

Keystone species in seed dispersal networks are mainly determined by dietary specialization

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A central issue in ecology is the definition and identification of keystone species, i.e. species that are relatively more important than others for maintaining community structure and ecosystem functioning. Network theory has been pointed out as a robust theoretical framework to enhance the operability of the keystone species concept. We used the concept of centrality as a proxy for a species' relative importance for the structure of seed dispersal networks composed of either frugivorous bats or birds and their food-plants. Centrality was expected to be determined mainly by dietary specialization, but also by body mass and geographic range size. Across 15 Neotropical datasets, only specialized frugivore species reached the highest values of centrality. Furthermore, the centrality of specialized frugivores varied widely within and among networks, whereas that of secondary and opportunistic frugivores was consistently low. A mixed-effects model showed that centrality was best explained by dietary specialization, but not by body mass or range size. Furthermore, the relationship between centrality and those three ecological correlates differed between bat- and bird-fruit networks. Our findings suggest that dietary specialization is key to understand what makes a frugivore species a keystone in seed dispersal networks, and that taxonomic identity also plays a significant role. Specialized frugivores may play a central role in network structuring and ecosystem functioning, which has important implications for conservation and restoration.

The relative importance of different species for the structure of a community has long been a central topic in ecology (Cottee-Jones and Whittaker 2012). Different concepts have been advanced, such as the original keystone species concept in rocky shore food webs (i.e. a species with disproportional importance in relation to its abundance, Paine 1966, 1969) and its versions created for several other terrestrial and aquatic systems (Mills et al. 1993). The keystone concept has been so extensively extrapolated that its original author (Paine 1995) and others have tried to refine and focus the concept, especially by looking for a better operational definition (Power et al. 1996). More recently, ecologists started to give attention to the keystone concept in a multispecies context, by studying the role of keystone species through mathematical simulations (Brose et al. 2005), or by extending the concept to whole communities and ecosystems

(Mouquet et al. 2013). However, most of these developments have focused on food webs, which are based on antagonistic interactions, whereas the role of keystones in mutualistic systems remains poorly studied. Here we focus on multispecies seed dispersal systems to determine which ecological and taxonomic factors lead a frugivore species to become a keystone element in the structure of a mutualistic network.

There are various ways in which a species can be important to its community, and quantifying this relative importance is challenging. In most cases, the importance of a given species has been inferred from its natural history, without experimental verification or mathematical quantification (Cottee-Jones and Whittaker 2012). Most importantly, species should not be considered in isolation, as they participate in complex networks of interspecific interactions (Bascompte and Jordano 2013). Mutualistic networks have their own set of emergent properties (such as nestedness, modularity and

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scale invariance, Bascompte 2009, 2010), but to understand how a species becomes a keystone in a web of mutualistic interactions we need to assess the species' importance in this complex context and through quantitative operational definitions. However, the task of quantifying a species' relative importance in a community is especially difficult when studying species-rich systems. A growing focus on multi-species systems with a well-defined taxonomic composition based on a particular kind of ecological interactions (i.e. ensembles, Fauth et al. 1996) is now leading to interesting insights into why species become keystones within complex ecological systems (Bascompte and Jordano 2013).

Recent theoretical analyses of complex networks have led to the use of centrality (i.e. the relative importance of an element to the structure of the whole system) as a proxy for the relative importance of species to community structuring (Lewinsohn and Cagnolo 2012). Centrality has also been used to assess a species' relative importance in the context of communities bound together by mutualistic interactions, also known as mutualistic networks (Dupont and Olesen 2009, Gonzalez et al. 2010, Mello et al. 2011b, 2013, Schleuning et al. 2014). A mutualist can be highly central to its network in two main ways: 1) by being a hub (i.e. a species with a disproportionally large number of interactions); or 2) by being a connector (i.e. a species that binds different modules of the network); some species can even be both. For instance, in pollination networks of oil flowers, the only hubs and connectors are always highly specialized oil bees of the genera *Centris* and *Epicharis*, which could be considered keystone mutualists (Mello et al. 2013). Thus, different sets of ecological traits may allow a species to play a central role in a mutualistic network. In the present study, we define a keystone mutualist as a frugivore species that is a potential seed disperser (i.e. it does not kill the seeds and carries some of them away from the mother plant, Fleming and Sosa 1994) and is also a hub, a connector, or both in its network.

The biological interpretation of different centrality metrics for animal or plant mutualists remains unclear, as well as the relationship between those metrics (but see some recent developments in Dupont and Olesen 2009, Gonzalez et al. 2010, Mello et al. 2011b, 2013, Santos et al. 2012, Schleuning et al. 2014). In food webs, it appears that the ecological role of important species is somewhat phylogenetically conserved (Estes et al. 2011). A recent study on seed dispersal networks of birds and their food-plants, which used metrics calculated from interaction frequencies, suggested that phylogeny had little influence on centrality metrics (Schleuning et al. 2014).

