Modularity in ecological networks between frugivorous birds and congeneric plant species

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Abstract: Ecological and evolutionary factors influence the presence of modules in species interaction networks, and these modules usually cluster functional similar species. But whether closely related species form modules is still unknown. We tested whether the interaction networks formed by frugivorous birds and *Miconia* plants are modular and evaluated how modules were divided. To do so, we gathered from the literature data concerning four networks of *Miconia* and their frugivorous birds (three from Brazilian savanna and one from a rain forest in Panama). We quantified modularity using binary and weighted algorithms and also tested the relationship between bird traits (body mass, dietary specialization, migratory behaviour and phylogeny) in relation to within- and among-module connectivity indices (*c* and *z* values). If considering only binary information, networks did not present distinct modular structure. Nevertheless, by including interaction strength, modules can be detected in all four *Miconia*-bird networks. None of the bird traits, however, was related with the connectivity indices. The possible fluctuation of frugivorous bird abundance coupled with the asynchronic fruiting period of *Miconia* might favour the formation of temporal modules comprising birds and plant species with phenological overlap, ensuring seed dispersal and facilitating the coexistence in sympatry. Bird traits had little effect on the role that each species plays within the modular network, probably because the frugivorous assemblages were dominated by small-bodied and opportunistic species.

Key Words: frugivory, Miconia, mutualistic networks, QuanBiMo, seed dispersal

INTRODUCTION

Interactions among species are not randomly structured and numerous studies have shown that networks of species' interactions show some recurrent patterns (Bascompte 2009). One such pattern is the presence of modules, i.e. subunits or compartments, with withingroup prevalence of interactions (Olesen *et al.* 2007, Vázquez *et al.* 2009a). Modules have been detected in distinct types of interaction networks, including plantpollinator (Martín González *et al.* 2012, Maruyama *et al.* 2003), host-parasite (Krasnov *et al.* 2012), plant-ant (Fonseca & Ganade 1996) and plant-frugivore networks (Donatti *et al.* 2011, Mello *et al.* 2011, Schleuning *et al.* 2014). Modular organization can also be found at different hierarchical levels; meaning that modules have been reported not only for communities, but also within population interactions performed by each individual of a species (Tur *et al.* 2015). Likewise, modules within modules are also expected in nature (Dormann & Strauss 2014). Organization of the interactions into distinct modules is theoretically expected to promote species coexistence and community stability as perturbations are unlikely to spread quickly across different modules in the network (Stouffer & Bascompte 2011, Tylianakis *et al.* 2010).

Once modules are identified, species in the network can also be classified according to distinct roles, whether they are important connectors of different modules and/or act as central components within a module (Olesen *et al.* 2007, Schleuning *et al.* 2014). Although modular structure is frequent in nature, this pattern might be less pronounced when analysing some subgroups within communities. For instance, plant-frugivore networks

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seem to be less modular than other types of interaction (Rezende *et al.* 2009), but this trend might reflect the overrepresentation of plant-bird networks in the available datasets which in fact comprise only one taxonomic and presumably few functional groups of seed dispersers (Donatti *et al.* 2011, Mello *et al.* 2011). Furthermore, most of the studies conducted so far are based on binary interaction data which might overestimate the role of rare and singleton species and/or underestimate highly interactive species (Dormann & Strauss 2014).

Plant-frugivore interactions are marked by large overlaps and resource share (Silva & Melo 2013, Terborgh & Diamond 1970), which ultimately lead to low levels of complementary specialization in relation to other types of interaction (Blüthgen et al. 2007). In spite of this, some assemblages of closely related animal-dispersed plants show apparent pattern of sequential fruiting, which might minimize the competition for seed dispersers and finally benefit the entire community of frugivores by providing constant supply of food resources (Maruyama et al. 2013, Poulin et al. 1999). In this sense, closely related plants which present similar fruits, thus impairing formation of morphology related modules, yet temporally segregating their fruiting phenology could be a good system to test whether temporal distribution of interactions drives formation of modules in small networks. By contrasting binary and weighted modularity algorithms, we can also demonstrate the importance of considering the strength of the interactions to detect subtle structural patterns in ecological networks (Dormann & Strauss 2014). Here we use data on interaction of four assemblages of Miconia (Melastomataceae) and their frugivorous birds from Neotropical habitats to test the following hypotheses: (1) networks centred on *Miconia* are modular and each module is composed of a Miconia species and their main partners; (2) modules in these networks can be efficiently detected by weighted algorithms and (3) dietary specialization is the bird trait that best explains species roles in the modular networks.

