

The modularity of seed dispersal: differences in structure and robustness between bat– and bird–fruit networks

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Abstract In networks of plant–animal mutualisms, different animal groups interact preferentially with different plants, thus forming distinct modules responsible for different parts of the service. However, what we currently know about seed dispersal networks is based only on birds. Therefore, we wished to fill this gap by studying bat–fruit networks and testing how they differ from bird–fruit networks. As dietary overlap of Neotropical bats and birds is low, they should form

distinct mutualistic modules within local networks. Furthermore, since frugivory evolved only once among Neotropical bats, but several times independently among Neotropical birds, greater dietary overlap is expected among bats, and thus connectance and nestedness should be higher in bat–fruit networks. If bat–fruit networks have higher nestedness and connectance, they should be more robust to extinctions. We analyzed 1 mixed network of both bats and birds and 20 networks that consisted exclusively of either bats (11) or birds (9). As expected, the structure of the mixed network was both modular ($M = 0.45$) and nested (NODF = 0.31); one module contained only birds and two only bats. In 20 datasets with only one disperser group, bat–fruit networks (NODF = 0.53 ± 0.09 , $C = 0.30 \pm 0.11$) were more nested and had a higher connectance than bird–fruit networks (NODF = 0.42 ± 0.07 , $C = 0.22 \pm 0.09$). Unexpectedly, robustness to extinction of animal species was higher in bird–fruit networks ($R = 0.60 \pm 0.13$) than in bat–fruit networks ($R = 0.54 \pm 0.09$), and differences were explained mainly by species richness. These findings suggest that a modular structure also occurs in seed dispersal networks, similar to pollination networks. The higher nestedness and connectance observed in bat–fruit networks compared with bird–fruit networks may be explained by the monophyletic evolution of frugivory in Neotropical bats, among which the diets of specialists seem to have evolved from the pool of fruits consumed by generalists.

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Introduction

Mutualistic interactions among animals and plants are vital for ecosystem functioning as they generate important

ecosystem services such as seed dispersal and pollination (Wright 2002). Network theory facilitates the understanding of the structure and dynamics of mutualisms, as it allows a traceable representation of their complexity and an assessment of the whole structure of their interactions at the community level, as well as simulations of extinctions or loss of interactions (Bascompte and Jordano 2007). This, in turn, is essential in assessing ecosystem services as a whole (Walker 1992). Despite some pervasive properties of mutualistic networks (such as nestedness; Bascompte et al. 2003), there are important differences between parts of each network. For instance, the hypothesis of mutualistic modules (Jordano 1987) states that networks consist of subsets composed of phylogenetically related species that play similar ecological roles.

Indeed, modules (i.e., cohesive subgroups of closely connected species) with a strong phylogenetic signal have already been detected in both ant–plant (Fonseca and Ganade 1996) and pollination networks (Olesen et al. 2007), and modularity seems to be another pervasive property of mutualisms (Fortuna et al. 2010). Modularity is also related to classic ecological theories, as interaction syndromes (van der Pijl 1972) and guilds (Root 1967). However, the novelty brought by the analysis of modularity is the possibility to test for a subgroup structure and to assess this structure based on the pattern of multi-species interactions. There is also much evidence supporting the hypothesis that closely related species tend to interact with similar subsets of partners (Oliver et al. 2008). A modular structure means that the ecosystem service rendered by the network consists of subsets of tightly-connected animals and plants, which are linked to each other by some species with interactions that reach beyond their own modules (i.e., connectors). Therefore, the concept of modules in network theory is related to the ecological concepts of guilds and functional groups (Blondel 2003), and hence may be used as a tool to test predictions derived from ecological theory. Modules may be complementary or redundant at different levels. It is therefore crucial to understand this mosaic of modules in order to comprehend how seed dispersal services are generated and how disturbances might affect their functioning.

Although there is strong evidence of a modular structure in pollination (Olesen et al. 2007) and myrmecophily systems (Fonseca and Ganade 1996), modularity has seldom been investigated in seed dispersal systems. Many animal groups are involved in seed dispersal (Fleming et al. 1987). This service is dominated by birds and bats in the Neotropics, as those two disperser groups are responsible for nearly 80% of the seed rain at some sites (Galindo-González et al. 2000), with other vertebrates, particularly primates and rodents, contributing as well (Fleming et al. 1987). However, our knowledge of seed dispersal networks is very limited, as almost only bird–fruit systems have been studied so far using a network approach (Bascompte and

Jordano 2007). Furthermore, in general, seed dispersal at community level has been much better studied in birds than in other animals.

Bats and birds are ecologically very similar since they are both highly mobile. They both feed on a wide range of fruit species (Terborgh et al. 2002), but dietary overlap is low between both groups in many Neotropical communities (Muscarella and Fleming 2007). Consequently, birds and bats appear to play complementary roles in seed dispersal, and thus, in a local network, birds and bats should belong to different mutualistic modules. Furthermore, in the Neotropics, strict frugivory evolved just once among bats (Datzmann et al. 2010), but several times independently among birds (Kissling et al. 2009). This means that frugivorous birds, which belong to several families, are more species-rich and phylogenetically much more diverse than frugivorous bats, which all belong to the family Phyllostomidae (Kissling et al. 2009; Lobova et al. 2009). Although frugivorous bats feed on plant species in at least 62 plant families, their diet is concentrated on five main genera (*Cecropia*, *Ficus*, *Piper*, *Solanum* and *Vismia*; Lobova et al. 2009), whereas frugivorous birds have a much more diversified diet (Kissling et al. 2009).