We analyzed 15 Neotropical seed dispersal networks with either bats or birds as dispersers, to understand the ecological traits leading a species to become central in a mutualistic network. From a network perspective, a central disperser would also play a keystone species role in the mutualistic community, which is a part of the whole ecological community. We expected specialized frugivores (i.e. bats and birds that depend on fruits for living) to occupy the network's most central position, as they need to feed on a broader variety of fruit species on a regular basis (Muscarella and Fleming 2007). We also expected large-bodied frugivores to be more central than small-bodied frugivores (Woodward et al. 2005) and frugivores with broader geographic ranges

(Ollerton and Cranmer 2002) to be more central than narrowly distributed frugivores, as in both cases those species are expected to feed on a larger number of fruit species. Finally, we expected the relationship between centrality metrics, dietary specialization, body mass, and geographic range to differ between bat- and bird-fruit networks, as frugivorous bats have much higher phylogenetic relatedness than frugivorous birds (Mello et al. 2011b). Therefore, there should be larger variation in centrality metrics and their relationship with ecological attributes among birds than among bats.

Methods

Datasets

We analyzed 15 seed dispersal datasets from the Neotropics: seven formed by birds and eight by bats. Most datasets came from published studies and some came from the Interaction Web Database (www.nceas.ucsb.edu/interactionweb/), Supplementary material Appendix 1). Only data from sampling periods of at least one year were included, in order to comprise seasonal variations in diet. Interactions between plants and frugivores were recorded through fecal analysis, roost inspection or direct observation. For simplicity, we considered all frugivorous bats and birds as seed dispersers, even if a few of them may actually be seed predators (for instance, *Chiroderma* bats; Nogueira and Peracchi 2003). In any case, only a few potential seed predators are present in each of the analyzed communities, they also disperse some seeds (Jordano et al. 2009), and they were not yet found to occupy central positions in frugivory and seed dispersal networks (Mello et al. 2011b). Datasets were organized as adjacency matrices, in which bat or bird species are represented in the rows and plant species in the columns (vertices), and records of fruit consumption are computed in the cells (edges).

We decided to use only binary data in our analysis, i.e. simple qualitative links between species, because binary matrices allow pooling data obtained with different methods, such as fecal analysis, observation, and inspection of roosts, while weighted data become very hard to interpret when different sampling methods are mixed. Furthermore, most studies on mutualistic networks so far are based on binary data, which makes comparisons easier. All networks were represented as bipartite graphs, using the package bipartite 2.03 for R (Dormann et al. 2008) and Pajek 3.15 (Batagelj and Mrvar 1998). Although the original datasets were binary, as explained, for most centrality analyses we transformed the bipartite networks into niche overlap networks, as explained in detail in the next sections.

Centrality metrics

Centrality is defined as the relative position of a vertex (here a species) within a network: how many links it has and how these links are distributed among different parts of the network (Nooy et al. 2005). As different metrics of centrality provide information on distinct aspects of a species' interaction pattern, we calculated three widely used metrics

(relative degree, closeness centrality, and betweenness centrality – all in their binary versions) and one novel metric (accessibility, with two variants: accessibility to direct and indirect neighbors – both in their weighted versions), which we explain here in detail.

The first metric of centrality is the simplest: ‘relative degree’ (k_r), i.e. the number of interactions made by a species (i.e. its degree, k) in relation to the total number of interactions it could make in the network (Nooy et al. 2005). This metric was calculated from the original bipartite networks with two sets of species (animals and plants). Albeit simple, relative degree is an informative metric. For instance, for plant-pollinator networks it has been suggested that species that make more interactions are more important for maintaining the whole system (Bezerra et al. 2009, Memmott et al. 2004). Because the sizes of networks vary, relative degree (k_r) is better than degree (k) for comparing species of different networks.

Although relative degree is informative in a multi-species context, it is important to assess not only the number of interactions, but also how these interactions are distributed among different parts of the network, as even a species with few interactions may be important for being a connector. We used two other metrics of centrality (Nooy et al. 2005), calculated in Pajek 3.15, which have proved to be useful for studying mutualistic plant–pollinator networks, as they provide this additional information of the importance of least-connected species (Gonzalez et al. 2010): closeness centrality and betweenness centrality. Those two other metrics were calculated from a niche overlap network, in order to assess how frugivore species share the seed dispersal service among themselves. This unipartite projection is indeed a niche overlap network: two frugivore species are connected to each other, when they feed on at least one common plant species. Although we built weighted unipartite projections of each original bipartite network, in which the strength of each link is based on how many plant species are shared between the two frugivores that it connects, for calculating closeness centrality and betweenness centrality we considered only the binary versions.

