

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

Marco Aurelio Ribeiro Mello · Flávia Maria Darcie Marquitti · Paulo R. Guimarães Jr. · Elisabeth Klara Viktoria Kalko · Pedro Jordano · Marcus Aloizio Martinez de Aguiar

Received: 9 August 2010 / Accepted: 22 March 2011  
© Springer-Verlag 2011

**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 =  $0.53 \pm 0.09$ ,  $C = 0.30 \pm 0.11$ ) were more nested and had a higher connectance than bird–fruit networks (NODF =  $0.42 \pm 0.07$ ,  $C = 0.22 \pm 0.09$ ). 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.

Communicated by Steven Johnson.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00442-011-1984-2) contains supplementary material, which is available to authorized users.

M. A. R. Mello (✉) · E. K. V. Kalko  
Institut für Experimentelle Ökologie, Universität Ulm,  
Biologie 3, Albert-Einstein-Allee 11, 89069 Ulm, Germany  
e-mail: marmello@gmail.com

F. M. D. Marquitti  
Programa de Pós-graduação em Ecologia, Universidade Estadual  
de Campinas, Cidade Universitária Zeferino Vaz s/n, Campinas,  
SP 13083-970, Brazil

P. R. Guimarães Jr.  
Departamento de Ecologia, Universidade de São Paulo,  
Rua do Matão, Trav. 14, n. 321, São Paulo, SP 05508-900, Brazil

P. R. Guimarães Jr. · P. Jordano  
Integrative Ecology Group, Estación Biológica de Doñana,  
CSIC, Apartado 1056, 41080 Sevilla, Spain

E. K. V. Kalko  
Smithsonian Tropical Research Institute,  
Balboa, Ancon, Republic of Panamá

M. A. M. de Aguiar  
Instituto de Física ‘Gleb Wataghin’, Universidade Estadual  
de Campinas, Campinas, SP 13083-970, Brazil

**Keywords** Complex networks · Ecosystem services · Food webs · Guilds · Mutualisms

## 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

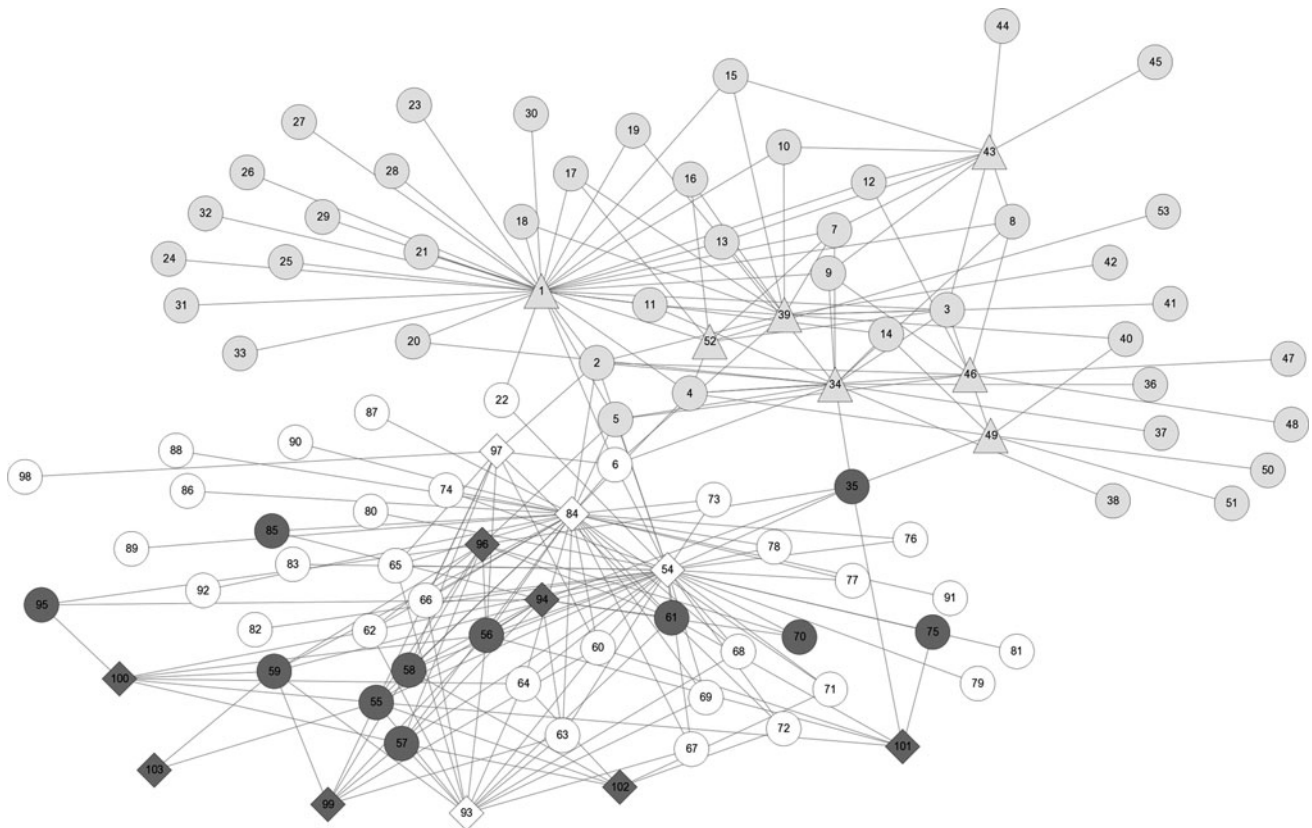
Differences between bat– and bird–fruit networks were tested with general linear models (GLM) in the package PASW Statistics for Mac 18.0. In each model, the network index (NODF,  $C$ , Ppa, Ppa', PI, or  $M$ ) was the dependent variable, the disperser group (bat–fruit or bird–fruit) was the fixed factor, 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<sub>bats</sub> = 0.65,  $P < 0.001$ ; NODF<sub>birds</sub> = 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).