Thus, on average, each bird species probably interacts with a larger number of plant species in each network, whereas each bat species probably has a narrower dietary spectrum but interacts with a higher proportion of the plants available in the network. Consequently, connectance should be higher and average path length (i.e., the number of direct and indirect links that separate on average every two species in the network) shorter in bat–fruit networks than in bird–fruit networks, as more interactions are likely to occur within them. Similarly, nestedness should also be higher in bat–fruit networks, as the diet of species with few interactions is probably a subset of the diet of species with many interactions, as observed for instance in *Carollia* bats (Thies and Kalko 2004).

Finally, because bird–fruit networks are ecologically more diverse, there should be a larger proportion of species playing peripheral roles, which cause smaller changes to the whole structure if removed, and consequently these networks should be more robust to random extinctions of single species than the ecologically less diverse bat–fruit networks. We tested these hypotheses and present evidence on the modularity of seed dispersal networks and on the ecological complementarity of bat and bird dispersal services.

Materials and methods

Datasets

To compare the structure and robustness of bat– and bird–fruit networks, we analyzed 17 published datasets,

consisting of 11 bat–fruit networks, 9 bird–fruit networks, and 1 mixed network with both bats and birds (Online Resource 1). Six of those datasets were obtained from the Interaction Web Database (<http://www.nceas.ucsb.edu/interactionweb/>). The mixed network was analyzed both as a whole and as separate bird– and bat–fruit subnetworks (i.e., subsets of a complete network, in this case based on taxonomy). For our analysis, we used 13 datasets based on data from fecal analysis obtained through mist-netting at ground level, and 3 datasets containing data from fecal analysis combined with other methods, such as focal observations and roost inspections. We included only studies in which sampling was carried out for at least 1 year, all frugivore and plant species were sampled without an a priori selection of particular groups, and all or most animals and plants were identified to the species. Although a few bird and bat species also act as seed predators (e.g., *Chiroderma* bats; Nogueira and Peracchi 2003), they are included in our network analysis as they represent only a very small proportion of all *frugivorous* species in each network (Jordano et al. 2009) and occasionally also disperse seeds. Therefore, we note that our networks really are of seed dispersal and not only frugivory, as most animals studied here are legitimate dispersers (Fleming and Sosa 1994). In the analysis of networks, similar problems are observed as in the analysis of communities, mainly sampling biases related to rare species (Blüthgen et al. 2008). In our study on seed dispersal networks, those biases are not particularly problematic, because we focused on the structure of interactions and the seed dispersal service as a whole and not on the niche of each species. As in other network studies (Bascompte et al. 2003), differences in sampling completeness among studies are viewed here as an advantage, as they allow for testing our hypotheses with an heterogeneous dataset that represents the diversity of information available in the literature.

Network analysis

We transformed all datasets into binary adjacency matrices of animals and plants, with bat or bird species as A rows and fruit species as P columns, in which 1 represents records of frugivory and 0 represents lack of records. Thus, vertices in those networks are species of animals or plants and edges are interactions of frugivory. The networks were represented as two-mode graphs in the “bipartite” package of R (Dormann et al. 2008).

To test whether bats and birds in the mixed network belong to different subgroups we used a modularity analysis based on a simulated annealing algorithm (Guimerà and Amaral 2005). The network module concept is very straightforward as a surrogate to test the hypothesis of mutualistic modules. Modularity is a measure of how much

the network is structured as cohesive subgroups of vertices (modules) in which the density of interactions is higher within than among subgroups. Modularity was calculated with the index M (range 0–1) in the program Netcarto (kindly provided by R. Guimerà) (Guimerà and Amaral 2005), and its significance was estimated with a Monte Carlo procedure with 1,000 randomizations. Modules were identified in Netcarto, and the bipartite network plus its modules were represented as energy-minimization graphs in Pajek 2.02 (Batagelj and Mrvar 1998). We used the original bipartite networks in this analysis, following other studies on mutualistic networks (e.g., Olesen et al. 2007).

Seven descriptors of structure were used to compare the 20 separate networks with either bats or birds: network size, nestedness, connectance, complementary specialization, average path length, modularity, and average number of plants per animal. Network size (S) was defined as the total number of species in a network; i.e., species richness in the community. The average number of plant species per animal species (Ppa), also known as “species richness ratio” (Guimarães et al. 2007), was calculated by dividing the number of plant species by the number of animal species in each network. Because networks have different species richness, the species richness ratio was also calculated as a proportion in relation to the total of partners available in the network (Ppa').

