

Meta-analyses

Combining plant–frugivore networks for describing the structure of neotropical communities



Adriana de Almeida and Sandra Bos Mikhich

A. de Almeida (<http://orcid.org/0000-0003-2352-909X>) (adri_dealmeida@hotmail.com), Programa de Pós-Graduação em Biologia Animal, Inst. de Biociências, Letras e Ciências Exatas, Univ. Estadual Paulista “Júlio de Mesquita Filho”. Rua Cristóvão Colombo 2265, 15054-000, São José do Rio Preto, SP, Brazil. Present address: Bioenv Monitoramento Ambiental, Rua Pilulares 17, 29199-072, Aracruz, ES, Brazil. – *S. Bos Mikhich* (<http://orcid.org/0000-0002-2641-1508>), Embrapa Florestas, Empresa Brasileira de Pesquisa Agropecuária, Colombo, PR, Brazil.

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Frugivory and seed dispersal are key processes for the maintenance of biodiversity. This is particularly true in the Neotropics, where most plant species depend on animals to disperse their seeds and most birds and mammals include fruits in their diets. We performed a continental-scale literature review to build a database of interactions between neotropical fruits and fruit-eating birds and mammals. Our objective was to evaluate the viability of combining literature data from different studies to describe the structure of highly diverse fruit–frugivore neotropical communities. We investigated sites that had been the focus of studies of at least four different avian and/or mammalian taxonomic orders and we included in our database only those conducted for at least a 6-month period in order to account for the seasonality in fruit availability. In spite of a large number of study sites investigated for frugivory ($n = 156$), we found a huge gap in the knowledge of community-wide fruit–frugivore interactions in the Neotropics, since most studies focused on single or a few species. Nevertheless, we were able to construct diverse plant–frugivore qualitative networks for 17 areas unevenly spread throughout the neotropical region. Using complex network analyses, we found that these networks were highly informative and non-randomly organized. Most networks were both significantly nested and modular, characteristics related to stability and resilience in biological systems. We concluded that it is possible to use merged data to build networks for sites of conservation interest. The main advantage of using this approach is to optimize resources, avoiding exhaustive, costly and time-consuming fieldwork when data is already available. Whilst bearing in mind the shortcomings of this methodology, these results can be used in studies aiming to understand the ecological processes structuring different communities in the neotropical region and to support conservation and restoration actions.

Introduction

Mutualisms between plants and animals are among the main processes capable of generating and maintaining the biodiversity on our planet (Odum and Barrett 2008). In tropical forests, about 90% of all woody plants depend on animals to complete their

reproductive cycles, such as for pollination or seed dispersal (Jordano 2000). Similarly, up to 80% of the biomass of birds and mammals can be represented by animals that primarily depend on fruit in their diet (Terborgh 1986).

The application of the 'network theory' (Estrada 2011) for the study of ecological interactions between species has proven to be an effective approach and enables the examination of how organisms interact, the evolution of current observed patterns, and the effects of ecosystem changes (Bascompte and Jordano 2007, Bascompte 2010, Nuismer et al. 2013). Networks of ecological interactions are representations of interactions (links) between species (nodes or vertices) that assemble a community (network) (Blüthgen et al. 2008). The network approach is able to simplify complex interactions uncovering patterns and characteristics of a species in a community (Jordano 1987, Bascompte and Jordano 2007). For example, modules in pollination and in seed dispersal networks have been found to be related with their respective syndromes (Donatti et al. 2011, Danieli-Silva et al. 2012, Carstensen et al. 2016), that are morphological traits of flowers or fruits associated with plant visitation or fruit consumption by different taxa of vertebrates. This approach is also an appropriate way to test the various factors involved in the dynamics of coevolution of animals and plants, such as phylogenetic history and climatic changes, and to examine the potential effects of the extinction or addition of species in a community through simulations and statistical modelling (Olesen et al. 2002, Memmott et al. 2004, Bascompte et al. 2006, Valdovinos et al. 2009, Thébault and Fontaine 2010, Guimarães Jr. et al. 2011).

Studies of communities based on the network approach can also provide important information for decision makers regarding species conservation, management, and restoration (Tylianakis et al. 2010, Devoto et al. 2012, Kaiser-Bunbury and Blüthgen 2015). Devoto et al. (2012), for example, studied 30 quantitative plant–pollinator networks along a managed successional gradient using theoretical and empirical approaches in order to identify which species should be given restoration priority, according to different restoration targets. Kaiser-Bunbury and Blüthgen (2015) also used the study of plant–pollinator interactions to aid conservation action and improve management success by building a framework that integrates conservation practitioners and network ecologists. Network structure can also be incorporated into conservation monitoring, as suggested by Tylianakis et al. (2010).