METHODS

Plant species

Miconia (Melastomataceae) with *c*. 1100 described species is one of the richest genera among Neotropical angiosperms. *Miconia* species can present many habits including shrubs, herbs, epiphytes, treelets and trees, and are usually associated with edges and natural gaps in the vegetation (Ellison *et al.* 1993). Plants from this group can be found in a range of environments, from open habitats as grasslands to savannas and extremely humid tropical rain forests (Romero & Martins 2002). One important characteristic of *Miconia* is a tight association

to frugivorous animals for seed dispersal. The small carbohydrate-rich fruits contain numerous tiny seeds and are eaten and dispersed by several species of bird, including many generalist species (Maruyama *et al.* 2013, Snow 1981). Furthermore, species of *Miconia* are among the most important resources for fruit-eating birds in Neotropical environments (Maruyama *et al.* 2013, Stiles & Rosselli 1993). Commonly, assemblages of *Miconia* species show asynchronous and complementary fruiting period (Maruyama *et al.* 2013, Poulin *et al.* 1999) which is believed to reduce interspecific competition for dispersal agents (Wheelwright 1985) and might contribute to the high number of species of this genus occurring in sympatry.

Interaction data

Data on interaction of *Miconia* and frugivorous birds came from four distinct communities, three from the Neotropical savannas in Brazil and one from the rain forest of Panama. Savanna networks were collected at Caça e Pesca (18°55'S, 48°17'W, Maruyama et al. 2013), Panga (19°10'S, 48°23'W, Borges 2010, Appendix 1) and Duratex (18°50'S, 47°49'W, Paniago 2014, Appendix 2), all areas with remnants of native vegetation in the region. In each of these sites, interactions among species of Miconia and frugivore birds were recorded through focal observations, where the observers remained about 10 m distant from the focal tree and recorded the fruit-eating interactions. From these records, we constructed bipartite interaction matrices with each cell representing the number of interaction events, i.e. instances in which a bird visited a plant individual, of the corresponding plant-bird pair. For the Panamanian network, data were collected at Soberania National Park (09°10'N, 79°07'W, Poulin et al. 1999) and instead of visits, interaction strength among a pair of species is represented by the number of fruit records in regurgitation or faecal samples collected from mist-netted birds (Poulin et al. 1999). Although differences in the methods to record the interaction exist, this should not affect our overall interpretation of the results as we are characterizing the networks pattern within each of the communities. After constructing these matrices considering the frequencystrength of the interaction, we also constructed for each of the matrices a binary version, representing the presence or absence of interaction among a pair of plant and bird. Networks used in our study were the only ones in literature that are collected specifically for Miconia assemblages which ensured an equivalent sampling for each plant species. Hence, although some broader community-wide networks containing Miconia species are available in the literature, we did not include those here.

Network analysis

To measure the binary modularity in the networks, we used the software MODULAR (Marquitti *et al.* 2014), quantifying the modularity using the metric proposed by Barber (2007) for bipartite networks:

$$Q_B = \sum_{i=1}^{N_M} \left[\frac{E_i}{E} - \left(\frac{k_i^C \cdot k_i^R}{E^2} \right) \right],$$

where N_M is the number of modules, E_i is the number of links in module *i*, *E* is the number of links in the complete network, k_i^C is the sum of the degrees of the nodes within module *i* that belong to set *C* and k_i^R is the sum of the degrees of the nodes within module *i* that belong to set *R*. The significance of the bipartite modularity was compared against 1000 random networks, generated by two null models. The first one is the Erdős–Rényi model (Erdős & Rényi 1959), where each pair of nodes has the same probability of being connected by a link and the second is null model 2 (Bascompte *et al.* 2003), where the probability of a pair being connected by an edge is proportional to the number of edges that the nodes have.