Nestedness is a topological pattern in which interactions involving species with few connections represent a subset of the interactions involving highly-connected species (Bascompte et al. 2003). Nestedness is hypothesized as a characteristic of facultative mutualisms (Guimarães et al. 2007) and is assumed to result in higher robustness of the whole system (Bastolla et al. 2009). We used the software Aninhado 3.0 to calculate the degree of nestedness with the metric NODF, which varies from 0 to 100 (Almeida-Neto et al. 2008); we normalized values so they ranged from 0 (non-nested) to 1 (perfectly nested). The significance of NODF was estimated with a Monte Carlo procedure with 1,000 randomizations, using null model C_e , in which the interaction probability between an animal and a plant is proportional to their total number of interactions.

Connectance (C) was defined as the proportion of realized interactions in relation to the total of interactions possible in the network. It varies from 0 (no interactions) to 1 (all species connected to each other) (Jordano 1987). For seed dispersal networks, connectance is calculated as $C = I/(AP)$, where I is the total number of interactions observed in the network, A represents the number of animal species involved, and P is the number of plant species. Connectance is considered as a surrogate for complementary specialization in mutualistic networks (Jordano et al. 2003) and describes the proportion of realized interactions

in the network. Here, specialization is not defined based on dietary preferences or coevolutionary relationships but only as the number of interactions established by the species in relation to all possible interactions. As there is some criticism of the use of connectance as a surrogate for specialization (Blüthgen et al. 2007), because it is strongly correlated with network size, we calculated H_2' for comparison (Blüthgen et al. 2006). H_2' depicts how much the interactions of each species differ from each other in the network. However, three networks could not be included in this analysis as they contained only binary data and H_2' requires weighted data (i.e., frequency of interaction).

Average path length (PI) represents the average length of all shortest paths between any two vertices in the network; the shortest path between two vertices is calculated as the number of interactions in the shortest possible path (geodesic) between them (Nooy et al. 2005). For instance, if two species i and j are connected to each other, the path length between them is 1; if two species i and j are indirectly connected by a third species k , which is a common partner of both, the path length between i and j is 2. Average path length is a surrogate for cohesiveness in the network (Watts and Strogatz 1998). To calculate path lengths, we transformed each network into an unipartite projection of only animal species, in which links represent niche overlap (i.e., species that have at least one food plant in common), using Pajek 2.02.

To test for the robustness of networks to cumulative random extinctions of single species, we used the analysis proposed by Burgos et al. (2007). In this analysis, extinctions were simulated by cumulatively and randomly removing species from the network. When a species was connected only to the removed species, it was also removed from the network (secondary loss). This way, an extinction curve was generated by plotting the number of remaining species against the cumulative number of species removed (100 randomizations). Removals were carried out from each side of the network separately. Ultimately, we obtained one curve for plants and one for animals for each network. The area below each curve (R) was calculated as a measure of the robustness of the system to the loss of animal or plant species, i.e., how quickly the network collapses after cumulative extinctions. $R = 1$ corresponds to a slow decrease in the curve, and thus represents a system in which most plants remain after the removal of most animals, or vice versa. $R = 0$ corresponds to a network that collapses quickly after the first removals. This analysis was carried out in the package bipartite for R (Dormann et al. 2008). It is important to say, though, that the removal of a species from a seed dispersal network does not mean an actual extinction in its ecological community, but a removal from the local seed dispersal service.

Statistical analysis

Differences between bat– and bird–fruit networks were tested with general linear models (GLM) in the package PASW Statistics for Mac 18.0. In each model, the network index (NODF, C , Ppa, Ppa', PI, or M) was the dependent variable, the disperser group (bat–fruit or bird–fruit) was the fixed factor, and network size (S) was the covariate, because network size is correlated with many network parameters (Dormann et al. 2009). For comparison of robustness in bat– and bird–fruit networks with regard to cumulative extinctions, we used separate GLMs for animals and plants. In the GLMs for robustness, R was the dependent variable, the disperser group (bat–fruit or bird–fruit) was the fixed factor, and the covariates were S , NODF, and M . We arcsine-transformed proportions and transformed counts to their square root in order to increase normality.

In these analyses, we assumed that the more a network is nested, the more robust it is, because fragile species (i.e., with few interactions) are connected to resistant species with many interactions (“hubs”) (Bastolla et al. 2009). We also assumed that the more a network is modular, the less robust it might be, as a modular structure comprises different subsets which are connected in some cases by a single or a few species. In case those connectors are eliminated, the system tends to become unstable and even to be divided into fragments that are not connected to each other anymore. In extreme cases, there may even be a system collapse, inducing a large change in topology (i.e., a ‘phase shift’) (Bascompte 2009; Scheffer et al. 2009).

Results

The mixed network with bats and birds together comprised 7 bird species, 11 bat species, and 85 plant species. About equal numbers of plant species were eaten exclusively by birds ($n = 40$) or by bats ($n = 39$), and only 6 plant species were eaten by both groups. Consequently, the network was highly modular ($M = 0.45$, $P < 0.001$) with three modules, two with only bats and one with only birds (Fig. 1; species names are given in Online Resource 1). At the same time, the whole network was also nested (NODF = 0.31, $P < 0.001$). Additionally, in the mixed network, birds (Ppa = 14.6, Ppa' = 0.17) interacted with more plant species than bats (Ppa = 7.7, Ppa' = 0.09). When considering the subsets of this network, the bat–fruit subnetwork and the bird–fruit subnetwork were both nested (NODF_{bats} = 0.65, $P < 0.001$; NODF_{birds} = 0.45, $P < 0.001$) and modular ($M_{bats} = 0.23$, $P < 0.001$; $M_{birds} = 0.35$, $P < 0.001$).