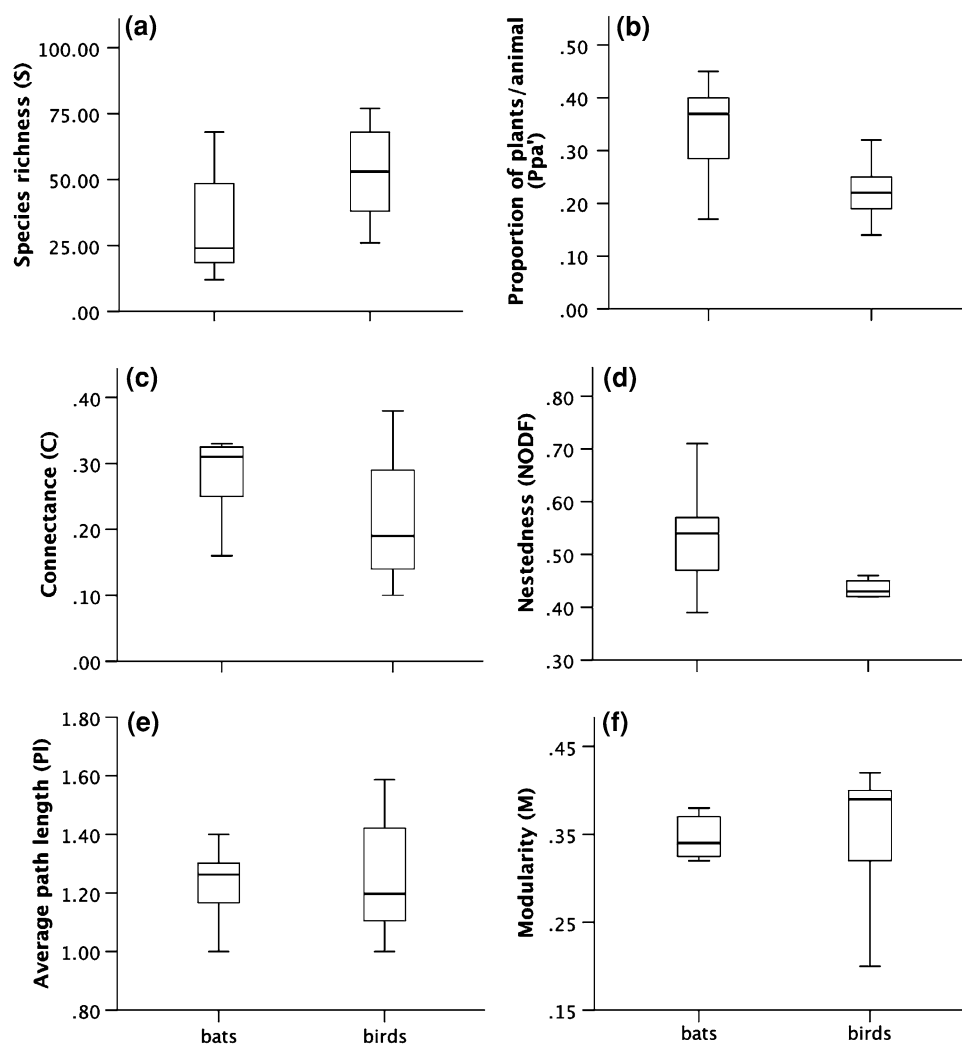
Bat–fruit networks ( $NODF = 0.53 \pm 0.09$ , all  $P < 0.01$ ) were on average more nested than bird–fruit networks ( $NODF = 0.42 \pm 0.07$ , all  $P < 0.02$ ), and differences were again explained mostly by the disperser group (GLM:  $df = 18$ ,  $F = 3.96$ ,  $P = 0.03$ ; disperser:  $F = 4.10$ ,  $P = 0.05$ ; 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 <sup>a</sup>	Disperser	PI	NODF	C	H <sub>2</sub> '	Ppa	Ppa'	M	S	P	A	R <sub>animals</sub>	R <sub>plants</sub>
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 (*H<sub>2</sub>'*), 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<sub>animals</sub>*), and robustness to the extinction of plants (*R<sub>plants</sub>*)

