1 | Network structure, resource availability and seasonality

The studied plant–pollinator networks were more specialized during the dry season, when floral resource availability was lower. Previous studies in binary temporal networks showed that metrics such as

FIGURE 2 Comparison of network metrics between dry and rainy season, as well as between complete and peak season networks for the four studied sites. We show the comparison for the raw metric values as well as Δ transformed values using two distinct null models, and functional diversity values (functional dispersion—FDis and functional evenness—FEve). The plots depict the mean and standard deviation for all the metrics. *denotes significant difference between seasons. See Table S2 for the actual metric values and Section 2 for further details on their calculations [Colour figure can be viewed at wileyonlinelibrary.com]
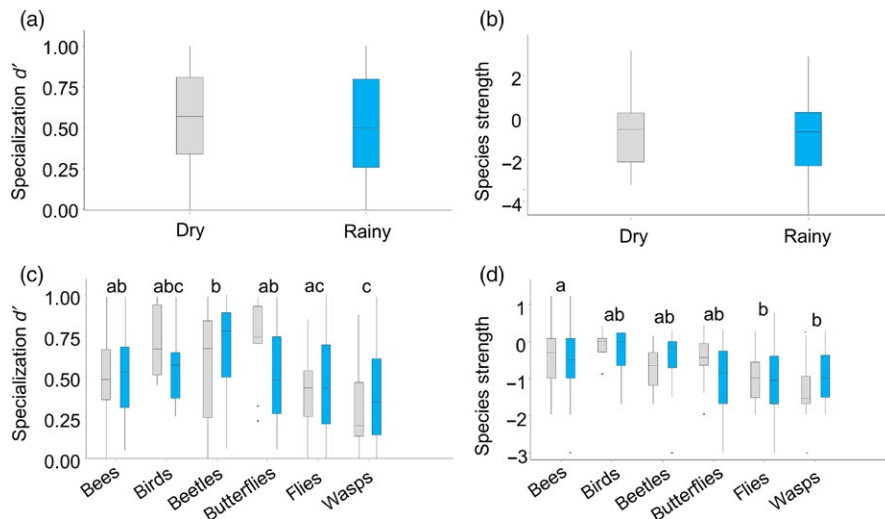
FIGURE 3 (a) Species-level specialization d' and (b) species strength for plants species according to seasons; (c) Species-level specialization d' and (d) species strength for each functional group of pollinators. The horizontal line in the boxes indicates the median for each index with upper and lower limits of the boxes indicating the lower and upper quartiles (25% and 75%, respectively). For the functional groups of pollinators, significant differences according to the post hoc Tukey tests are indicated by different letters (Tukey test: $p < .05$). Species strength values were $\log_{10}$ transformed to improve model fit [Colour figure can be viewed at wileyonlinelibrary.com]

connectance, nestedness and modularity vary significantly within a single year (e.g. Basilio, Medan, Torretta, & Bartoloni, 2006). Other studies from temperate regions showed that these values are highly conserved between successive plant reproductive seasons (e.g. Alarcón, Waser, & Ollerton, 2008; Burkle & Irwin, 2009; Dupont et al., 2009; Fang & Huang, 2012; Olesen et al., 2008; Petanidou et al., 2008).

An important ecological factor that influences specialization is the availability of resources, which can vary at small scales both temporally and spatially (Carstensen, Sabatino, Trøjelsgaard, & Morellato, 2014; González-Castro, Yang, Nogales, & Carlo, 2012). When resource availability and diversity are higher, the number of pollinators coexisting in the network may be greater, and higher levels of specialization may be expected (Fontaine et al., 2006; Ghazoul, 2006). Moreover, according to optimal foraging theory, an opposite decrease in resource availability should lead to an increase in diet breadth, leading to higher generalization (Fontaine et al., 2008; Robinson & Wilson, 1998; Schoener, 1971). Thus, changes on resource availability reflect directly on the structure of the interaction networks, with expected higher specialization associated to higher resource availability and diversity (Fontaine et al., 2006). Nevertheless, the greater specialization in the dry period recorded here, is related to lower floral availability and lower richness of plant species blooming, as well as a lower diversity and activity of pollinators in the studied areas (see also Dupont, Hansen, & Olesen, 2003; Smith-Ramírez, Martinez, Nuñez, González, & Armesto, 2005). It is possible that considerably lower availability of floral resources, even though coupled with lower availability of pollinators, still leads to changes in animal foraging behaviour owing to higher competition, ultimately resulting in overall higher degree of specialization (Tinoco, Graham, Aguilar, & Schleuning, 2017).

Interestingly, while floral resource availability showed clear seasonal patterns, floral FD that quantifies diversity in terms of the distribution of species traits (Diaz & Cabido, 2001; Fornoff et al., 2017; Plein et al., 2013) did not differ between seasons. Consequently, plants in the communities offer similarly diverse floral resources

across seasons in spite of differences on overall resource availability and network structure. Similar lack of concordance between FD and network structure has been reported for other mutualistic systems such as frugivorous birds and fruiting plants (Plein et al., 2013) although for flowering plants and hummingbirds, a consistent association of network structure to hummingbird FD was found (Maglianesi, Blüthgen, Böhning-Gaese, & Schleuning, 2015). Our results suggest that in our system, when including distinct functional groups of pollinators, network structure correlates to changes in the abundance of floral resources, rather than their assemblage-level trait composition. Since many species, especially pollinators, have longer or even year-around activity span in the tropics, it is possible that turnover of species between communities is higher at the spatial than the temporal gradient, and that community structure in terms of trait composition varies less than in terms of how interactions are organized across time. To test the generality of such a trend, however, will require the availability of more temporarily and spatially discrete data in the future.