The separate bat–fruit networks ($n = 11$, $S = 33 \pm 19$ species) had on average half the size of the bird–fruit networks ($n = 9$, $S = 68 \pm 54$ species) ($df = 18$,

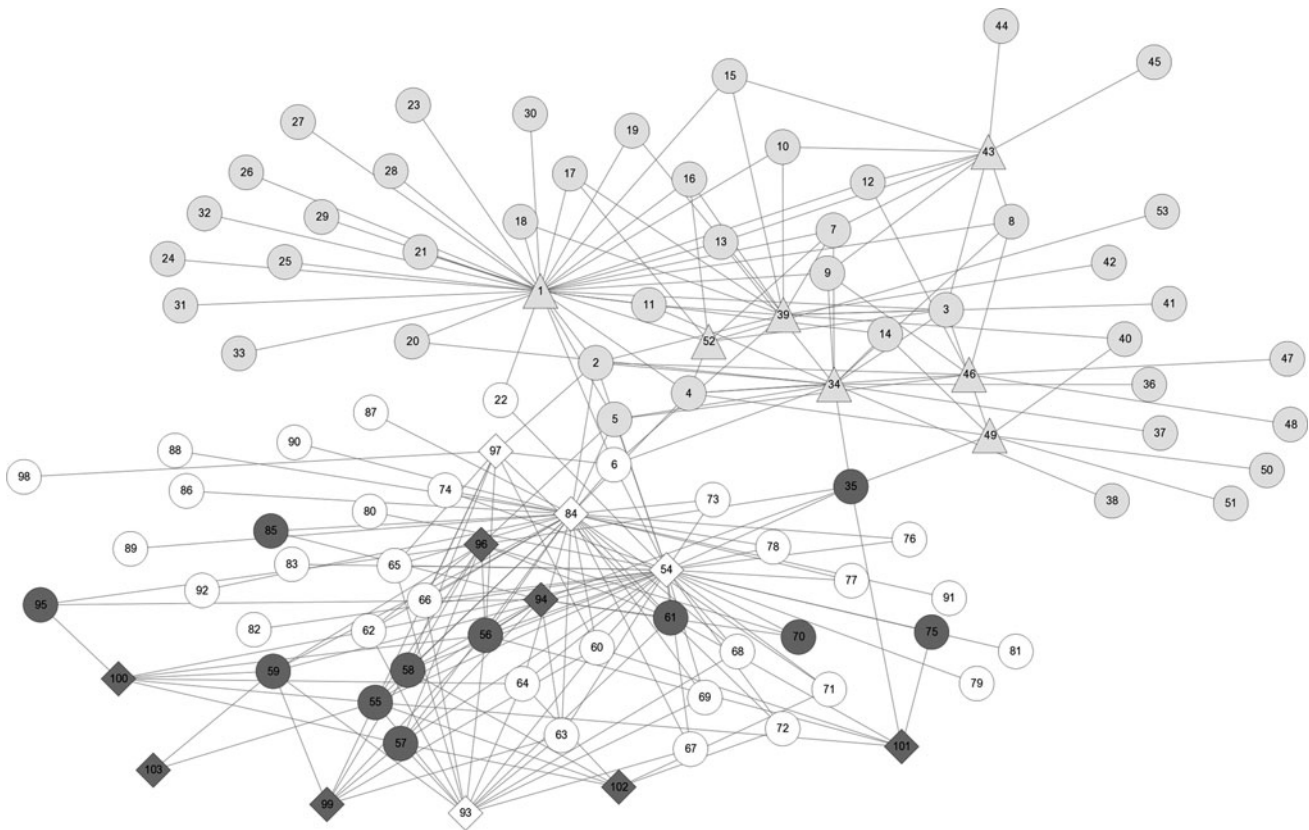


Fig. 1 The seed dispersal network by Neotropical frugivorous birds and bats in a forest in the Peruvian Amazon (data from Gorchov et al. 1995; see Online Resource 1). Birds (triangles), bats (diamonds) and food-plants (circles) that are in separate modules (gray tones) are more densely connected to each other than to other species in the

same network. Each line (edge) represents a frugivory interaction. Species with a large number of interactions (hubs) or species that connect different parts of the network (connectors) are closer to the center. Species names are given in Online Resource 1

Student's $t = -2.39$, $P = 0.03$) (Online Resource 2). On average, birds ($Ppa = 11 \pm 10$) interacted with almost 60% more plant species than bats ($Ppa = 7 \pm 4$). Differences were explained mainly by the disperser group; moreover, larger networks also had larger animal linkage level (GLM: $df = 18$, $F = 47.28$, $P < 0.001$; disperser: $F = 4.41$, $P = 0.05$; size: $F = 86.04$, $P < 0.001$, $B' = 2.92$). Bats ($Ppa' = 0.34 \pm 0.09$) interacted with a higher proportion of available plants than birds ($Ppa' = 0.22 \pm 0.06$); differences were explained exclusively by the disperser group (GLM: $df = 18$, $F = 7.17$, $P = 0.006$; disperser: $F = 4.58$, $P = 0.04$; size: $F = 2.79$, $P = 0.11$) (Fig. 2, Table 1).