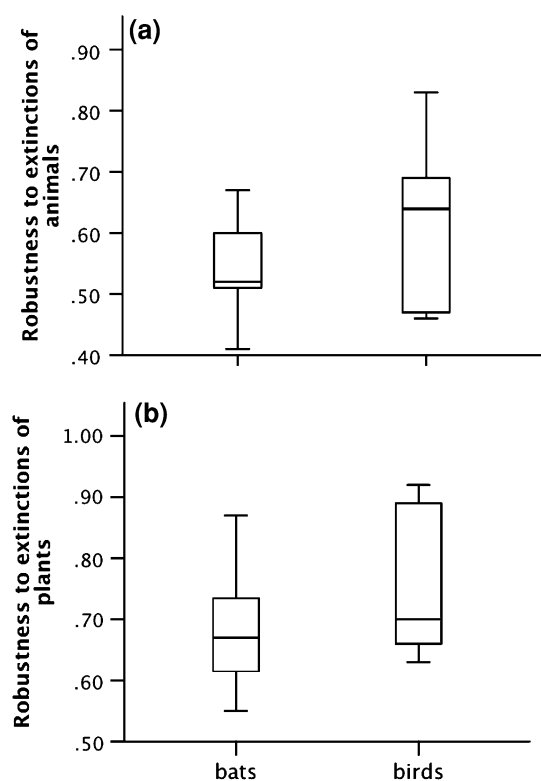
<sup>a</sup> For details of networks, see Online Resource 1

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.

**Acknowledgments** We are especially grateful to all people who made their data available in papers, monographs or databases. Carsten Dormann, Mário Almeida-Neto, Nico Blüthgen, Roger Guimerà and Vladimir Batagelj helped us use their network software. Theodore Fleming made invaluable suggestions on an early version of this manuscript. Diego Vazquez created the Interaction Web Database (<http://www.nceas.ucsb.edu/interactionweb/>), from which we took some datasets. Many colleagues, especially Wibke Thies, helped to complement the ‘Kalko BCI dataset’ after its first publication in 2004. Fundação de Amparo à Pesquisa do Estado de São Paulo (Brazil) funded this project by giving Grants to M.A.R.M. (2006/00265-0), F.M.D.M., M.A.M.A. and P.R.G. M.A.R.M. was also supported by the Alexander von Humboldt Foundation (Germany, 1134644). E.K.V.K. was supported by the Deutsche Forschungsgemeinschaft (Germany), and P.J. by the Consejo Superior de Investigaciones Científicas (Spain). Experiments comply with the current laws of Germany, Brazil and Spain.

## References

- Almeida-Neto M, Guimarães PR, Guimarães PR Jr, Loyola RD, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117:1227–1239
- Bascompte J (2009) Disentangling the web of life. *Science* 325:416–419
- Bascompte J, Jordano P (2007) Plant–animal mutualistic networks: the architecture of biodiversity. *Annu Rev Ecol Evol Syst* 38:567–593
- Bascompte J, Jordano P, Melian CJ, Olesen JM (2003) The nested assembly of plant–animal mutualistic networks. *Proc Natl Acad Sci USA* 100:9383–9387
- Bastolla U, Fortuna MA, Pascual-García A, Ferrera A, Luque B, Bascompte J (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458: U1018–U1091
- Batagelj V, Mrvar A (1998) Pajek—a program for large network analysis. *Connections* 21:47–57
- Bezerra ELS, Machado ICS, Mello MAR (2009) Pollination networks of oil-flowers: a tiny world within the smallest of all worlds. *J Anim Ecol* 78:1096–1101
- Blondel J (2003) Guilds or functional groups: does it matter? *Oikos* 100:223–231
- Blüthgen N, Menzel F, Blüthgen N (2006) Measuring specialization in species interaction networks. *BMC Ecology* 6:1–12
- Blüthgen N, Menzel F, Hovestadt T, Fiala B, Blüthgen N (2007) Specialization, constraints, and conflicting interests in mutualistic networks. *Curr Biol* 17:341–346
- Blüthgen N, Frund J, Vazquez DP, Menzel F (2008) What do interaction network metrics tell us about specialization and biological traits? *Ecology* 89:3387–3399
- Boucher DH, James S, Keeler KH (1982) The ecology of mutualism. *Annu Rev Ecol Syst* 13:315–347
- Burgos E, Ceva H, Perazzo RPJ, Devoto M, Medan D, Zimmermann M, Marìa Delbue A (2007) Why nestedness in mutualistic networks? *J Theor Biol* 249:307–313
- Cazetta E, Schaefer H, Galetti M (2009) Why are fruits colorful? The relative importance of achromatic and chromatic contrasts for detection by birds. *Evol Ecol* 23:233–244
- Cipollini ML, Levey DJ (1997) Why are some fruits toxic? Glykoalkaloids in *Solanum* and fruit choice by vertebrates. *Ecology* 78:782–798