4.2 | Species roles and seasonality

Although dry season networks were more specialized, we did not find the same pattern when considering species-level specialization and species strength of all plant and pollinator species. Only plants that occurred in both seasons showed higher specialization in the dry season. The overall lack of consistent pattern at the species level for pollinators can be illustrated by two of the most abundant pollinator species that occurred in both seasons. The honeybee *A. mellifera* occurred in all studied formations and in high abundance in all seasons, tending to be more specialized in the dry season (d' rainy = 0.50; d' dry = 0.57) and to have higher species' strength in the rainy season (strength rainy = 11.79; strength dry = 8.46; Table S4). Owing to its high abundance and tendency to focus on the most abundant flowers with high floral constancy (Grant, 1950; Gross, 2001; Grüter, Moore, Firmin, Helanterä, & Ratnieks, 2011; Magrach et al., 2017), *A. mellifera* interacts with

more species during the rainy than dry season, when there are not many massive flowering species (Table S4). In contrast, *Bombus morio*, the most common native pollinator, had higher value of specialization (d' rainy = 0.78; d' dry = 0.54) and species' strength (strength rainy = 9.14; strength dry = 5.95; Table S4) in the rainy season in Pantanal. During periods of higher resource availability, bumblebees may show higher levels of specialization to specific plants, but at the same time being the most frequent visitors of many of these plant species (hence higher species strength), than during the dry season when resources are scarcer (Robinson & Wilson, 1998).

The lack of consistent differences between seasons in species-level indices, except for plants blooming in both seasons, indicates that higher network level specialization is an emergent property only seen when considering the entire network. It is possible that the lack of difference on overall species-level specialization, coupled to lower resource availability during the dry season, generates the observed network-wide higher specialization. Finally, the fact that bees presented higher values of specialization and species strength in relation to some other groups suggests that plant species that are visited by bees are frequently used only by this group. Such plants include abundant species in the communities with specialized floral resources common in the tropics, for example, oil producing plants (e.g. Malpighiaceae, Plantaginaceae and Iridaceae species; Vogel, 1990) that are frequently visited by bees and rarely or never visited by other groups of pollinators. Conversely, abundant plant species with more generalist flowers are visited by several groups of pollinators, explaining the fact that other groups of pollinators such as flies and wasps tend to be more opportunistic and visit a wide range of plant species, reducing their specialization and also promoting plants to depend less on them (e.g. Aoki & Sigrist, 2006; Freitas & Sazima, 2006; Ollerton, 2017).

5 | CONCLUSIONS

Our study is, to the best of our knowledge, the first to provide a quantitative description of the seasonal changes in the metrics of plant–pollinator interaction networks in tropical areas that also includes different functional groups of plants and pollinators. Importantly, we also show that targeted data collection during peak flowering season generates higher estimates of network specialization and lower estimates for nestedness (after corrected by a null model). Such results may be caused by longer activity periods of pollinators than the targeted monitoring frame. Hence, depending on the period when the data collection is undertaken, different structural values for the networks of interactions may be returned. By showing that temporal scale, and especially seasonality, has consequences for the description of network structure for communities in the tropics, we indicate caution with tropical network sampling. Ideally, sampling should include all seasons and not just the few months of spring and summer during the peak flowering season, especially when attempting cross network comparisons with temperate area networks which are usually sampled for most of their

flowering season. The use of targeted sampling has been argued for since aggregating temporally extensive data generates many temporal "forbidden links" (e.g. Carstensen et al., 2014; Carvalheiro et al., 2014). However, when such choices are made, assumptions regarding temporal forbidden links and variability of network structure are not usually checked, even though these are important for structuring interaction networks (Jordano, Bascompte, & Olesen, 2003; Vizentin-Bugoni, Maruyama, & Sazima, 2014). It should be noted that we are not advocating to simply gathering and aggregating all the interactions, but ideally identifying the networks through the contained temporal identities (Sajjad et al., 2017), since comparing seasonal or sequential webs more explicitly reveals otherwise unnoticed network dynamics (CaraDonna et al., 2017). In sum, our results indicate that much about the temporal dynamics of plant-pollinator networks is still unknown, and such limitation is especially important for species-diverse and year-round active tropical networks. Finally, variation in resource availability across space and time offers the opportunity to learn about the processes that determine patterns in the structure of interaction networks. Thus, studies that consider temporal variation in networks of interactions on a global scale should be encouraged.

AUTHORS' CONTRIBUTIONS

C.S.S., P.K.M., C.A., M.R.S. and A.C.A. conceived the ideas; C.S.S., C.A., M.R.S. and A.C.A. designed sampling methodology; C.S.S. and C.A. collected the data; C.S.S. and P.K.M. analysed the data and wrote the initial version of the manuscript. All the authors participated in the conception of the manuscript, discussions of the results and contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5g10870 (Souza et al., 2018).

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