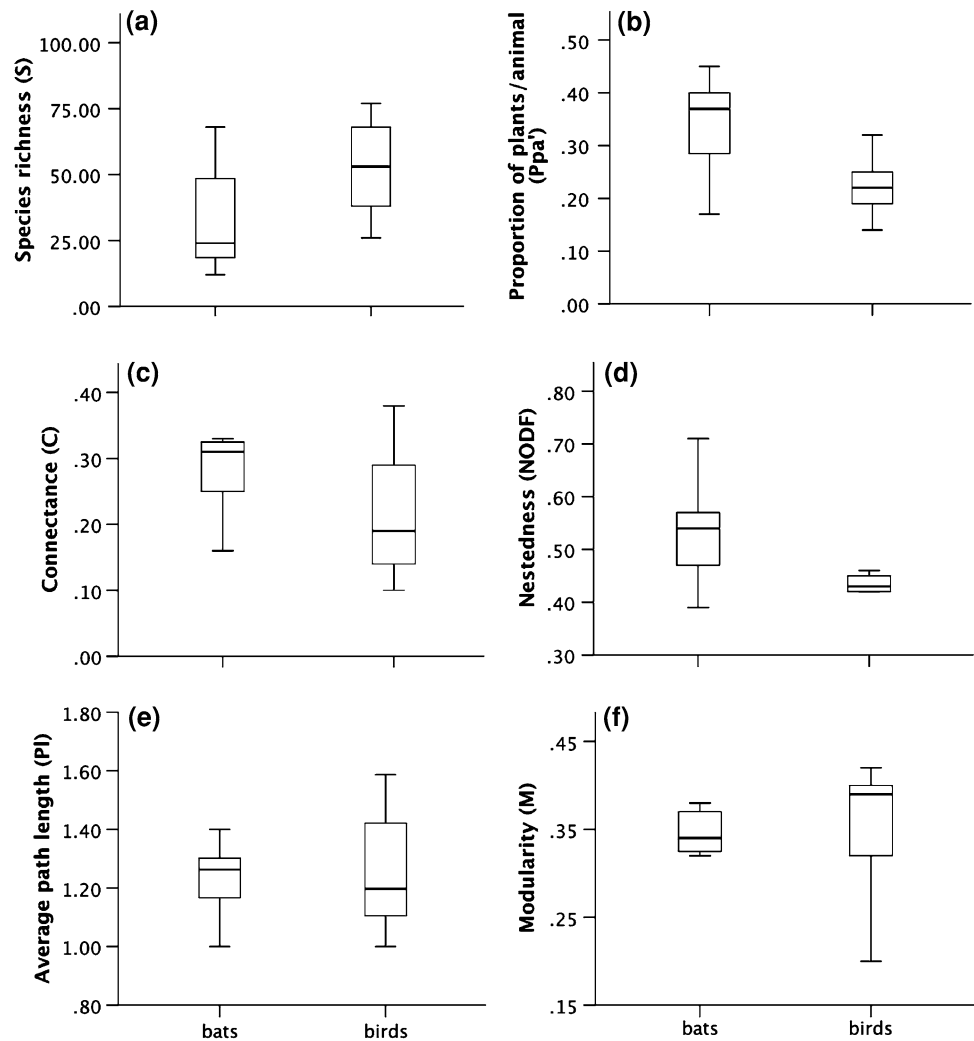
Bat–fruit networks ($NODF = 0.53 \pm 0.09$, all $P < 0.01$) were on average more nested than bird–fruit networks ($NODF = 0.42 \pm 0.07$, all $P < 0.02$), and differences were again explained mostly by the disperser group (GLM: $df = 18$, $F = 3.96$, $P = 0.03$; disperser: $F = 4.10$, $P = 0.05$; size: $F = 0.50$, $P = 0.49$) (Online Resource 2). Connectance was also higher in bat–fruit networks ($C = 0.30 \pm 0.11$) than in bird–fruit networks ($C = 0.22 \pm 0.09$), but in this case differences were explained mostly by network

size, as larger networks had lower connectance (GLM: $df = 18$, $F = 6.30$, $P = 0.009$; disperser: $F = 0.26$, $P = 0.62$; size: $F = 7.89$, $P = 0.01$, $B' = -0.31$).

Bat–fruit and bird–fruit networks did not differ in terms of H_2' (GLM: $df = 15$, $F = 0.62$, $P = 0.55$). Furthermore, there were no differences between bat–fruit ($PI = 1.24 \pm 0.11$, $M = 0.34 \pm 0.07$) and bird–fruit networks ($PI = 1.24 \pm 0.20$, $M = 0.35 \pm 0.07$) either in average path length (GLM: $df = 18$, $F = 0.35$, $P = 0.71$) or in modularity (GLM: $df = 18$, $F = 0.19$, $P = 0.83$) (Fig. 2, Table 1).