- Datzmann T, von Helversen O, Mayer F (2010) Evolution of nectarivory in phyllostomid bats (phyllostomidae gray, 1825, chiroptera: mammalia). *BMC Evol Biol* 10:165
- Dormann CF, Gruber B, Fründ J (2008) Introducing the bipartite package: analyzing ecological networks. *R News* 8:8–11
- Dormann CF, Fründ J, Blüthgen N, Gruber B (2009) Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecol J* 2:7–24
- Fleming TH, Sosa VJ (1994) Effects of nectarivorous and frugivorous mammals on reproductive success of plants. *J Mammal* 75:845–851
- Fleming TH, Breitwisch R, Whitesides GH (1987) Patterns of tropical vertebrate frugivore diversity. *Annu Rev Ecol Syst* 18:91–109
- Fonseca CR, Ganade G (1996) Asymmetries, compartments and null interactions in an Amazonian ant–plant community. *J Anim Ecol* 66:339–347
- Fortuna MA, Stouffer DB, Olesen JM, Jordano P, Mouillot D, Krasnov BR, Poulin R, Bascompte J (2010) Nestedness versus modularity in ecological networks: two sides of the same coin? *J Anim Ecol* 79:811–817
- Galindo-González J, Guevara S, Sosa VJ (2000) Bat and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conserv Biol* 14:1693–1703
- Guimaraes PR, Rico-Gray V, Oliveira PS, Izzo TJ, dos Reis SF, Thompson JN (2007) Interaction intimacy affects structure and coevolutionary dynamics in mutualistic networks. *Curr Biol* 17:1797–1803
- Guimarães PR, Machado G, de Aguiar MAM, Jordano P, Bascompte J, Pinheiro A, dos Reis SF (2007) Build-up mechanisms determining the topology of mutualistic networks. *J Theor Biol* 249:181–189
- Guimerà R, Amaral LAN (2005) Cartography of complex networks: modules and universal roles. *J Stat Mech Theory Exp* P02001
- Howe HF, Smallwood J (1982) Ecology of seed dispersal. *Annu Rev Ecol Syst* 13:201–228
- Jordano P (1987) Patterns of mutualistic interactions in pollination and seed dispersal—connectance, dependence asymmetries, and coevolution. *Am Nat* 129:657–677
- Jordano P, Bascompte J, Olesen JM (2003) Invariant properties in coevolutionary networks of plant–animal interactions. *Ecol Lett* 6:69–81
- Jordano P, Vázquez D, Bascompte J (2009) Redes complejas de interacciones mutualistas planta–animal. In: Medel R, Aizen M, Zamora R (eds) *Ecología y evolución de interacciones planta–animal*. Editorial Universitaria, Santiago, pp 17–41
- Kalko EKV, Ayasse M (2009) Study and analysis of odor involved in behavioral ecology of bats. In: Kunz TH, Parsons S (eds) *Ecological and behavioral methods for the study of bats*, 2nd edn. The Johns Hopkins University Press, Baltimore, pp 491–499
- Kissling WD, Gaese KB, Jetz W (2009) The global distribution of frugivory in birds. *Glob Ecol Biogeogr* 18:150–162
- Korine C, Kalko EKV, Herre EA (2000) Fruit removal by bats and birds from a community of strangler figs in Panama. *Oecologia* 123:560–568
- Levey DJ, Silva WR, Galetti M (2002) Seed dispersal and frugivory : ecology, evolution, and conservation. CABI Publishing, New York
- Lobova TA, Geiselman CK, Mori SA (2009) Seed dispersal by bats in the Neotropics. New York Botanical Garden Press, New York
- Melo FPL, Rodriguez-Herrera B, Chazdon RL, Medellín RA, Ceballos GG (2009) Small tent-roosting bats promote dispersal of large-seeded plants in a Neotropical forest. *Biotropica* 41:737–743
- Mills LS, Soule ME, Doak DF (1993) The keystone-species concept in ecology and conservation. *Bioscience* 43:219–224
- Muscarella R, Fleming TH (2007) The role of frugivorous bats in tropical forest succession. *Biol Rev* 82:573–590
- Nogueira MR, Peracchi AL (2003) Fig-seed predation by 2 species of *Chiroderma*: discovery of a new feeding strategy in bats. *J Mammal* 84:225–233
- Nooy W, Mrvar A, Batagelj V (2005) Exploratory social network analysis with Pajek. Cambridge University Press, New York
- Olesen JM, Bascompte J, Dupont YL, Jordano P (2006) The smallest of all worlds: pollination networks. *J Theor Biol* 240:270–276
- Olesen JM, Bascompte J, Dupont YL, Jordano P (2007) The modularity of pollination networks. *Proc Natl Acad Sci USA* 104:19891–19896
- Oliver TH, Leather SR, Cook JM (2008) Macroevolutionary patterns in the origin of mutualisms involving ants. *J Evol Biol* 21:1597–1608
- Root RB (1967) The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol Monogr* 37:317–350
- Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, van Nes EH, Rietkerk M, Sugihara G (2009) Early-warning signals for critical transitions. *Nature* 461:53–59
- Terborgh J, Pitman N, Silman M, Schlichter H, Núñez VP (2002) Maintenance of tree diversity in tropical forests. In: Levey DJ, Silva WR, Galetti M (eds) *Seed dispersal and frugivory : ecology, evolution, and conservation*. CABI Publishing, New York, pp 1–17
- Thies W, Kalko EKV (2004) Phenology of Neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). *Oikos* 104:362–376
- van der Pijl L (1972) Principles of dispersal in higher plants. Springer, Berlin
- Walker BH (1992) Biodiversity and ecological redundancy. *Conserv Biol* 6:18–23
- Watts DJ, Strogatz SH (1998) Collective dynamics of small-world networks. *Nature* 393:440–442
- Wendeln MC, Runkle JR, Kalko EKV (2000) Nutritional values of 14 fig species and bat feeding preferences in Panama. *Biotropica* 32:489–501
- Wilmers CC, Sinha S, Brede M (2002) Examining the effects of species richness on community stability: an assembly model approach. *Oikos* 99:363–367
- Wright SJ (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130:1–14

## Appendix 1

### 1a. Datasets used

We used 17 Neotropical datasets in our analyses, which provided us with 11 bat-fruit networks, 9 bird-fruit networks and 1 mixed network with bats and birds. Some of these datasets were downloaded from the Interaction Web Database

(<http://www.nceas.ucsb.edu/interactionweb/>).