Studies of frugivory usually focus on one frugivorous species or one group of frugivores with similar behaviour, like bats, birds or primates. Although such studies provide useful knowledge on particular species and can contribute with their conservation, it is essential to assess their interactions with the rest of the community in which they are found (Tylianakis et al. 2010). However, few studies to date have used this approach in order to understand the observed patterns in highly diverse communities (Fontaine et al. 2011, Dáttilo et al. 2016, Genrich et al. 2017). Even studies

that considered only one type of interaction (i.e. plant–frugivore) still fail to consider the several groups involved in these interactions and base their conclusions on observations of only one taxonomic group (e.g. plants–birds or plants–bats). Thus, there are only a few studies (Silva et al. 2007, Donatti et al. 2011, Hawes and Peres 2014, Stevenson et al. 2015) that have evaluated the interactions considering the whole community of frugivores. This scarcity of information is due, in part, to sampling limitations since different taxonomic groups usually demand different sampling techniques and it is usually not feasible to sample different groups at the same time (Litvaitis 2000, Vidal et al. 2013).

Given the amount of data collected through different studies and the need to broaden the knowledge about the interactions between plants and frugivores in highly diverse neotropical communities, this study sought to evaluate the viability of combining literature data from different studies in order to describe the structure of mutualistic fruit–frugivore communities in the neotropical region. We expected our combined qualitative interaction networks to have: 1) similar structure to empirical mutualistic networks described in the literature, concerning qualitative indices of network characterization; 2) empirical structural indices with statistical significance in relation to null models, which indicates the presence of ecological factors influencing the community structure (Gotelli and Graves 1996, Sebastián-González et al. 2015); and 3) nestedness and modularity showing a positive relationship with the richness of frugivores, since networks have been found to become more structured with increased complexity (Bascompte et al. 2003, Olesen et al. 2007, Bastolla et al. 2009, Donatti et al. 2011).

We believe that the combination of data already available in the literature can be used as a surrogate for the study of interaction networks in neotropical communities, that today are restricted to individual studies dealing with subsets of frugivores, while more complete studies of community-level interactions between plant and frugivores are not available. The combined networks might potentially assist in community-level conservation strategies and restoration plans.

Material and methods

Data collection

We built a database of interactions between neotropical plant and fruit-eating birds and mammals, after a comprehensive review of the literature. We searched for studies about frugivory by mammals or birds in the Neotropics in all databases of the Web of Science (<<http://apps.webofknowledge.com>>), from 1990 to 2015, in Google Scholar (<<https://scholar.google.com.br/>>), and an online repository of theses and dissertations (<<http://bancodeteses.capes.gov.br/>>), in addition to direct searches of references

cited in the analysed studies. We then searched for study sites with data on at least four different taxonomic orders of birds and/or mammals to build binary (presence–absence) fruit–frugivore interaction networks. Studies reporting fruit and seed consumption and/or seed dispersal by bird or mammals were used. The following data were collected from the selected studies: taxonomic information on plants (to the lowest taxonomic rank available in the study) and frugivores (always to species level), name and location of the study site (country and geographical coordinates), and sampling duration (in months). As we built a binary network, all interactions between a given fruit taxa and a bird/mammal species were included in our database but computed only once for each study site. Additionally, since patterns of plant–animal interactions are not constant throughout the year, especially due to seasonality in fruit availability (van Schaik et al. 1993), only studies conducted during at least one dry and one wet season (a six-month period or more) were used to build the networks. A map with the distribution of study sites was built using the software QGIS ver. 2.16.0-Nødebo (QGIS Development Team 2016).

The different studies that formed our database used various methods for the collection of the interaction data, which included direct and indirect records of fruit consumption. Also, these studies had time periods varying from 6 to 120 months (Supplementary material Appendix 1 Table A1). We acknowledge that the use of different methods for data collection have distinct detection probabilities of species interactions, but we expected to minimize the negative effects of these discrepancies by only considering qualitative descriptors of the networks.

Network topology

Species-rich mutualistic networks are usually organized in a nested pattern, which means that the more specialist species interact with subsets of species interacting with generalists. This type of non-random organization has been found to make communities more resilient to perturbations because the most generalist species interact cohesively among them creating a dense core of interactions (Bascompte et al. 2003). Another commonly observed pattern inherent to mutualistic networks is modularity. This type of structure is also related to network stability and is characterized by groups of strongly connected species weakly connected to other species belonging to other groups of strongly connected species in the network (Olesen et al. 2007). Both structural patterns are expected to have a positive correlation with network size (Olesen et al. 2007).