This way, the second metric calculated was ‘closeness centrality’ (CC), which measures the proximity of a species to other species in the same network. Proximity is measured as the length of a small path: the smallest number of links that separate two species in the network. The closeness centrality of a frugivore species is calculated as the number of other frugivore species in the niche overlap network divided by the sum of the lengths of all small paths between that species and all others. In ecological terms, a frugivore species has high closeness centrality, when it feeds on plant species that are also consumed by many other frugivores in the same network, and it has low closeness centrality, when its diet is more unique.

The third metric used was ‘betweenness centrality’ (BC), i.e. the importance of a vertex as a connector between the different parts of the network. A vertex with a high value of betweenness centrality is assumed to be an important element that keeps different parts of the network together. We calculated the betweenness centrality of a species as the proportion of all geodesics (i.e. shortest possible paths, measured as number of links) between pairs of other species

that include that species. Ecologically, a connector species bridges two or more different guilds within the mutualistic community.

To assess other aspects of a species’ relative importance in comparison to previous studies on mutualistic networks, we calculated a novel index in the context of ecological networks, which is known as ‘accessibility’ (A) (Travençolo and Costa 2008, Viana et al. 2012). Accessibility has been mainly used to investigate street networks in cities; it is defined as the potential that a vertex has in accessing or being accessed by other vertices of the same network. Accessibility can be measured to direct (A1) and indirect neighbors (A2). A direct neighbor in the niche overlap network is a species that is directly connected to the target species; an indirect neighbor is indirectly connected to the target species through connections with its neighbors. In a mutualistic network, it measures a species’ accessibility to species that actually share some food-plants with it (direct neighbors), and to species that share food-plants not directly with it, but with its neighbors (indirect neighbors). Details on the calculation of accessibility are provided in Supplementary material Appendix 2. Accessibility assesses how many connections of niche overlap a frugivore makes in the niche overlap network, and how unique those overlaps are. A frugivore with intermediate to high accessibility either disperses the seeds of several plant species or focuses on the plants that are dispersed by most other frugivores; a frugivore with a very high accessibility probably combines both characteristics. A frugivore that feeds on a few plant species may reach an intermediate accessibility, if those plants are visited by many other frugivores. A frugivore with low accessibility feeds on a few plants, which are visited only by one or a few frugivores. Furthermore, accessibility allows assessing these properties at different levels (direct and indirect neighbors). This is useful because the influence (e.g. through competition for food or sharing ecological services) of a species on other species of the same network may be far-reaching or not.

Ecological traits

In order to understand what makes some frugivores more important than others to the structure of the whole network, we tested for a relationship between the five centrality metrics and three core ecological traits of species: dietary specialization (hereafter ‘level of frugivory’), body mass, and geographic range size.

We classified bat and bird species according to their level of frugivory as specialized, secondary, or opportunistic frugivores. The diets of all bird species in our database were compiled from a comprehensive literature survey (Şekercioğlu et al. 2004). We used an updated version (31 January 2009) of this database (Kissling et al. 2012), and defined specialization as how strongly a species depends on fruits relative to other possible food items (e.g. seeds, leaves, nectar, pollen, insects and vertebrates, Kissling et al. 2009, 2012). This concept allows quantifying dietary specialization across a large number of species and taxa (Kissling et al. 2009). It is derived independently of network metrics as it does not take into account 1) the number of fruit species consumed by a frugivore in the network (Bascompte et al. 2006), 2) the difference between a species’ interaction

pattern and that of other species in the same network (Blüthgen et al. 2006), or 3) a species' preference for particular fruit taxa (Heithaus 1982). For bats, we followed the general consensus that phyllostomids of the subfamilies Carollinae and Stenodermatinae depend strongly on fruits (specialized or 'obligate' frugivores), whereas most members of the Glossophaginae and Lonchophyllinae have fruits as a secondary food (secondary frugivores), and members of the Phyllostominae feed on fruits only occasionally (opportunistic frugivores) (Fleming and Kress 2013, Heithaus 1982, Lobo et al. 2009) (see Supplementary material Appendix 3 for species-specific information). For the Glossophaginae and Lonchophyllinae, we refined our classification using a literature database on bat–plant interactions (updated from Lobo et al. 2009), which provided us with information on the number of records of frugivory and nectarivory for each species, therefore assigning species either as secondary or opportunistic frugivores. As specialized frugivory in bats evolved only in two subfamilies of the Phyllostomidae (Datzmann et al. 2010, Dumont et al. 2012, Rojas et al. 2012), and the other subfamilies have only either secondary or opportunistic frugivores, there is a strong phylogenetic signal in frugivory among Neotropical bats (Fleming and Kress 2013). For birds, the level of frugivory was initially scored for each bird species, ranging from 0 (never eats fruits) to 10 (totally dependent of fruits) (Kissling et al. 2012). The bird fruit classification was then adjusted to match the bats' classification by simplifying the diet ranks (species classified from 7 to 10 were categorized as 'specialized', species from 4 to 6 as 'secondary', and species from 1 to 3 as 'opportunistic').