To quantify the modularity in the weighted networks, we used the algorithm QuanBiMo (Dormann & Strauss 2014). This algorithm detects the presence of modules in weighted bipartite networks based on a hierarchical representation of species link weights and optimal allocation to modules (Dormann & Strauss 2014). The algorithm is a modification of the Newman's quantity of modularity Q (Barber 2007):

$$Q = \frac{1}{2N} \sum_{ij} \left(A_{ij} - K_{ij} \right) \delta \left(m_i, m_j \right),$$

where *N* is the total number of interactions in the network; A_{ij} is the number of interactions between frugivorous species *i* and plant species *j*; K_{ij} represents the random expected probability of interactions within a module; the function (m_i, m_j) is 1 when species *i* and *j* are in the same module $(m_i = m_j)$ and 0 if they are in different modules $(m_i \neq m_j)$. The modularity *Q* ranges from 0 (no support for division of modules) to 1 (maximum degree of modularity). The QuanBiMo algorithm was run with the function computeModules in R-package bipartite (Dormann *et al.* 2009).

The absolute value of Q is dependent on network size and number of links (Dormann & Strauss 2014), so we tested the estimates of modularity Q with 1000 randomizations generated by two null models: Patefield null model (r2dtable) – which uses fixed marginal totals to distribute the interactions and produce a set of networks in which all species are randomly associated (Blüthgen *et al.* 2008); and the null model proposed by Vázquez *et al.* (2007), which retain the number of interactions per species and the network connectance (*vaznull*). To identify species roles in modular network we estimated for each species the within-module degree *z* and the among-module connectivity *c*-scores (Guimerà & Amaral 2005, Olesen *et al.* 2007):

$$c = 1 - \sum_{t=1}^{N_M} \left(\frac{k_{it}}{k_i}\right)^2, \ z = \frac{k_{is} - k_s}{SD_{ks}}$$

where, k_{is} is number of links of *i* to other species in its own module *s*; k_s and SD_{ks} are average and standard deviation of within module *k* of all species in *s*; k_i is degree of species *i*; k_{it} is number of links from *i* to species in module *t*. As binary networks did not show significant modularity, we only calculated the weighted version of these indices, which are computed based on species strength instead of number of links (Dormann & Strauss 2014). For calculations of weighted *c* and *z*-scores, we used the function czvalues in bipartite.

Bird traits

In order to relate network role of birds to their ecological traits, we gathered data on bird body mass, migration behaviour, dietary specialization and taxonomic family. As the morphology of the Miconia berries in this study is very similar (Maruyama et al. 2007), bill gape width should not constrain the interaction, therefore, it was not considered here. The fruit-eating birds were classified into three dietary categories following Kissling et al. (2007) as (1) obligate frugivores species that have fruits as the major food items in their diet; (2) partial frugivores – species that include other major food items in diet; and (3) opportunistic fruit-eaters – species that only occasionally eat fruits as supplementary food resource. Data on the diet of birds were gathered from published studies, and for savanna areas also included personal observations in the areas of studies (del Hoyo et al. 2015, Sick 1997). Bird body mass influences food choices and the number of fruits consumed (Wotton & Kelly 2012), thus it might be related to the network role. For each bird species we obtained data on average body mass of adult specimens from the literature (Dunning 2008). As temporal distribution of species in a community might constrain the partners to interact with (Vázquez et al. 2009b, Vizentin-Bugoni et al. 2014), we classified the migratory behaviour of the bird species as: (1) resident - sedentary species that remain year-round in the area; (2) nomad – a species that perform irregular moments in response to resource availability; and (3) migratory – species that make short or long and well-defined seasonal movements. Movement information was gathered from Loiselle & Blake (1991), Nunes & Tomas (2008), del Hoyo *et al.* (2015) and personal observations. Finally, as many traits in birds are phylogenetically conserved (Losos

Table 1. Values of modularity in binary and weighted versions of four *Miconia*-frugivore bird networks: Caça e Pesca (Maruyama *et al.* 2013), Panga (Borges 2010), Duratex (Paniago 2014) and Panama (Poulin *et al.* 1999); and the significance against the null models. Null 1 = Erdős and Rényi model (Erdős & Rényi 1959); Null 2 = "null model 2" of Bascompte *et al.* (2003); r2dtable = Null model Patefield (Patefield 1981); vaznull = Null model proposed by Vázquez *et al.* (2007); Q_{obs} = value of modularity Q observed in the networks; Q_{null} = value of mean modularity Q generated by 1000 null models.