For graph and network analyses of neotropical plant–frugivore webs, we built a binary matrix of adjacencies A_{ij} for each site. Frugivorous species were arranged in i rows and plant taxa were arranged in j columns. The interactions resulting from these matrices generate representations in the form of bipartite graphs, since interactions do not occur between entities of the same trophic level (Bascompte and Jordano 2006).

Since our networks were built from the combination of different studies, we were able to calculate qualitative measurements only. We used six indices to describe the structure of neotropical fruit–frugivore networks: network size (S), connectance or connectivity (C), mean number of links per species (\bar{L}_s), niche overlap, nestedness ($NODF$), and modularity (M).

Network size, which consists of the sum of animal and plant species, can be considered as species richness, species density or a biodiversity measure of the network, and indicates the maximum number of interactions possible (Olesen and Jordano 2002). The level of generalization of the network can be measured through the connectance (Jordano 1987), which is equivalent to the proportion of interactions that actually exist in the network in relation to the total number of possible interactions (number of animals multiplied by the number of plants) (Olesen and Jordano 2002). The mean number of links per species corresponds to the total number of links observed in the network divided by the total number of species. Niche overlap indicates the mean similarity in the pattern of interactions between species of the same trophic level, in this case the frugivores. It was determined by the ‘Horn’ index (Dormann et al. 2009), and can vary from 0 (no niche overlap) to 1 (total niche overlap). All these indices were determined using the ‘Bipartite’ package ver. 2.04 (Dormann et al. 2008, 2009) implemented in the software R ver. 3.1.2 (< www.r-project.org >).

Nestedness is a feature intrinsic to mutualistic networks, such as pollination or seed dispersal, and it is characterized by non-random interactions between species, which has been found to make networks particularly robust (Bascompte et al. 2003). In this study, the nestedness was determined by the NODF index (Almeida-Neto et al. 2008) using the software ANINHADO ver. 3.0.3 (Guimarães and Guimarães 2006).

Modularity is also commonly observed in ecological networks. For its determination, we chose the Barber modularity index M_B (Barber 2007), which determines how many interactions a species has within its module than expected at random. This index was specifically designed for bipartite networks and proved to be the most suitable for detecting modularity in presence–absence matrices (Thébault 2013). The calculations were made using the software MODULAR ver. 0.21 (Marquitti et al. 2014). Network modules were identified using the software NetCarto (Guimerà and Amaral 2005a, b) and graphically designed using the software Pajek ver. 3.13 (Batagelj and Mrvar 2013) in order to optimize the node positioning inside their modules.

Analyses

The patterns observed in the networks can be caused by biological processes, but can also be a byproduct of sampling intensity, sampling biases, or a result of species abundance (Blüthgen et al. 2008). An efficient way for evaluating if the structural patterns are caused by these stochastic processes is

to compare the observed values with values generated by null models (Gotelli and Graves 1996, Gotelli and Colwell 2001).

The statistical significance of the indices C , \bar{L}_x , and niche overlap among frugivores was also calculated using the 'Bipartite' package after comparison with values obtained from 1000 random matrices, created based on the 'null model 2': where each simulated network is the same size of each empirical network and the probability of an interaction between one animal species and one plant species is proportional to the total number of interactions (Bascompte et al. 2003). The statistical significance of the index M_B was calculated using the same procedure, but with the software MODULAR. In order to determine if the network was more nested than expected at random because of species richness and heterogeneity of interactions, the expected value of NODF was compared to the value of NODF estimated from 1000 random matrices created based on the null model CE of the software ANINHADO, equivalent to Bascompte's "null model 2" (Bascompte et al. 2003).

The effect of the richness of frugivorous species on the modularity and nestedness of the networks was analysed using two linear regression models, where the values of NODF and M_B were the dependent variables of their respective models and the log-transformed number of frugivorous species was the predictive variable in both models. The number of frugivorous species was log-transformed in order to yield a better fit for the data. Linear regression models were run with the R commander ver. 2.1-2 package for R (Fox 2005).

Results

We were able to build 17 plant–frugivore interaction networks for the neotropical region (Table 1, Fig. 1). The study sites are mainly remnants of native vegetation protected by public or private administration and with a wide variation in sizes (Supplementary material Appendix 1 Table A2). In some sites, the diversity of frugivores reached up to 15 different orders (Table 1).