Body mass can be an important driver of plant–animal interactions (Fleming 1991, Jordano 1995) and also of mutualistic network structure (Vázquez et al. 2009, Woodward et al. 2005). We obtained data on average body mass (in g) for each species from the literature, representing average values of adults across sexes (Nowak 1994, Dunning 2008, Gardner 2008). We considered the average body mass for each bird or bat species and used the same value for all networks, as local data on body mass were not available in all studies included in our dataset.

Frugivore species that have broader geographic ranges are subjected to a variety of environmental conditions, including for instance different availability of plants species. Therefore, they are likely able to feed on a larger number of fruit species, which could lead to higher centrality. So we tested whether the geographic range size of a species, a basic ecological characteristic (Brown et al. 1996), explains its centrality scores. Range size data were obtained by georeferencing digitized distribution maps of bats (IUCN's Red List of Threatened Species, ver. 2009.1: <www.iucnredlist.org>) and birds (Ridgely et al. 2011). Using ArcGIS 10, we projected the original distribution maps to a Behrmann projection and then calculated the area (in km²) for each distribution polygon. This way of quantifying geographic range size represents the extent of occurrence of a species (Gaston and Fuller 2009).

Statistical analyses

First, we quantified variations in the centrality metrics (k_p , CC, BC, A1 and A2) and ecological traits (level of frugivory,

body mass and range size) across all species and networks (median, minimum and maximum values). We further calculated correlations between centrality metrics, using Spearman correlations with bootstrapping (10 000 randomizations stratified for disperser group, i.e. bats or birds).

In order to test whether the three chosen ecological traits explain variations in the five calculated centrality metrics, we used a multivariate general linear mixed effects model with bootstrapping (10 000 randomizations). In our model, the five centrality metrics were considered as response variables, disperser group (i.e. bats or birds) and level of specialization in frugivory were considered as fixed factors, and body mass and range size were considered as covariates. In other words, we assumed that disperser group and level of frugivory determine the centrality of a species in a seed dispersal network, that body mass and range size may affect this relationship, and that this relationship varies depending on whether the network is formed by bats or birds.

All statistical analyses followed Zar (1996) and Manly (2007), and were performed in SPSS Statistics for Mac 20.0. We decided to base our mixed model on bootstrapping because we worked with different kinds of data, which are not always normally distributed, but follow different statistical distributions. Thus, we chose bootstrapping over making several different kinds of data transformation or building separate generalized linear mixed models for each centrality metric. Significance was estimated by comparing the calculated value of each statistics to the distribution of randomized values generated from the same dataset (10 000 iterations).

Results

The 15 Neotropical seed dispersal networks were composed on average of 63 ± 74 plant and animal species (mean $\pm$ SD) (Supplementary material Appendix 4). Overall, 32 bat species, 125 bird species and 443 plant species were analyzed. In the following, we do not mention plants because we transformed all networks into niche overlap networks of animals for all subsequent analyses except for relative degree. Relative degree varied from 0.02 to 1.00 (median = 0.16), which shows that the number of interactions of each species varies greatly within and among local networks. The pattern of interactions of each species in each local network also differed greatly among species of the same and different networks, as closeness centrality varied from 0.00 to 1.00 (median = 0.85), betweenness centrality varied from 0.00 to 0.17 (median = 0.00), accessibility to direct neighbors varied from 0.03 to 0.96 (median = 0.67), and accessibility to indirect neighbors varied from 0.05 to 0.97 (median = 0.83). Specialized frugivores were most frequent in the studied seed dispersal networks (bats = 25 spp., birds = 38 spp.), although many secondary and opportunistic frugivores were also observed. The studied frugivores ranged from small to large animals, as body mass of bats varied from 8 to 88 g (median = 18 g) and of birds from 6 to 1135 g (median = 34 g). There were also large differences among species in the distributional areas they occupy, as geographic range size of bats varied from 5 to 15 288 792 km² (median = 8 337 978 km²) and of birds from 7 to 24 811 474 km² (median = 1 426 637 km²) (Supplementary material Appendix 3).