Robustness to extinction of animal species was lower in bat–fruit networks ($R_{\text{animals}} = 0.54 \pm 0.09$) than in bird–fruit networks ($R_{\text{animals}} = 0.60 \pm 0.13$). Differences were not explained by disperser group, but by the covariates: larger networks were slightly more robust, whereas more nested and more modular networks were less robust to removals (GLM: $df = 18$, $F = 7.67$, $P = 0.001$; disperser: $F = 0.93$, $P = 0.35$; size: $F = 5.76$, $P = 0.03$, $B' = 0.02$; nestedness: $F = 5.82$, $P = 0.03$, $B' = -0.74$; modularity: $F = 19.57$, $P < 0.001$, $B' = -1.57$). Bat–fruit networks ($R_{\text{plants}} = 0.68 \pm 0.09$) were also less robust to extinction of

Fig. 2 Characteristics of Neotropical bat–fruit and bird–fruit seed dispersal networks: **a** species-richness, **b** proportion of plants available, **c** connectance, **d** nestedness, **e** path length, and **f** modularity. The horizontal line represents the median, boxes represent quartiles, and whiskers depict 95% intervals



plant species than bird–fruit networks ($R_{\text{plants}} = 0.75 \pm 0.12$). In this case, differences were explained only by network size. Larger networks were slightly more robust than smaller networks (GLM: $df = 18$, $F = 6.42$, $P = 0.003$; disperser: $F = 0.06$, $P = 0.80$; size: $F = 18.23$, $P = 0.001$, $B' = 0.03$; nestedness: $F = 0.09$, $P = 0.76$; modularity: $F = 2.05$, $P = 0.17$) (Fig. 3, Table 1).

Discussion

In this paper, we show for the first time with a network approach that the distinct evolutionary trajectories of bats and birds lead, at the community level, to modularity in seed dispersal networks. This pattern has previously been observed in pollination networks (Olesen et al. 2007). Our results relate to general patterns in community ecology, in particular the separation of ecological communities into guilds or functional groups (Blondel 2003). Furthermore, they support the current notion that seed dispersal services

of bats and birds are largely separated, as first predicted by the theory of interaction syndromes (van der Pijl 1972) and observed in a few previous studies (Korine et al. 2000; Muscarella and Fleming 2007). In our study, we show how this separation is translated into patterns of interaction in seed dispersal networks and how it affects the system's structure and robustness. Interestingly, although there was large variation in sampling effort among the studies used in our database, results were relatively consistent among networks; therefore, we believe that our criteria for study selection (i.e., at least 1 year monthly sampling, identification to the species level, and inclusion of all species that ate fruits regardless of being specialists or not) are enough to allow a good representation of the systems analyzed. In summary, our results suggest that seed dispersal networks also represent, similar to pollination networks (see Olesen et al. 2006), 'small worlds'; i.e., networks in which vertices are very close to each other, because despite having subgroups of more densely vertices, those subgroups are connected to each other by some hubs (i.e., vertices with a

Table 1 Indexes for each network

Network ^a	Disperser	PI	NODF	C	H ₂ '	Ppa	Ppa'	M	S	P	A	R _{animals}	R _{plants}
Ayub 2008	Bats	1.35	0.48	0.16	0.37	10.27	0.31	0.44	45	33	12	0.52	0.67
Carvalho 2008	Bats	1.13	0.54	0.33	0.38	4.97	0.45	0.38	17	11	6	0.52	0.66
Faria 1996	Bats	1.25	0.56	0.32	0.36	6.24	0.39	0.33	24	16	8	0.58	0.69
Garcia et al. 2000	Bats	1.40	0.41	0.26	0.39	5.60	0.40	0.44	20	14	6	0.41	0.60
Gorchov et al. 1995	Bats	1.00	0.65	0.28	0.30	7.75	0.17	0.23	57	46	11	0.59	0.87
Hayashi 1996	Bats	1.29	0.51	0.32	0.53	3.18	0.26	0.32	19	12	7	0.51	0.63
Kalko BCI	Bats	1.26	0.39	0.18	N/a	14.63	0.31	0.36	68	47	21	0.67	0.75
Lopez and Vaughan 2007	Bats	1.32	0.46	0.24	0.34	8.26	0.22	0.36	52	37	15	0.65	0.77
Passos et al. 2003	Bats	1.20	0.55	0.33	0.44	9.17	0.40	0.34	29	23	6	0.51	0.72
Pedro 1992	Bats	1.29	0.58	0.31	0.54	4.02	0.37	0.33	18	11	7	0.41	0.55
Silveira 2006	Bats	1.13	0.71	0.58	0.18	2.65	0.44	0.20	12	6	6	0.61	0.59
Carlo et al. 2003 CACG	Birds	1.29	0.46	0.19	0.41	5.78	0.25	0.40	38	23	15	0.47	0.67
Carlo et al. 2003 CACI	Birds	1.42	0.43	0.14	0.46	7.11	0.22	0.39	53	33	20	0.47	0.63
Carlo et al. 2003 CACO	Birds	1.42	0.30	0.16	0.42	4.48	0.19	0.42	36	23	13	0.46	0.65
Galetti and Pizo 1996	Birds	1.59	0.34	0.14	N/a	9.12	0.25	0.39	68	36	32	0.69	0.70
Gorchov et al. 1995	Birds	1.00	0.45	0.29	0.26	14.56	0.32	0.35	53	46	7	0.50	0.89
Snow and Snow 1971	Birds	1.00	0.42	0.27	0.31	9.10	0.14	0.30	77	63	14	0.64	0.92
Snow and Snow 1988	Birds	1.13	0.53	0.38	0.30	9.32	0.27	0.20	55	35	20	0.83	0.78
Sorensen 1981	Birds	1.20	0.43	0.30	0.47	1.95	0.16	0.32	26	12	14	0.71	0.66
Wheelwright et al. 1982	Birds	1.11	0.42	0.10	N/a	34.51	0.21	0.40	207	167	40	0.66	0.89
Gorchov et al. 1995	Both	1.39	0.31	0.15	0.42	8.81	0.10	0.45	103	85	18	0.62	0.88