#### 1. Mixed: bats and birds together in the same network

1. Gorchov DL, Cornejo F, Ascorra CF, Jaramillo M (1995) Dietary overlap between frugivorous birds and bats in the Peruvian Amazon. *Oikos* 74:235-250.  
Obs: we used the complete network and also the bird- and bat-fruit subnetworks in our analysis

#### 2. Bats only

2. Ayub A (2008) Estrutura da rede de dispersão de sementes por morcegos. BSc Dissertation. Universidade Federal de Pernambuco, Departamento de Botânica. Recife
3. Carvalho MC (2008) Frugivoria por morcegos em floresta estacional semidecídua: dieta, riqueza de espécies e germinação de sementes após passagem pelo sistema digestivo. MSc Dissertation. Universidade Estadual Paulista, Departamento de Botânica. Botucatu

4. Faria DM (1996) Uso de recursos alimentares por morcegos filostomídeos fitófagos na Reserva de Santa Genebra, Campinas, São Paulo. MSc Dissertation. Universidade Estadual de Campinas Departamento de Zoologia. Campinas
5. Garcia QS, Rezende JL, Aguiar LMS (2000) Seed dispersal by bats in a disturbed area of southeastern Brazil. *Revista de Biologia Tropical* 48:125-128
6. Giannini NP, Kalko EKV (2004) Trophic structure in a large assemblage of phyllostomid bats in Panama. *Oikos* 105:209-220. This dataset was named 'Kalko BCI' in our study. The dataset was updated after its first publication in 2004 with new records made by colleagues in BCI, especially Wibke Thies.
7. Hayashi MM (1996) Morcegos frugívoros em duas áreas alteradas da fazenda Lageado, Botucatu, Estado de São Paulo. MSc Dissertation. Universidade Estadual Paulista, Instituto de Biociências. Botucatu
8. Lopez JE, Vaughan C (2007) Food niche overlap among neotropical frugivorous bats in Costa Rica. *Revista de Biologia Tropical* 55:301-313
9. Passos FC, Silva WR, Pedro WA, Bonin MR (2003) Frugivoria em morcegos (Mammalia, Chiroptera) no Parque Estadual Intervales, sudeste do Brasil. *Revista Brasileira de Zoologia* 20:511-517
10. Pedro WA (1992) Estrutura de uma taxocenose de morcegos da Reserva do Panga (Uberlândia, MG), com ênfase nas relações tróficas em Phyllostomidae (Mammalia: Chiroptera). MSc Dissertation. Universidade Estadual de Campinas, Departamento de Zoologia. Campinas
11. Silveira M (2006) Dispersão de sementes por morcegos frugívoros em uma área em processo de restauração vegetal na RPPN Parque Florestal São Marcelo

Mogi-Guaçu-SP. BSc Dissertation. Universidade Estadual de São Paulo,  
Instituto de Biociências. Rio Claro

### 3. Birds only

12. Carlo TA, Collazo JA, Groom MJ (2003) Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia* 134:119–131. Obs: this paper provided us with three bird-fruit networks used separately in our analyses.
13. Galetti M, Pizo MA (1996) Fruit eating birds in a forest fragment in southeastern Brazil. *Ararajuba* 4:71-79
14. Snow BK, Snow DW (1971) The feeding ecology of Tanagers and honeycreepers in Trinidad. *The Auk* 88:291-322
15. Snow BK, Snow DW (1988) *Birds and berries*. Academic Press, Calton
16. Sorensen AE (1981) Interactions between birds and fruit in a temperate woodland. *Oecologia* 50:242-249
17. Wheelwright NT, Haber WA, Murray KG, Guindon C (1984) Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* 16:173-192