		Binary				Weighted				
		Nul	11	Null 2			r2dtable		vaznull	
Area	Q _{obs}	Q _{null}	р	Q _{null}	р	Q _{obs}	Q _{null}	р	Q _{null}	р
Caça e Pesca	0.178	0.202	0.78	0.195	0.73	0.240	0.118	< 0.01*	0.143	< 0.01
Panga	0.294	0.265	0.33	0.260	0.30	0.399	0.183	$< 0.01^{*}$	0.233	< 0.01
Duratex	0.376	0.364	0.39	0.351	0.31	0.240	0.096	$< 0.01^{*}$	0.1463	< 0.01
Panama	0.352	0.331	0.31	0.323	0.24	0.245	0.126	< 0.01*	0.1697	< 0.01

2008), we also included the family of birds as a category in our analysis to reflect species relatedness. Classification and nomenclature of birds followed the South American Classification Committee (Remsen *et al.* 2015).

Statistical analysis

The relationship between network roles, as represented by *c* and *z* scores, and bird traits was evaluated with linear mixed-effects models (Bolker *et al.* 2009). We used as fixed factors the body mass, dietary specialization, migratory behaviour and taxonomic family. Bird species identity was included as a random effect to account for non-independence within observations of the same species in different networks (Bolker *et al.* 2009). For each of the response variables, *c* and *z*-scores, we ran the models separately. The full model including all factors and reduced models were fitted using the function dredge in R package MuMln and compared by their values of the Akaike information criterion corrected for small sample sizes (Bolker *et al.* 2009). Models with $\triangle AICc \leq 2$ were considered as equivalent.

RESULTS

Considering all networks, 66 species of bird, 12 *Miconia* species and 953 interactions were recorded. Thraupidae were the best-represented family with 24 species (36.4%), followed by Tyrannidae with 11 (16.7%). Seventeen (25.8%) species were classified as obligate frugivores, while 23 (34.8%) and 26 (39.4%) were classified as partial frugivores and opportunistic fruit-eaters, respectively. For migratory behaviour, 43 species (65.1%) are resident, 10 (15.2%) are nomad and 13 (19.7%) are migrant. Considering the body mass, most birds are small with 87.9% of the bird species weighing less than 100 g.

When considering binary matrices, none of the networks had values of modularity different from random,

irrespective of the null models used. All quantitative versions of the networks, in contrast, were modular with each presenting three modules (P < 0.01 for both null models; Table 1). Each module within these networks contained one or two *Miconia* species associated with their most common frugivores (Figure 1). Model selection showed that neither *c* nor *z*-scores can be associated to body mass, dietary specialization, migratory behaviour and bird family, as no model including fixed factors performed better than the model including only the intercept (Table 2).

DISCUSSION

Modules could only be found by incorporating the strength of the interactions in Miconia-bird networks. The importance of using weighted information, such as interaction strength in network analyses has been recognized as an important step in understanding the architecture of ecological communities (Gilarranz et al. 2012, Ings et al. 2009). Schleuning et al. (2014), in a study with 18 plant-frugivore networks, found that only one third presented significant modularity with binary data, while including information on the strength of interaction allowed the detection of modules in all but one of these networks. Similarly, although small binary pollination networks do not show distinct modular organization (Olesen et al. 2007), the inclusion of quantitative information led to the detection of modules even in species-poor hummingbird-plant pollination networks (Maruyama et al. 2014, 2015). Moreover, these modules are associated to the functional traits of the species (Maruyama et al. 2014, 2015). Overall, it seems that inclusion of quantitative information led to detection of finer partitioning in networks.

Interspecific competition among plants for dispersal agents is regarded as a force that can shape the structure of plant-frugivore interactions (Herrera 1981, Howe & Estabrook 1977, Howe & Smallwood 1982).



Figure 1. Modules identified by the QuanBiMo algorithm in four weighted *Miconia*-frugivore bird networks: Caça e Pesca (Maruyama *et al.* 2013) (a), Panga (Borges 2010) (b), Duratex (Paniago 2014) (c) and Panama (Poulin *et al.* 1999) (d). Warm tones represent a higher number of interactions and cool tones represent fewer interactions. The green boxes represent the modules identified and each row represents a *Miconia* species.