Average path length (*PI*), nestedness (*NODF*), connectance (*C*), complementary specialization (*H₂'*), number of plants/animal (*Ppa*), proportion of plants/animal (*Ppa'*), modularity (*M*), species richness (*S*), number of plant species (*P*), number of animal species (*A*), robustness to the extinction of animals (*R_{animals}*), and robustness to the extinction of plants (*R_{plants}*)

^a For details of networks, see Online Resource 1

very large number of links). We have evidence to propose that the mutualistic modules hypothesis (Jordano 1987), which proposed that phylogenetically related species form subgroups within those networks with similar patterns of interaction, is also valid for seed dispersal, since bats and birds belong to distinct modules in the mixed network, and since separate networks formed by bats and birds differ in structure and robustness. Those differences have important implications for the understanding of the overall structure of the system, as they corroborate the hypothesis that the ecosystem service of seed dispersal is a mosaic of sub-services performed by distinct groups of frugivores.

The observed complementarity of bat and bird seed dispersal, probably due to niche segregation, has already been suggested in previous studies but with other approaches (Muscarella and Fleming 2007). This hypothesis of separation between bats and birds is further corroborated by the strong modularity that we found in the mixed network. The presumed niche segregation may ultimately point to distinct differences in the phylogenetic history of frugivorous birds and bats, as frugivory evolved independently several times in birds and occurs in many families (Kissling et al. 2009), but evolved only once in Neotropical

bats and occurs in a single family (Datzmann et al. 2010). This possibly explains the less diversified diet of frugivorous bats compared with that of frugivorous birds. Interestingly, instead of feeding on a subset of the many fruits consumed by birds, bats apparently followed a separate evolutionary path in the use of fruit resources (Datzmann et al. 2010) and concentrated their diet on five phylogenetically distinct plant genera (Lobova et al. 2009). Although most of the diet of forest-dwelling frugivorous bats consists of pioneer species with small seeds (Muscarella and Fleming 2007), phyllostomid bats also feed on some climax trees and large-seeded plants (Lobova et al. 2009; Melo et al. 2009). Future studies at the community level should investigate the role of fruit characteristics in generating this modular structure, since differences in macronutrients (Wendeln et al. 2000), secondary metabolites (Cipollini and Levey 1997), visual clues (Cazetta et al. 2009), and olfactory clues (Kalko and Ayasse 2009) are considered as very important in fruit selection by bats, birds and other dispersers.

If a modular structure is common in bat–fruit and bird–fruit networks, it means that seed dispersal services are also rendered by subgroups specializing in different plant

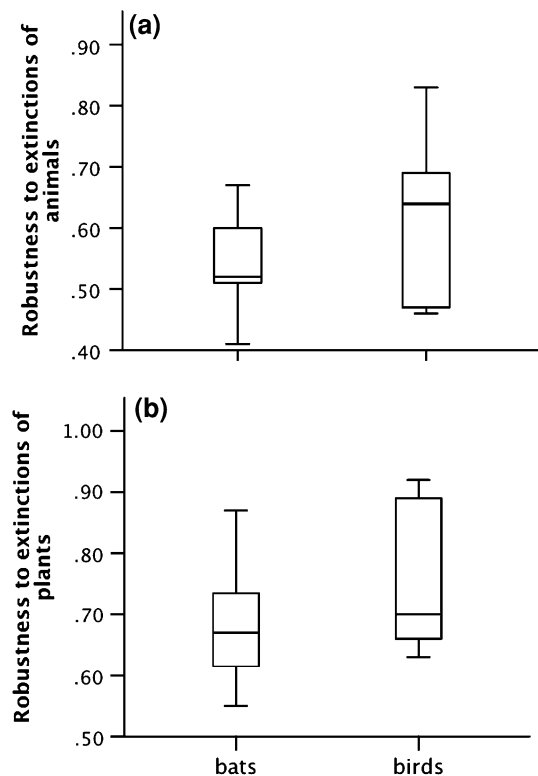


Fig. 3 Robustness of bird–fruit and bat–fruit networks to the extinction of **a** animal and **b** plant species. The horizontal line represents the median, boxes represent quartiles, and whiskers depict 95% intervals

subsets. However, those interactions appear more diffuse and less specialized than in pollination networks (Howe and Smallwood 1982). Furthermore, they also exhibit a lower level of complementary specialization (Blüthgen et al. 2007). Overall, if we also consider other groups of seed dispersers that feed on different plants than bats and birds, a modular structure is probably very common in seed dispersal networks. As a consequence, the ecosystem service of seed dispersal strongly depends on the variety of different animal taxa (birds, bats, primates, rodents, etc.) that form the modules. As modules do not fully replace each other following extinctions, conservation efforts need to be targeted at the maintenance of the diversity of dispersers.