### 1b. Species represented in Figure 1.

Number	Species	Group
1	Pipra_pipra	bird
2	Marcgravia_sp.301	plant
3	Miconia_duckei	plant
4	Souroubea_guianensis	plant
5	Havetiopsis_flavida	plant
6	Philodendrum_cuneatum	plant
7	Ossaea_cucullata	plant
8	Miconia_dolichorrhyncha	plant
9	Coussapoa_parvifolia	plant
10	Miconia_minutiflora	plant
11	Miconia_wittii	plant
12	Miconia_phanerostila	plant
13	Tococa_discolor	plant
14	Clidemia_hirta	plant
15	Henriettea_sp.	plant
16	Melastomataceae_2	plant
17	Rubiaeceae_1	plant
18	Miconia_ternatifolia	plant
19	Psychotria_alboviridula	plant
20	Ficus_americana	plant
21	Marcgraviaceae_1	plant
22	Phytolacca_rivinooides	plant
23	Clidemia_japurensis	plant
24	Ossaea_araneifera	plant
25	Miconia_poeppigii	plant
26	Miconia_tetragona	plant
27	Loreya_arborescens	plant
28	Palicourea_punicea	plant
29	Psychotria_sp.	plant
30	Anthurium_acaule	plant
31	Araceae_1	plant
32	Sorocea_sp.	plant
33	Iryanthera_grandis	plant
34	Tachyphonus_surinamus	bird
35	Coussapoa_villosa	plant
36	Melastomataceae_1	plant
37	Clusia_sp.	plant
38	Araceae_2	plant
39	Pipra_coronata	bird
40	Miconia_splendens	plant

41	Clidemia_epiphytica	plant
42	Psychotria_deflexa	plant
43	Machaeropterus_regulus	bird
44	Tococa_guianensis	plant
45	Dilleniaceae_1	plant
46	Tangara_schrankii	bird
47	Coussapoa_sp.	plant
48	Ficus_sp.	plant
49	Catharus_ustulatus	bird
50	Croton_schiedianus	plant
51	Codonanthe_sp.	plant
52	Manacus_manacus	bird
53	Alchornea_tripplinervia	plant
54	Carollia_perspicillata	bat
55	Cecropia_ficifolia	plant
56	Vismia_angusta	plant
57	Piper_aduncum	plant
58	Cecropia_distachya	plant
59	Ficus_sp.2	plant
60	Vismia_macrophylla	plant
61	Anthurium_sp.	plant
62	Piper_arboreum	plant
63	Cecropia_membranacea	plant
64	Solanum_lanceolatum	plant
65	Araceae_1	plant
66	Amaranthace	plant
67	Piper_sp.1	plant
68	Piper_sp.2	plant
69	Piperaceae_1	plant
70	Cecropia_sciadophylla	plant
71	Solanum_sp.	plant
72	Guttiferae_1	plant
73	Pothomorphe_peltata	plant
74	Piperaceae_2	plant
75	Ficus_sp.1	plant
76	Vismia_sp.1	plant
77	Philodendron_sp.	plant
78	Passifloraceae_1	plant
79	Vismia_sp.2	plant
80	Piper_sp.3	plant
81	Ficus_sp.42	plant
82	Passifloraceae_2	plant
83	Gesneriaceae_1	plant
84	Carollia_brevicauda	bat

85	Gurania_acuminata	plant
86	Solanum_jamaicens	plant
87	Physalis_sp.	plant
88	Thoracocarpus_bissectus	plant
89	Ficus_sp.9	plant
90	Cactacea_1	plant
91	Cucurbitaceae_1	plant
92	unidentified	plant
93	Carollia_castanea	bat
94	Phyllostomus_hastatus	bat
95	Ficus_sp.3	plant
96	Artibeus_jamaicensis	bat
97	Rhinophylla_pumilio	bat
98	Marcgravia_sp.	plant
99	Artibeus_lituratus	bat
100	Uroderma_bilobatum	bat
101	Artibeus_gnomus	bat
102	Sturnira_lilium	bat
103	Artibeus_obscurus	bat