Fourteen bat species and twenty-seven bird species occurred in two or more networks; five bat species and one bird species occurred in half or more of the sites. Most species that occurred in two or more networks had different values of centrality in different sites, varying from central to peripheral (Fig. 1). On the other hand, in most cases the highest values of centrality were reached by specialized frugivores in bat-fruit networks, and by specialized and secondary frugivores in bird-fruit networks (Supplementary material Appendix 5, Fig. 2).

Relative degree was significantly correlated with all other centrality metrics, although the strength of correlation differed among metrics (CC: $\rho = 0.58$, $p < 0.001$; BC: $\rho = 0.29$, $p < 0.001$; A1: $\rho = 0.63$, $p < 0.001$; A2: $\rho = 0.53$, $p < 0.001$) (Table 1). Similarly, there were also correlations between closeness centrality and accessibility to direct neighbors (CC $\times$ A1: $\rho = 0.87$, $p < 0.001$), closeness centrality and accessibility to indirect neighbors (CC $\times$ A2: $\rho = 0.53$, $p < 0.001$), and betweenness centrality and accessibility to indirect neighbors (BC $\times$ A2: $\rho = 0.29$, $p < 0.001$).

The multivariate general linear mixed effects models ($n = 153$ species) had high statistical power for most response variables (power of the corrected model > 0.659 for all response variables) (Supplementary material Appendix 5). The level of specialization in frugivory was the most important ecological trait, as it explained the variations in closeness centrality (effect size, measured as the partial $\eta^2 = 0.06$, $F = 4.28$, $p = 0.02$) and accessibility to indirect

neighbors (partial $\eta^2 = 0.06$, $F = 4.22$, $p = 0.02$) (Fig. 3). There were differences between bats and birds in the relationship between ecological traits and centrality metrics, as the variable 'disperser group' had a significant effect on closeness centrality (partial $\eta^2 = 0.08$, $F = 11.78$, $p = 0.001$), accessibility to direct neighbors (partial $\eta^2 = 0.03$, $F = 5.04$, $p = 0.03$), and accessibility to indirect neighbors (partial $\eta^2 = 0.06$, $F = 9.81$, $p = 0.002$). Variations in the centrality metrics tested were in most cases not explained by the other two ecological traits: body mass and range size (all $p > 0.05$, Supplementary material Appendix 6). However, range size explained part of the variation in relative degree (partial $\eta^2 = 0.03$, $F = 3.77$, $p = 0.05$). There was also a significant interaction between level of specialization in frugivory and disperser group for closeness centrality (partial $\eta^2 = 0.07$, $F = 5.13$, $p = 0.007$) and accessibility to indirect neighbors (partial $\eta^2 = 0.05$, $F = 3.93$, $p = 0.02$). In other words, centrality depends on how strongly frugivorous a species is and by its taxonomic identity.

Discussion

In the present study, we observed that the centrality of frugivorous bats and birds varied widely within and among a large set of Neotropical seed dispersal networks. Most importantly, our results suggest that dietary specialization was more important than body mass and geographic range