As interaction pressures are expected to be stronger among closely related species due to similarity in niches (Webb *et al.* 2002), sympatric congeneric species tend to have mechanisms to ensure their co-existence (Beltrán *et al.* 2012). Berries of the 12 *Miconia* species analysed are very similar in morphology and nutritional values (Maruyama *et al.* 2007), meaning that these traits play little role in selection of different dispersal agents, and hence in generating modules. However, the fruiting asynchrony observed, with no overlap in fruiting peak among the sympatric species (Maruyama *et al.* 2013, Poulin *et al.* 1999), potentially suffices to generate the modular structure and also facilitate the co-existence of species by promoting facilitation among plants (Poulin *et al.* 1999).

The abundance of bird populations fluctuates yearround, especially in seasonal environments, due to several factors, such as total or partial migration and

dispersal (Loiselle & Blake 1991). Moreover, more than one third of the species associated with the Miconia species perform seasonal movements. Frugivorous birds are subject to high resource fluctuations (Loiselle & Blake 1991), having greater tendency to seasonal movement compared with insectivorous species (Levey & Stiles 1992). Nevertheless, bird migration behaviour did not strongly associate to species role in the networks. One important point that should be noticed, though, is that consumer species may seasonally switch their foraging behaviour according to resource variability (Carnicer et al. 2009), e.g. insectivorous and omnivorous birds can change the proportion of fruits in their diet according to the availability of their main resources (Borghesio & Laiolo 2004) or with the life stage (Robbins 1981). Even within more specialized frugivorous birds, the availability of fruiting plants other than *Miconia* might change the relative attractiveness of these less-rewarding

Table 2. Comparisons of statistical models containing combinations of bird traits that explaining the within- and among-module connectivity indices (c and z scores) in four *Miconia*-frugivore bird networks (Borges 2010, Maruyama *et al.* 2013, Paniago 2014, Poulin *et al.* 1999). Models with \triangle AICc < 2 were considered equivalent and include here in the table. None of the bird trait models has more explanatory power than the models containing only the intercept.

Model	AICc	ΔAICc	AICc weight
c-score			
Intercept only	691.1	0.00	0.288
Dietary specialization	692.0	0.88	0.185
Body mass	692.5	1.38	0.145
Body mass + Dietary specialization	692.7	1.58	0.131
z-score			
Intercept only	726.3	0.00	0.181
Body mass	726.7	0.34	0.153
Body mass + Dietary specialization	726.7	0.41	0.148
Migratory behaviour	727.0	0.66	0.131
Dietary specialization	727.3	0.97	0.112
Body mass + Migratory behaviour	727.3	1.00	0.110
Body mass + Dietary specialization + Migratory behaviour	727.7	1.34	0.093
Dietary specialization + Migratory behaviour	728.2	1.86	0.072

carbohydrate-rich fruits (Maruyama *et al.* 2013). In this sense, this potential diet variation in frugivorous birds would function as a seasonal pattern in fruit consumption, which coupled with possible abundance fluctuation and asynchronic fruiting period in *Miconia* could favour the formation of modules comprising birds (or their seasonal diet preferences) and plant species with stronger phenological overlap.

None of the bird morphological traits or taxonomic relatedness affected the within- and among-module connectivity. In general, body mass has been shown to be an important driver in structuring ecological networks (Arim et al. 2011, Rezende et al. 2009), although it has been shown to have little explanatory power in the variation of centrality metrics in plantfrugivore networks (Mello et al. 2015). This lack of association might be especially likely if the assemblage of animals considered shows little variation in the trait. Birds associated with Miconia are mostly passerines, a group composed by small- to medium-sized species. Fruit-eating bird assemblages dominated by small-bodied species tend to be less specialized (Menke et al. 2012), resulting in modularity roles more evenly distributed among bird species. Furthermore, Saavedra et al. (2014) found little effect of morphological traits in interaction strength in the forest-edge frugivore networks, where Miconia species are widespread and small-bodied birds are predominant. Considering the dietary specialization, obligate and partial frugivorous had within- and amongmodule connectivity values higher than opportunistic ones in most community-wide plant-frugivorous bird networks (Schleuning et al. 2014). Once again, the fact that most birds associated with Miconia are generalist, small-bodied birds is probably related to the lack between

diet and network roles, since even generalist frugivores have important roles in dispersing the seed of these species (Howe 1993, Maruyama *et al.* 2013, Poulin *et al.* 1999, Snow 1981). Nevertheless, this independence from specific groups of dispersal agents may ensure the seed dispersal services from a variety of species (Jordano *et al.* 2007) which is especially important for high-fecundity pioneer species with small-seeded fruits (Howe 1993).