The mean size of the networks was $\bar{S}=171$, varying between $S=64$ and $S=415$ nodes, and included networks with four to 114 frugivorous species (Table 2, Supplementary material Appendix 1 Table A3) and 57 to 317 plants (Table 2, Supplementary material Appendix 1 Table A4). The indices C , \bar{L}_x and niche overlap were statistically different from the null models in all 17 networks ($p < 0.001$). Connectance was generally low, with a mean value of $C=0.12 \pm 0.08$ (mean \pm SD), reaching a maximum value of $C=0.35$ in the MGSP network (Table 2). The mean number of links per species was $\bar{L}_x=1.94 \pm 0.76$, but this differed greatly between trophic levels. The mean number of links for frugivores was $\bar{L}_{HL}=13.48 \pm 7.24$, and mean number of links for plants was $\bar{L}_{LL}=2.62 \pm 1.40$. Niche overlap was low among frugivores, with a mean value of $NO_{HL}=0.17 \pm 0.09$, indicating a low overlap in resource use among frugivores. Fifty-nine percent of networks were significantly nested ($p < 0.05$), and

the mean value for nestedness was $NODF=24.18 \pm 11.08$. Similarly, 71% of the networks were significantly modular ($p < 0.05$), and the mean observed value was $M_B=0.51 \pm 0.07$ (Table 2). The networks had an average of five modules (5.00 ± 0.94), a number that varied from four to seven (Fig. 2). Fifty-three percent of all networks were both significantly nested and modular (Table 2).

Contrary to what was expected, modularity exhibited a significant negative relationship with frugivorous richness (lm: $R^2=0.042$, $F=3.848$, $df=15$, $p=0.034$, Fig. 3 a). Additionally, nestedness did not exhibit any significant relationship with frugivorous richness ($R^2=0.005$, $F=1.184$, $df=15$, $p=0.147$, Fig. 3 b).

Discussion

Our study suggests that using combined networks created after literature data for specific fruit–frugivore communities can provide useful and non-random information on animal–plant interactions in the tropics. Yet, we face a huge spatial gap in the knowledge of community-wide fruit–frugivore interactions in the Neotropics. The 17 networks analysed in this study are not evenly distributed throughout this geographical region, but concentrated in areas such as southeastern Brazil and Central America. Highly biodiverse ecosystems such as the Amazon, Andean forests, Araucaria forest, Cerrado, and the Yungas remain poorly sampled. Although studies on the frugivorous diet of vertebrates were carried out in some of these areas, they have either focused on a few species or were conducted for less than a six-month period, so that they were not included in our analyses.

In general, the networks studied here exhibited a similar structure to other mutualistic networks previously described in the literature, in terms of their nestedness and modularity. For example, Bascompte et al. (2003) found that 75% of 52 mutualistic networks were significantly nested, and Olesen et al. (2007) found that 57% of 51 pollination networks were significantly modular. The nested pattern is a common trait in mutualistic networks and is caused by multiple ecological and evolutionary processes (Nuismer et al. 2013). This complex and non-random network structuring is believed to be among the main causes for the stability of ecological systems (Bascompte 2010). Nestedness can enhance the number of coexisting species, by reducing interspecific competition (Bastolla et al. 2009), and increase the robustness of the network to species extinctions (Memmott et al. 2004), and habitat loss (Fortuna and Bascompte 2006). Evolutionary constraints also seem to have favoured modularity – semi-independent compartments of highly connected species – in mutualistic networks. This compartmentalization is thought to be a result of morphological, functional, or phylogenetic constraints (Lewinsohn et al. 2006). It can also be a direct consequence of climatic seasonality (Schleuning et al. 2014). Although mostly significant, modularity values in our networks were usually low. Indeed, these values have been found

Table 1. Characteristics of 17 interaction networks created based on literature data for different groups of fruit-eating birds and mammals in the Neotropics.