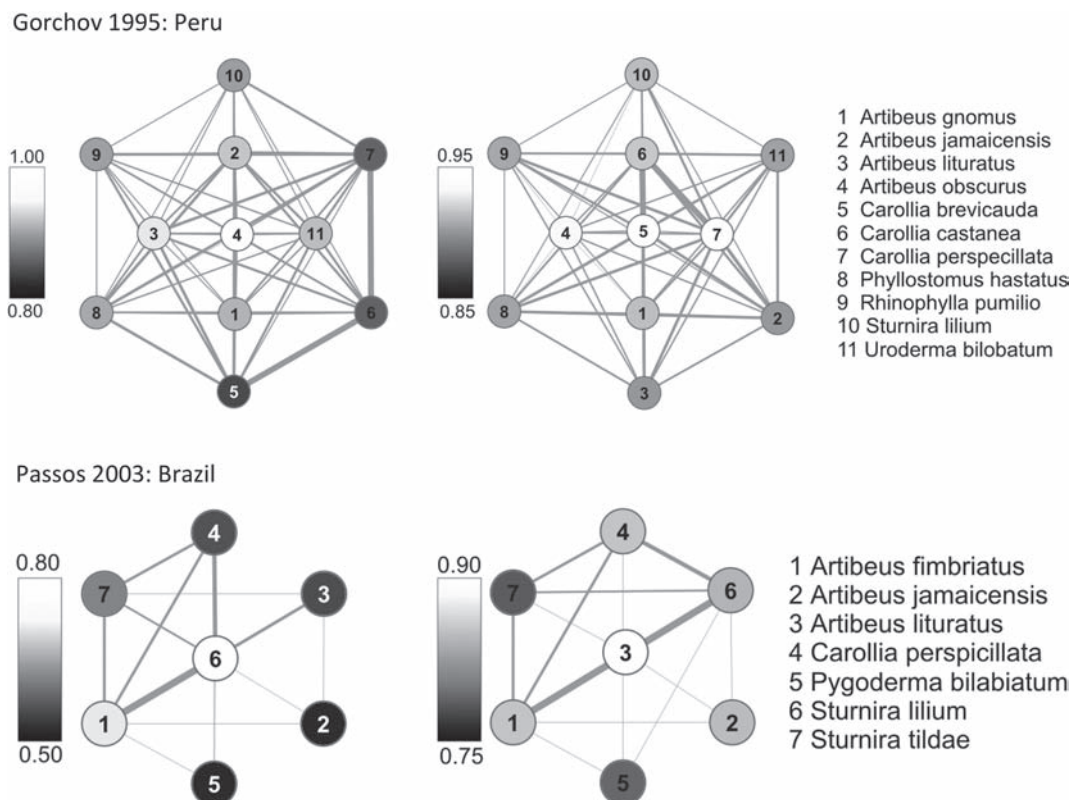


Figure 1. The centrality of frugivore species varied among local seed dispersal networks. The networks presented here are unipartite projections of the original bipartite networks (niche overlap networks); vertices represent frugivore species; two species are connected to each other if they feed on at least one common plant species (the weight of the links are proportional to the number of plant species being shared). Shades of grey represent values of accessibility to direct (left-hand side, directly connected to the target species) and indirect neighbors (right-hand side, connected indirectly through another species) for each frugivore species.

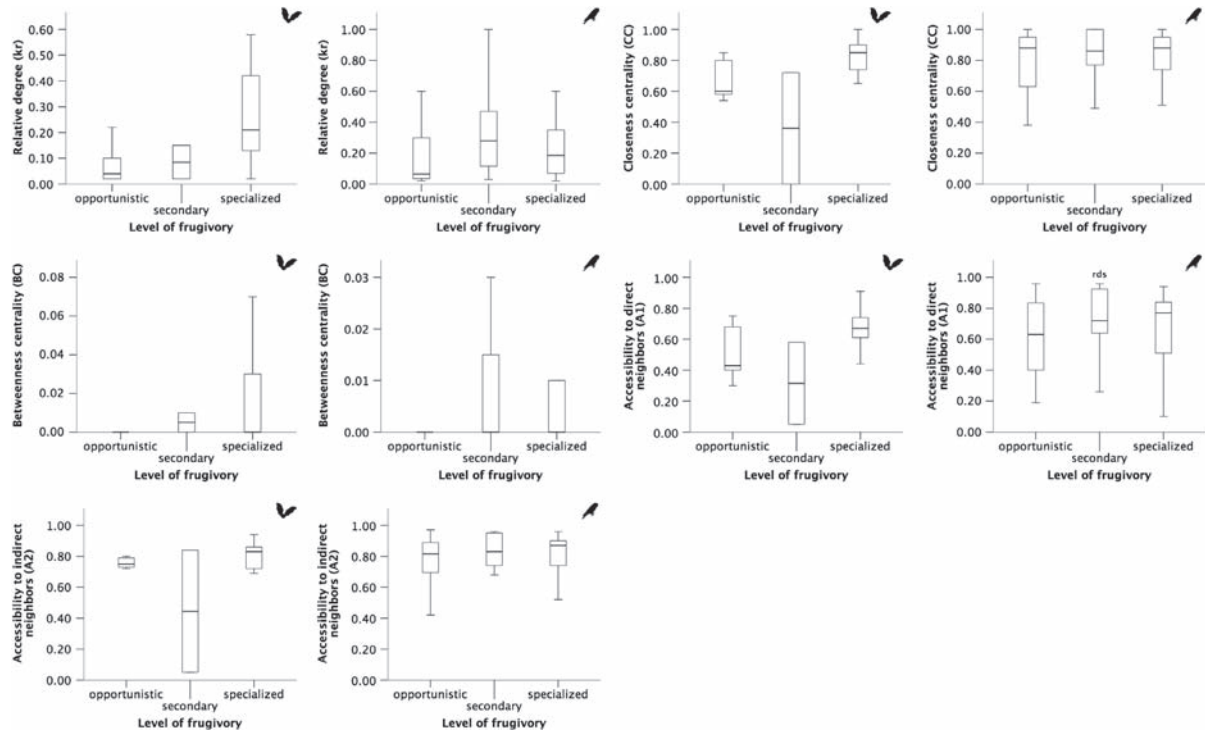


Figure 2. The relationship between centrality metrics and level of specialization in frugivory differs between bats and birds (disperser groups are represented by symbols). Specialized frugivores tend to have higher values of closeness centrality and accessibility to indirect neighbors, but this relationship is stronger for bats than for birds. Specialized frugivorous bats showed higher variation in relative degree and betweenness centrality, and are those that reach the highest values. There is no similar trend for birds. Boxes represent quartiles, the mid line represents the median, and whiskers represent the 95% confidence interval.