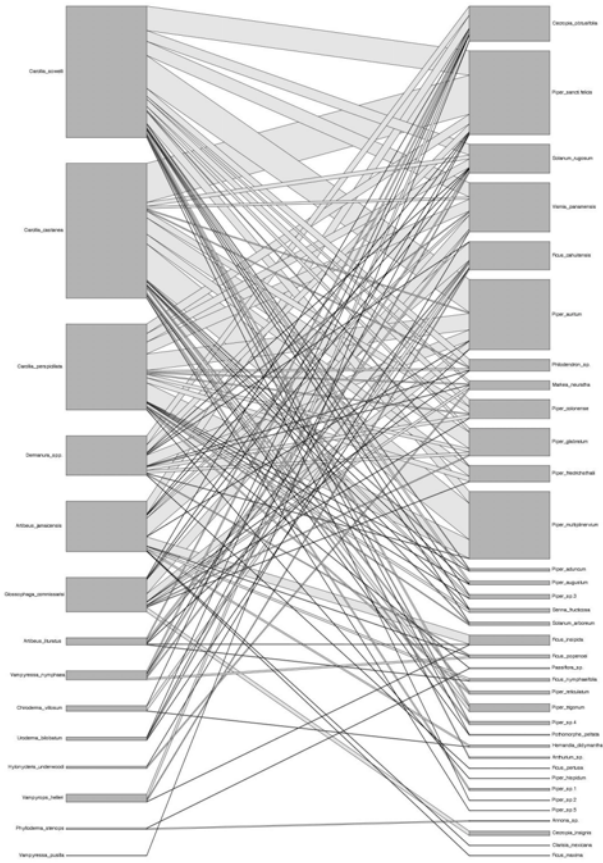




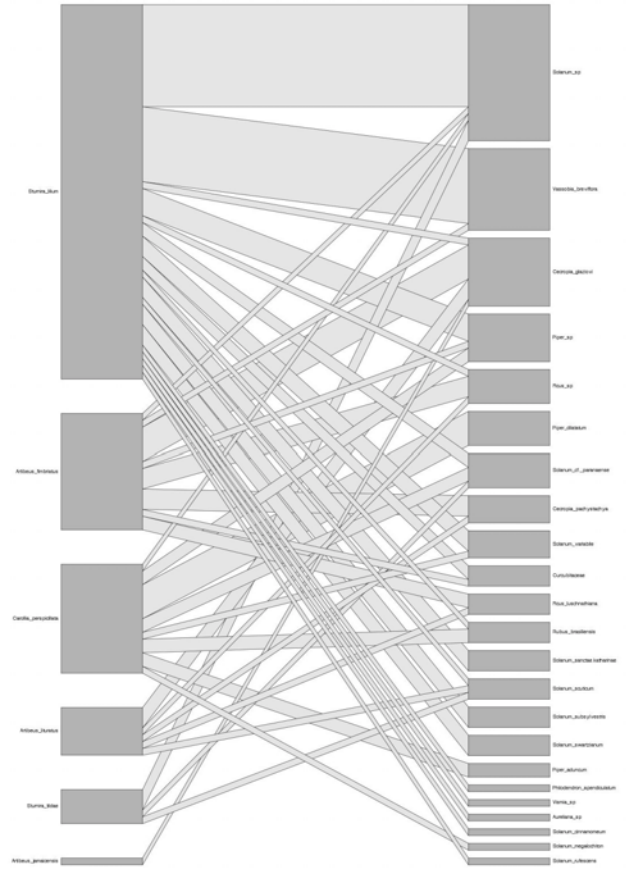




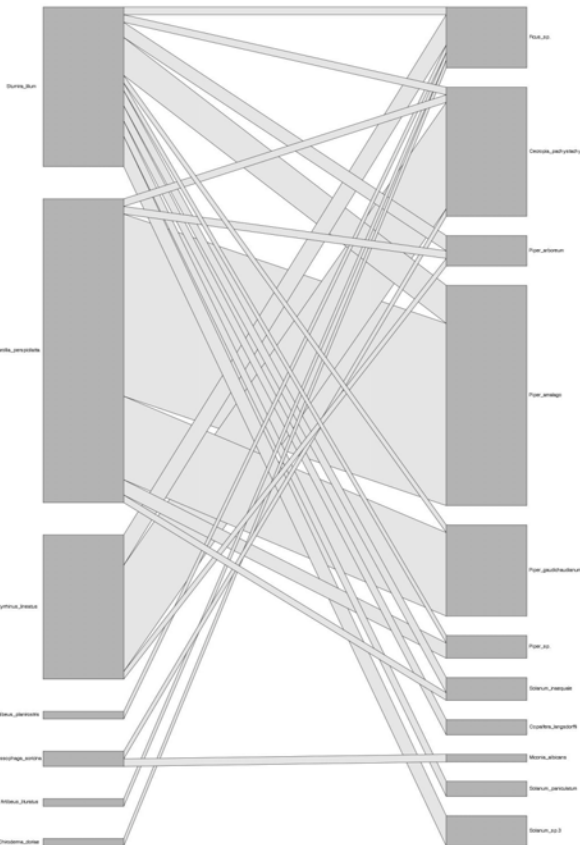
Lopez & Vaughan 2007



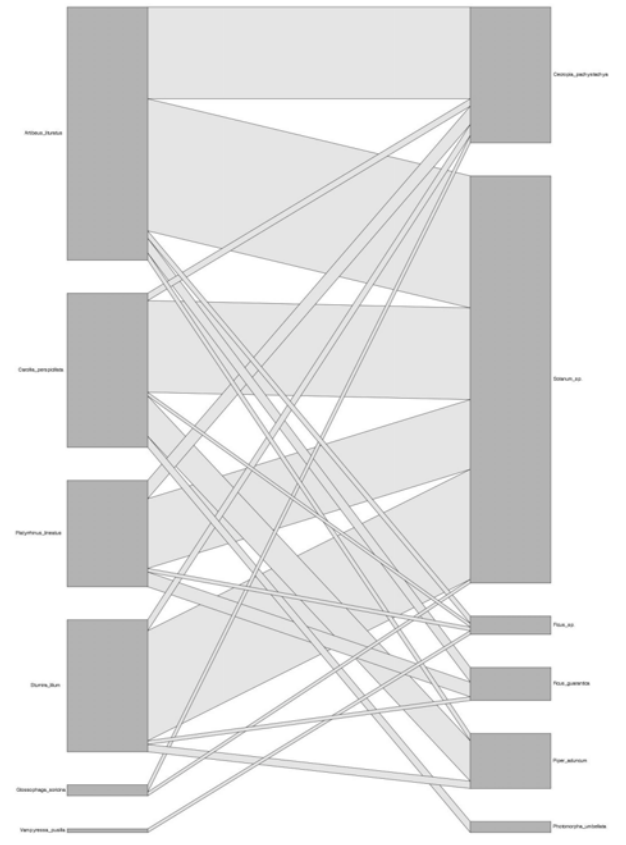
Passos et al. 2003