Network name	Site	Country	Latitude	Longitude	Animal group	Orders	No. of animal species	No. of plant species	Network size (A+P)	References ¹
BCI	Barro Colorado Island	Panama	9.16	-79.85	mammal	4	34	257	291	1–15
CSPR	Caraca Sanctuary Private Reserve	Brazil	-20.10	-43.49	mammal	4	4	60	64	16–19
GCVEPA	Gama-Cabeça de Veado Environmental Protection Area	Brazil	-15.93	-47.90	bird/mammal	4	31	57	88	20–24
HPIN	Hato Piñero	Venezuela	8.93	-68.08	bird/mammal	4	12	64	76	25–28
INP	Iguaçu and Iguazú National Parks	Argentina/Brazil	-25.67	-54.36	mammal	4	10	60	70	29–33
ISP	Intervalles State Park	Brazil	-24.31	-48.27	bird/mammal	15	114	61	415	34–41
LTBR	Los Tuxtlas Biosphere Reserve	Mexico	18.56	-95.15	bird/mammal	7	43	110	153	42–52
MCFBR	Monteverde Cloud Forest Biological Reserve	Costa Rica	10.42	-84.83	bird/mammal	7	42	189	231	53–54
MGSP	Mata dos Godoy State Park	Brazil	-23.45	-51.25	mammal	4	5	71	76	55
MNP	Manu National Park	Peru	-12.04	-71.72	mammal	4	13	191	204	42; 56–61
PABR	Poço das Antas Biological Reserve	Brazil	-22.52	-42.28	bird/mammal	7	52	89	141	62–68
PONP	Pontal do Paranapanema	Brazil	-22.53	-52.30	bird/mammal	4	6	90	96	69–70
RNBAF	Rio Negro and Barranco Alto farms	Brazil	-19.55	-56.53	bird/mammal	14	52	63	115	71–73
SGR	Santa Genebra Reserve	Brazil	-22.82	-47.11	bird/mammal	7	45	113	158	74–81
SPNINR	Saut Pararé/Nouragues Natural Reserve	French Guiana	4.09	-52.67	bird/mammal	5	18	317	335	42; 82–89
SRNP	Santa Rosa National Park	Costa Rica	10.81	-85.69	mammal	4	16	173	189	42; 90–102
VRESSP	Vila Rica do Espírito Santo State Park	Brazil	-23.91	-51.96	bird/mammal	12	84	124	208	103–104

¹References used as data sources for the construction of fruit–frugivore interaction networks: 1) Kaufmann 1962; 2) Hladik and Hladik 1969; 3) Oppenheimer 1968; 4) Morrison 1978; 5) Bonaccorso 1979; 6) Oppenheimer (*apud* Freese and Oppenheimer 1981); 7) Glanz et al. 1983; 8) Oppenheimer 1983; 9) Russell 1983; 10) Smythe et al. 1983; 11) Bonaccorso and Humphrey 1984; 12) Handley et al. 1991; 13) Wehncke et al. 2003; 14) Giannini and Kalko 2004; 15) Andrade et al. 2013; 16) Silva and Talamoni 2003; 17) Alvarenga and Talamoni 2006; 18) Talamoni and Assis 2009; 19) dos Santos et al. 2012; 20) Motta-Júnior 1991; 21) Miranda 1997; 22) Vilela 1999; 23) Vilela 2007; 24) Camargo et al. 2011; 25) Barreto et al. 1997; 26) Miller 1998; 27) Bertsch and Barreto 2008; 28) Aranguren et al. 2011; 29) Brown and Zunino 1990; 30) Casella 2006; 31) Hirsch 2009; 32) Sánchez et al. 2012; 33) Tujaque et al. 2016; 34) Rodrigues 1991; 35) Vieira and Izar 1999; 36) Galetti et al. 2000; 37) Passos et al. 2003; 38) Leiner and Silva 2007; 39) Izar 2008; 40) Mello et al. 2008; 41) Amatuzzi 2009; 42) Beck 2005; 43) Estrada and Coates-Estrada 1984; 44) Estrada et al. 1984; 45) Orozco-Segovia et al. 1985; 46) van Dorp 1985; 47) Galindo-González et al. 2000; 48) Herrera et al. 2001; 49) Puebla-Olivares and Winker 2004; 50) Asensio et al. 2007; 51) Amato and Estrada 2010; 52) Dunn et al. 2010; 53) Wheelwright et al. 1984; 54) Dinerstein 1986; 55) Rocha 2001; 56) Janson 1975; 57) Kiltie 1981; 58) Janson 1985; 59) Foster et al. 1986; 60) Tobler et al. 2010; 61) Palma and Stevenson 2010; 62) Correia 1997; 63) Dietz et al. 1997; 64) Carvalho et al. 1999; 65) Pinheiro et al. 2002; 66) Mello et al. 2004; 67) Carvalho et al. 2005; 68) Macedo et al. 2010; 69) Tófoli 2006; 70) Goulart 2007; 71) Keuroghlian et al. 2009; 72) Donatti et al. 2011; 73) Munin et al. 2012; 74) Galetti 1992; 75) Galetti 1993; 76) Chiarello 1994; 77) Galetti and Morellato 1994; 78) Galetti and Pedroni 1994; 79) Paschoal and Galetti 1995; 80) Faria 1996; 81) Galetti and Pizo 1996; 82) Julien-Laferrère 1993; 83) Guillotin et al. 1994; 84) Julliot 1996; 85) Simmen and Sabatier 1996; 86) Charles-Dominique and Cockle 2001; 87) Julien-Laferrère 2001; 88) Erard et al. 2007; 89) Lobova et al. 2009; 90) Fleming et al. 1977; 91) Freese 1977; 92) Heithaus and Fleming 1978; 93) Janzen 1982; 94) Williams 1984; 95) Fleming and Heithaus 1986; 96) Chapman 1987; 97) Fleming 1988; 98) Chapman 1989; 99) Chapman and Fedigan 1990; 100) Fleming 1991; 101) MacKinnon 2006; 102) Valenta and Fedigan 2008; 103) Mikich 2001; 104) Bianconi 2009.