At what hierarchical level or with what kind of information, i.e. binary and weighted, modules can be detected in ecological systems is still only beginning to be addressed in the literature (Schleuning et al. 2014, Tur et al. 2015). We showed that modular structure can be detected within closely related sympatric species, but only when using weighted information incorporating the strength of the interactions. The use of quantitative information has been argued for in recent studies (Dormann & Strauss 2014, Schleuning et al. 2014) and we hope our study illustrated how finer partitioning of interactions can be detected by using it. Even when evaluating the role of species within networks, analysing quantitative data may deeply affect how we quantify the importance of each species in a network (Scotti et al. 2007). The next question to answer is at what hierarchical level the detection of modular organization has real impact on how we assess the stability and dynamics of ecological systems. Modules have been detected for a myriad of ecological systems, from entire assemblage/community to within species/populations individual-based networks (Donatti et al. 2011, Tur et al. 2015). Closely related sympatric species also show a modular interaction pattern, possibly related to asynchronous fruiting period, but not with morphological and behavioural traits of birds such as

body mass, diet and migratory behaviour. How each of these modular patterns, present at distinct layers of hierarchy, can promote co-existence of species and hence the functioning of ecological systems, deserve further investigation in the future.

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Appendix 1. Frugivory interaction matrix between three *Miconia* species and 17 bird species in a Neotropical savanna in Brazil (Panga; 19°10'S, 48°23'W). Frugivory interactions were recorded from April to November 2007 with 30–42 h of focal-plant observation per *Miconia* species. Source: Borges (2010).

	Miconia	Miconia	Miconia	
	theaezans	albicans	chamissois	Total
Tangara cayana	28	0	2	30
Dacnis cayana	6	0	4	10
Tachyponus rufus	4	1	3	8
Antilophia galeata	2	0	5	7
Elaenia sp.	4	1	0	5
Volatinia jacarina	0	5	0	5
Saltator similis	1	0	3	4
Turdus leucomelas	0	0	4	4
Ramphocelus carbo	0	0	4	4
Schistochlamys melanopis	2	0	1	3
Cyanocorax cyanopogon	0	2	1	3
Tangara palmarum	0	1	2	3
Sporophila nigricollis	0	3	0	3
Pipraeidea melanonota	0	0	1	1
Tersina viridis	0	0	1	1
Lanio cucullatus	0	0	1	1
Euphonia chlorotica	0	0	1	1
Total	47	13	33	

Appendix 2. Frugivory interaction matrix between four *Miconia* species and 17 bird species in a Neotropical savanna in Brazil (Duratex; $18^{\circ}50'S$, $47^{\circ}49'W$). Frugivory interactions were recorded from August 2012 to December 2013 with about 35 h of focal-plant observation per *Miconia* species. Source: Paniago (2014).

	Miconia	Miconia	Miconia	Miconia	
	albicans	elegans	leucocarpa	ligustroides	Total
Elaenia sp.	8	1	82	52	143
Piranga flava	14	0	0	0	14
Tangara cayana	8	0	4	0	12
Zonotrichia capensis	12	0	0	0	12
Tangara palmarum	7	1	3	0	11
Cyanocorax cristatellus	0	0	3	3	6
Hemithraupis guira	5	0	0	0	5
Turdus leucomelas	4	0	0	0	4
Sporophila sp.	2	0	1	1	4
Aratinga aurea	0	0	0	4	4
Saltator maximus	3	0	0	0	3
Antilophia galeata	0	3	0	0	3
Dacnis cayana	2	0	0	0	2
Euphonia chlorotica	2	0	0	0	2
Lanio cucullatus	1	0	0	0	1
Tangara sayaca	1	0	0	0	1
Volatinia jacarina	0	0	1	0	1
Total	69	5	94	60	