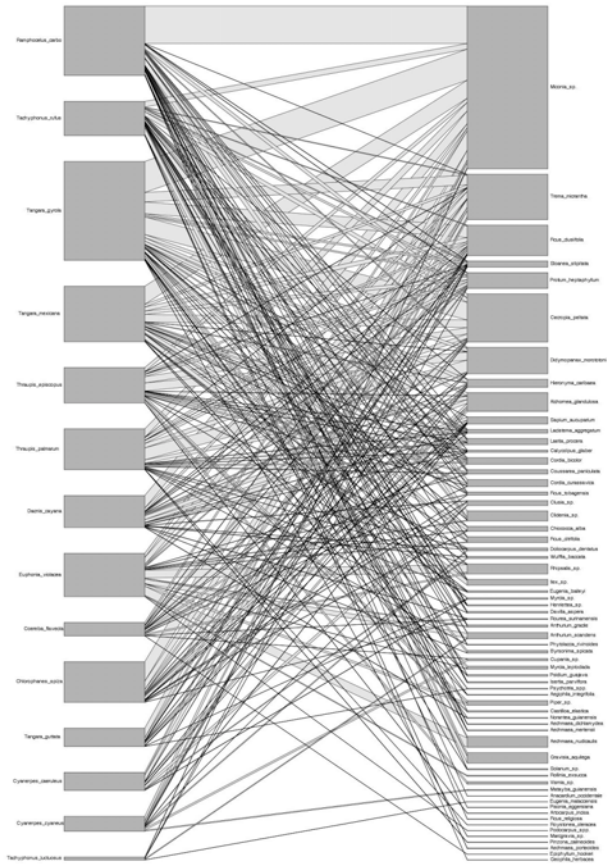
Pedro 1992



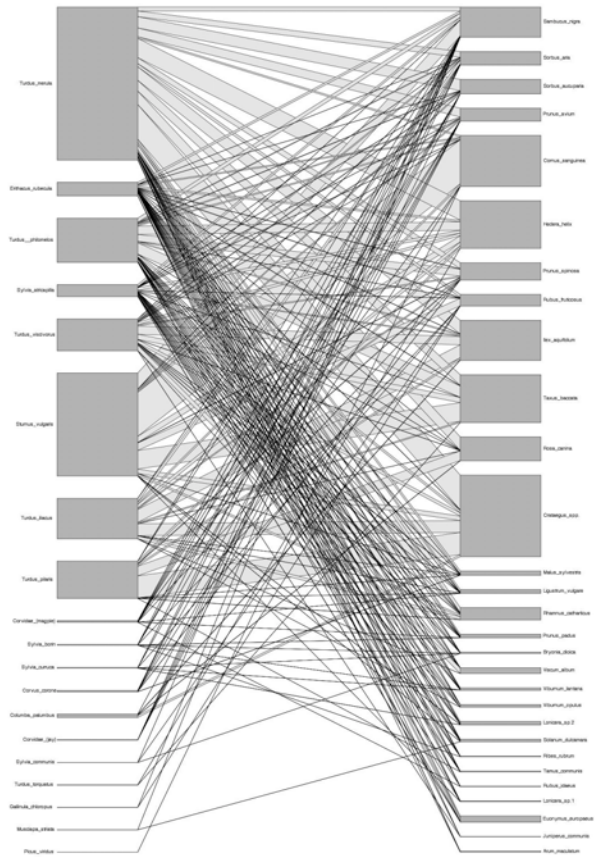
Silveira 2006



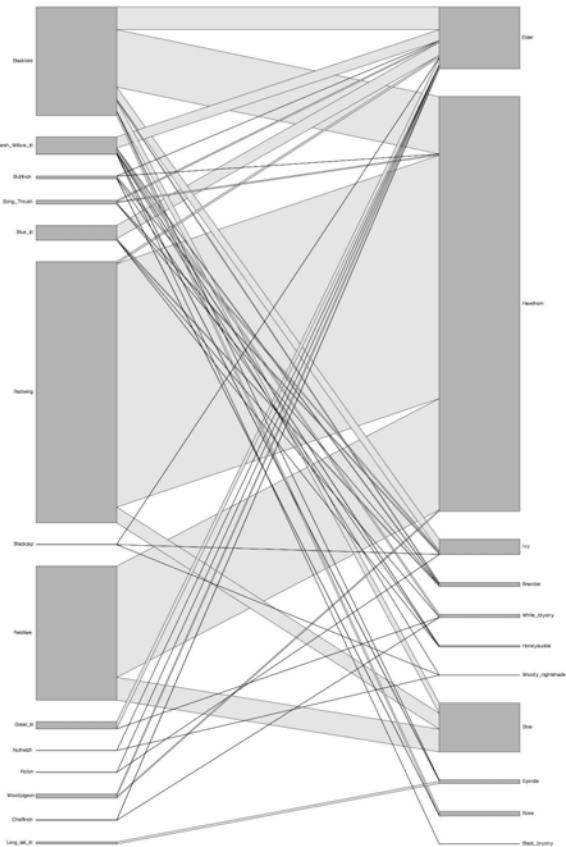
Snow & Snow 1971



Snow & Snow 1988



Sorensen 1981



Wheelwright et al. 1982