Figure 1. Location of the study sites for which plant–frugivore interaction networks were constructed based on literature data.

to be low in tropical seed-dispersal systems (Schleuning et al. 2014). Modularity, like nestedness, is related with community stability and resilience because any perturbations are retained within a single module, minimizing the impact in the rest of the network (Donatti et al. 2011, Sebastián-González et al. 2015).

Other qualitative indices of network structure also revealed a non-random organization of our 17 fruit–frugivore webs. A low average connectance is common for mutualistic networks, indicating a low generalization and high specialization, and thus low competition between species in the same trophic level (Jordano 1987). As connectance is correlated with the number of links in a network (Blüthgen et al. 2006), it was expected that the mean number of links would also be low. Although, when examined separately, \bar{L} showed great variation since \bar{L} for animals was much higher than \bar{L} for plants. This difference may be determined by the extremely asymmetrical matrix architecture of most webs, where the number of plant species greatly exceeds the number of frugivore species. This pattern could occur due to the seasonal variation in fruiting, which forces animal species to switch between fruit species during the annual cycle according to their availability. A high resource richness may be the cause of a low niche overlap between frugivores, because seed-dispersal systems are known to be the less specialised compared to other types of mutualism such as plant–ant and plant–pollinator interactions (Blüthgen et al. 2007). High fruit species richness reduces the overlap between the diets of frugivores because it reduces interspecific competition (Ramos-Robles et al. 2016).

The statistical significance of the binary indices from the empirical networks we created in relation to null models confirmed the influence of biological and ecological processes in community structuring, eliminating the possibility that the observed patterns are only a result of stochastic processes (Gotelli and Graves 1996). In other empirical mutualistic networks reported in the literature, the network structure has been found to be a result of multiple processes such as species abundance, morphological trait matching, species spatio-temporal distribution, and phylogenetic relationships, and usually a combination of such processes is what dictates

Table 2. Structural descriptors of 17 neotropical fruit–frugivore interaction networks. The indices calculated were: network size (S), number of frugivorous and plant species, connectance (C), niche overlap (NO), nestedness (NODF), modularity (M_B), mean number of links per species (\bar{L}_x), mean number of links per frugivorous species (\bar{L}_{HL}) and mean number of links per plant species (\bar{L}_{LL}). Significance levels in relation to the null model 2 of nestedness and modularity indices are indicated by: *, $p < 0.05$; **, $p < 0.01$; NS, non-significant.

Network name	Type	n frugivores	n plants	S	C	NO	NODF	M_B	\bar{L}_x	\bar{L}_{HL}	\bar{L}_{LL}
BCI	mammal	34	257	291	0.07	0.14	35.74**	0.50**	2.06	17.62	2.33
CSPR	mammal	4	60	64	0.27	0.04	7.29 ^{NS}	0.63**	1.00	16.00	1.07
GCVEPA	mixed	31	57	88	0.09	0.18	17.29 ^{NS}	0.48 ^{NS}	1.90	5.39	2.93
HPIN	mixed	12	64	76	0.13	0.14	24.17*	0.57*	1.33	8.42	1.58
INP	mammal	10	60	70	0.18	0.24	27.57 ^{NS}	0.54**	1.50	10.50	1.75
ISP	mixed	114	301	415	0.04	0.07	14.68**	0.43**	3.31	12.05	4.56
LTBR	mixed	43	110	153	0.05	0.31	26.33**	0.61**	1.54	5.47	2.14
MCFBR	mixed	42	189	231	0.09	0.20	26.62**	0.43**	3.03	16.67	3.70
MGSP	mammal	5	71	76	0.35	0.35	39.11 ^{NS}	0.40 ^{NS}	1.62	24.60	1.73
MNP	mammal	13	191	204	0.09	0.03	8.48 ^{NS}	0.57 ^{NS}	1.11	17.46	1.19
PABR	mixed	52	89	141	0.06	0.21	13.68 ^{NS}	0.52**	1.96	5.33	3.11
PONP	mixed	6	90	96	0.21	0.20	9.69 ^{NS}	0.55 ^{NS}	1.19	19.00	1.27
RNBAF	mixed	52	63	115	0.09	0.13	29.09**	0.51**	2.62	5.79	4.78
SGR	mixed	45	113	158	0.07	0.11	28.12**	0.51**	2.13	7.47	2.97
SPNNR	mixed	18	317	335	0.09	0.10	27.21**	0.52 ^{NS}	1.57	29.17	1.66
SRNP	mammal	16	173	189	0.11	0.21	28.97**	0.54**	1.66	19.63	1.82
VRESSP	mixed	84	124	208	0.07	0.20	47.09**	0.36**	3.51	8.69	5.89