The differences observed between bat–fruit and bird–fruit networks in structural properties support the hypothesis that those two disperser groups form different mutualistic modules. Some differences were mainly explained by the disperser group per se, whereas other differences were related mostly to network size. Firstly, although it is assumed that seed dispersal networks in general exhibit a low level of interaction specialization (Blüthgen et al. 2007; Jordano 1987), there are important differences between bats and birds within those networks because bats interact with fewer plants but with a higher proportion of the plants available. Hence, within their own networks, bats seem to be

more generalized than birds. However, when we look at results for the mixed network, we see that each bird species, on average, interacted with a higher proportion of available plants. As this result is based on only one example, caution is needed when interpreting the degree of specialization in seed dispersal networks. A larger sample size and more complete sampling of seed dispersal networks might reveal a higher degree of specialization in the interactions.

The higher nestedness and connectance of bat–fruit compared with bird–fruit networks (despite the lack of a difference in H_2') corroborate the initial hypothesis that bats are more generalized within their subnetworks than birds, and that the diets of specialists overlap more with the diets of generalists in bat–fruit networks. This is probably explained, at least in part, by the lower phylogenetic and ecological diversity of frugivorous bats in the Neotropics. Compared with that of the species-rich birds, the more specialized diet of frugivorous bat species probably initially evolved in closely related species (as can be inferred from the phylogeny by Datzmann et al. 2010), so that specialists feed on a subset of the plants consumed by generalists. Frugivorous birds, by contrast, evolved fruit-eating habits several times independently (Levey et al. 2002), most likely leading to higher dietary diversification. This could explain the higher nestedness in bat–fruit networks. There are some well-documented examples of more specialized bat species feeding on a subset of fruits consumed by more generalistic species, as observed in bats of the genus *Carollia*. The diet of the generalist *C. perspicillata* is very broad, including a wide range of fruits in addition to *Piper*. In contrast, the diet of the more specialized *C. castanea* comprises almost only fruits of *Piper* (Thies and Kalko 2004), and is nested within the diet of *C. perspicillata*.

Overall, bat–fruit and bird–fruit networks were rather similar in terms of path length and modularity, in spite of some structural differences. Since facultative mutualisms generate very cohesive systems with much higher connectivity than obligate mutualisms (Boucher et al. 1982), all networks of facultative mutualisms are probably ‘small worlds’. A small world structure has already been observed in many pollination networks (Olesen et al. 2006), including modules within those networks (Bezerra et al. 2009). Average path length was very close to 1, the shortest possible length in all networks analyzed, for both bats and birds. This means that impacts on one species are likely to quickly affect many other species directly and indirectly (Guimaraes et al. 2007). Furthermore, this high proximity of species within the seed dispersal networks makes them ‘tiny worlds’, i.e., even smaller worlds (Bezerra et al. 2009).

Bird–fruit networks were more robust to cumulative random extinctions than bat–fruit networks, not because of

any intrinsic characteristic of bird–fruit interactions but mainly because they were larger. It is important to remember that in our study extinctions are contextualized in the seed dispersal service, so they do not necessarily mean extinction of the respective dispersers as a species in the ecological community, as some of the studied species do not depend only on fruits for living and thus may switch diet. A positive effect of species richness on community stability has been known since the early works of Charles Elton, and has since been confirmed by a range of approaches and studies indicating that richer communities are better buffered against loss of species than species-poorer communities (Wilmers et al. 2002). In the case of food webs, more species make random losses more affordable without collapsing the whole system, since more species are likely to play peripheral and less important roles, and loss of those peripheral or redundant services may be lost with little consequences for the whole system. However, directed removal of central species (i.e., those that are more important for maintaining the structure of the system) has larger impacts in such systems than has been observed in predation food webs (Mills et al. 1993) and in mutualistic networks (Bezerra et al. 2009). This finding reinforces the need to aim at conserving the highest possible biodiversity in natural communities to ensure maintenance of ecosystem stability and function (Walker 1992); however, as in many cases some priorities have to be established, the network properties of each species may also be considered in conservation strategies. It is interesting to note that modularity also played a role in determining robustness to extinction, in particular for animals. As modular networks are bound together not only by hubs (i.e., species with a large number of interactions) but also by connectors (i.e., species that bind together different modules), their structure is more sensitive to random removal of vertices (i.e., species and their services). The negative effect of nestedness on robustness to extinction in animals was unexpected, as nestedness is assumed to enhance robustness (Bastolla et al. 2009). Based on our data, we suggest that conservation strategies should pay special attention to species that play the roles of hubs and connectors in natural communities, as they seem to be essential for the overall functioning and robustness of the systems.

In summary, our findings suggest that, despite being a less specialized interaction than pollination (Howe and Smallwood 1982), seed dispersal is also organized in subgroups of phylogenetically close species. Therefore, species within different modules may follow different coevolutionary pathways, leading to morphological differences among plants and morphological and physiological differences among frugivores.

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