size in explaining the observed variation in centrality metrics. Therefore, we infer that specialized frugivores, considered to be potential seed dispersers, may be keystone mutualists of seed dispersal networks.

Some relationships between centrality metrics and dietary specialization differed between bat– and bird–fruit networks, supporting the hypothesis that different seed disperser taxa form networks with different structure. The local pattern of interaction plays also a role in determining centrality, as most widespread frugivorous bats and birds had varying scores of centrality in different local networks. Abundance might explain part of this inter-network variation in centrality (Vázquez et al. 2007), but we could not test this hypothesis, as we did not have abundance data in our dataset. The ecological role or relative importance of species in a food web seem to be phylogenetically conserved (Estes et al. 2011),

but a recent study on seed dispersal networks (Schleuning et al. 2014) found no phylogenetic dependence of the centrality of frugivorous birds (measured as network functional roles). Nevertheless, a phylogenetic signal is embedded in the centrality of frugivorous bats, as true dietary specialists belong to only two subfamilies, while secondary and opportunistic frugivorous bats are distributed in only three other subfamilies, and all five subfamilies with varying levels of frugivory belong to the Phyllostomidae (Fleming and Kress 2013). This is also evidence that mutualistic networks formed by different taxa have different structures and that those structures depend also on the higher taxonomic level considered, as networks formed by phylogenetically close species of a single taxon are different from networks formed by a mixture of different taxa (as pointed out by Bezerra et al. 2009, Mello et al. 2011a, Sarmento et al. 2014).

Table 1. Results of Spearman correlations (ρ) between centrality metrics (relative degree = k_r , closeness centrality = CC, betweenness centrality = BC, accessibility 1 – A1, and accessibility 2 – A2) measured for each frugivore species in 15 Neotropical seed dispersal networks ($n = 153$). Correlation significances were estimated through a bootstrap procedure (10 000 randomizations); * $p < 0.05$.

		Relative degree	Closeness centrality	Betweenness centrality	Accessibility to direct neighbors	Accessibility to indirect neighbors
k_r	ρ	1.00	0.58*	0.29*	0.63*	0.53*
CC	ρ	0.58*	1.00	−0.03	0.87*	0.80*
BC	ρ	0.29*	−0.03	1.00	−0.12	−0.29*
A1	ρ	0.63*	0.87*	−0.12	1.00	0.86*
A2	ρ	0.53*	0.80*	−0.29*	0.87*	1.00

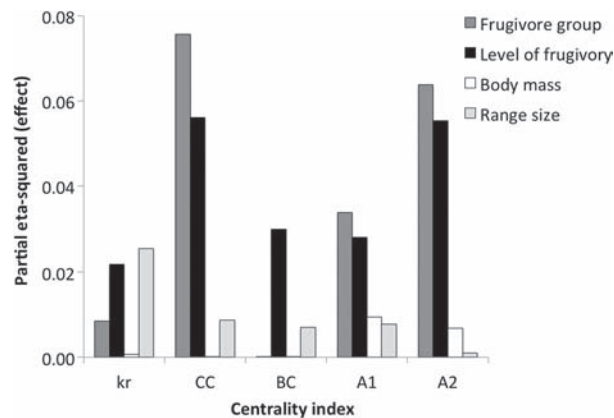


Figure 3. Dietary specialization as an important factor explaining variation in centrality indices in seed dispersal networks. Relative importance is measured by standardized effect scores (partial eta-squared), as obtained from a mixed-effects model (Supplementary material Appendix 5). Frugivore centrality in a seed dispersal network was related to its taxonomic affiliation (bats, birds) and level of specialization in frugivory. Centrality was weakly related to body mass or geographic range size. Boxes represent quartiles, the mid line represents the median, and whiskers represent 95% confidence intervals.