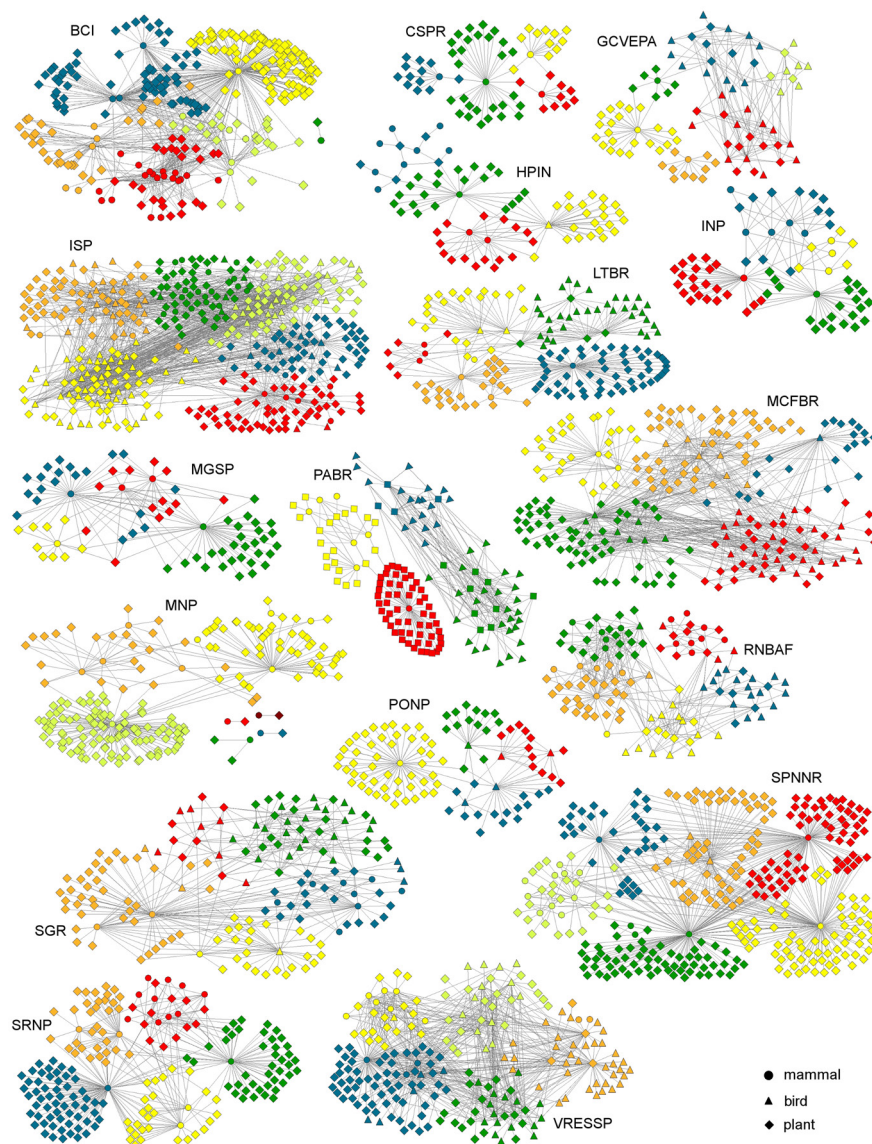


Figure 2. Networks of interactions (lines) among plants (diamonds) and frugivores (birds: triangles; mammals: circles) in 17 neotropical communities. Different colours represent different modules of the networks.

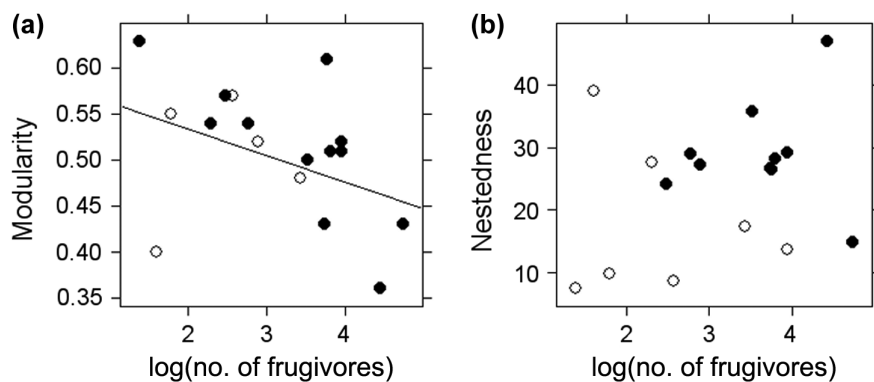


Figure 3. Relationships between frugivorous richness and both modularity (a) and nestedness (b) in 17 neotropical plant–frugivore interaction networks. Full circles represent networks with significant measures of modularity and nestedness, and empty circles represent networks with non-significant measures of modularity and nestedness.

the interaction events between individuals (Vázquez et al. 2009a, b).

The studied networks did not exhibit a significant relationship between size and nestedness, although it tended to be positive. This relationship was expected since a nested structure allows greater species coexistence, even with a low number of interactions (Bascompte et al. 2003, Bastolla et al. 2009). Nestedness can be both a result of network richness but it is also related to the complexity of the system, that is the number of links for a given number of species (Bascompte et al. 2003). The 17 neotropical networks studied here exhibited a low mean number of links, a result greatly biased by the low mean number of links in the lower trophic level (plants). Modularity, in turn, exhibited a surprisingly significant, although low, negative relationship with an increase of species number, contrary to what was expected. The modular structure of networks involving frugivores and plants usually reflects species diversity (Donatti et al. 2011, Mello et al. 2011), but it can also be influenced by a synergy of multiple processes. Both network patterns have been found to be more significant with an increase in size, but a high density of interactions between the generalist species can explain reductions in modularity level for some networks (Olesen et al. 2007). Modularity is also expected to be low in networks characterized by low interaction specificity (Lewinsohn et al. 2006), which is the case for fruit–frugivore interactions.

We acknowledge that our approach has shortcomings. The studies used here to build the networks were conducted in different periods, had different time spans, and data were collected by several methods, but we are confident that by only considering qualitative descriptors of the networks these differences do not affect our analyses. Special attention is also required when analysing data from old studies due to possible changes in species composition and/or density. It is known that many of these factors influence the interactions between species and how they are recorded by researchers. For example, sampling quality is expected to be directly linked with sampling effort (Falcão et al. 2016). Also, some species exhibit conflicting ecological traits, such as different phenologies or morphological mismatch, known as forbidden links, and it means that there are biological constraints limiting the interactions between two species and, irrespective of sampling effort, they will remain unobservable (Jordano et al. 2003, Jordano 2016). The metrics used to characterize networks are highly influenced by the number of observations, the sampling period, and the size of the networks (Blüthgen et al. 2006, Blüthgen 2010, Fründ et al. 2016). Species abundances and foraging behaviours of the animals also influence the recording of plant–animal interactions (Silva et al. 2007). Nevertheless, even the most comprehensive study will fail in collecting all the interactions occurring in any given ecological community, but it is still possible to achieve valid conclusions by analysing major ecosystem compartments (Jordano 2016). Nestedness, for example, is not found to be very sensitive to sampling effort (Nielsen and Bascompte 2007). Metrics based on binary

data, although not as robust as weighted metrics, have shown to be effective for describing the macroecological structure of seed dispersal networks, for example (Sebastián-González et al. 2015), and in general they present similar results to corresponding quantitative metrics (Corso et al. 2015).

Combined interaction networks can be used to assess the structure of frugivore assemblages in neotropical systems, and as traditional interaction networks they are potentially applicable to aid conservation efforts such as determining keystone species (Mello et al. 2015, Stevenson et al. 2015), understanding the effects of species loss (Kaiser-Bunbury et al. 2010, Vidal et al. 2013), and addition of invasive species (Aizen et al. 2008), and evaluating ecosystem functioning after restoration (Ribeiro da Silva et al. 2015).

Conclusions

This study presented a novel way for studying the interactions between plants and frugivores, combining data already available from the literature to build complex networks of interactions with a high diversity of animal species. While this approach is not able to completely substitute costly, extensive, and time-consuming fieldwork it can reveal some important patterns of the structure of plant–frugivore interaction networks. Despite this, the Neotropics still is poorly explored in terms of its highly diverse communities of frugivores, with gaps in important biodiverse ecosystems such as the Amazon. The combined networks presented characteristics similar to those of mutualistic networks already described in the literature. Whilst bearing in mind the shortcomings of this methodology, these results can be used in studies aiming to understand the ecological processes structuring different communities in the neotropical region, as well as to predict possible consequences of disturbances caused by the extinction of species in these systems.

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Supplementary material (available online as Appendix oik-04774 at <www.oikosjournal.org/appendix/oik-04774>). Appendix 1.