As expected, the correlations between centrality metrics point out to some degree of redundancy in measures of relative importance for network structure. Relative degree, the most fundamental centrality metric, was positively correlated with all other four centrality metrics, showing that more sophisticated metrics, such as accessibility, partly contain information conveyed by relative degree. Nevertheless, this does not mean that more complex metrics of centrality should be abandoned in favor of simpler ones, as the Spearman rank ρ -values of all correlations were low, meaning that complex metrics account only for part of the variation in centrality. It should be further noted that relative degree explained only a small portion of the variation in betweenness centrality, and that the latter was only correlated with accessibility to indirect neighbors. This suggests that betweenness centrality, at least in seed dispersal networks, is the most unique centrality metric. It is also worth remembering that betweenness centrality is the only one of the five centrality metrics that assesses the power of a species in binding different parts of the network, and as such, this metric plays a unique role for understanding the relative importance of a species for the network structure. Therefore, we suggest that the relative importance of a keystone mutualistic species in its network should be assessed with at least two different metrics, especially one that focuses on hubs and another one that focuses on connectors.

The relationship between geographic range size and relative degree corroborates the hypothesis that mutualists with larger geographic ranges tend to interact with more partners (Thompson 2005), and are therefore highly influential within seed dispersal networks. In addition, there was also large variation in the centrality of the same frugivore species among local networks. Therefore, a seed disperser cannot be considered equally important for network topology in all the sites where it occurs. Considering that some specialized frugivores have a preference for particular plant families (Levey et al. 2002, Şekercioğlu 2006), a low centrality might be interpreted as a locally narrower and more specialized diet. Some primary

frugivores probably show higher values of centrality where their preferred food-plants are less abundant, simply because they might be forced to include more fruit species in their diets (assuming optimal diet theory, Pyke 1984). This relationship between fruit availability, fruit preferences, and frugivore centrality could be investigated in future studies. Furthermore, the relationship between the level of specialization in frugivory and closeness centrality and accessibility to direct neighbors suggests that specialized frugivores are more important than other species to maintain the network structure.

Our results corroborate the hypothesis that some species are relatively more important than others to the structure of their network. Unfortunately, we did not have local information on seed dispersal effectiveness in our dataset (Schupp et al. 2010). Despite this shortcoming, several of the specialized frugivore species identified in the study networks are considered legitimate seed dispersers (Lobova et al. 2009), such as bats *Carollia perspicillata* (Thies and Kalko 2004) and *Sturnira lilium* (Mello et al. 2008). Therefore, our results suggest that specialized frugivores probably play keystone roles in seed dispersal networks. This supports similar observations from antagonistic food webs (Pimm 2002), pollination networks (Dupont and Olesen 2009) and bat–fruit networks (Mello et al. 2011b), in which ecological specialists were found to have larger relative importance than generalists to community structuring. Interestingly, some opportunistic frugivores, such as the bat *Trinycteris nicefori* (primarily insectivorous) (network Kalko BCI, Supplementary material Appendix 5), although being connected to only a few plant species, reached intermediate to high values of accessibility 2, as it feeds on very ‘popular’ plants, such as *Piper* species. Results of our mixed effects model are consistent with the hypothesis that specialized frugivores are the keystone species in seed dispersal networks, as in most networks they were the only ones to reach the highest centrality scores. However, patterns depended on the disperser group, as the relationship between dietary specialization and centrality differed between bat- and bird-fruit networks.

Although body mass and range size are considered to be relevant to frugivory interactions at the population level (Ollerton and Cranmer 2002, Woodward et al. 2005), they did not play an important role in determining centrality at the species level in our study. Furthermore, the mutualists’ taxonomic identity (i.e. bats or birds) seems to influence the structure of mixed-taxon networks, as observed for topological indices measured for seed dispersal (Mello et al. 2011b) and pollination networks (Bezerra et al. 2009, Olesen et al. 2007, Santos et al. 2010, Mello et al. 2011b). These findings suggest that the complex structure of interactions observed at the network level is only in part derived from the set of ecological traits studied here, which may affect disperser–plant relationships at both the organism and population levels.

In conclusion, our findings reinforce the need for studying the ecological correlates of centrality in mutualistic networks. We also stress the need for considering the taxonomic level and identity of disperser species, as evidence is growing that single-taxon and multi-taxon networks differ from each other in topology. We suggest that care should be taken when assessing ‘network specialization’ in mutualistic systems (a problem pointed out first by Blüthgen 2010, Blüthgen et al. 2008). The first step is to clearly distinguish between ecological and network concepts, the latter being surrogates

for the former. As ecologists we are interested in studying biological entities and phenomena, whereas network metrics are one of the quantitative tools we use to assess the biology of complex interaction webs. The problem is not which metric is used: the problem is that it is not wise to use the tool to define the ecological concept. We cannot state that a bat or a bird is specialized based only on network metrics, but we can define specialization on ecological terms and then assess how the degree of specialization affects the interaction pattern of the species within its network. This theory-oriented approach may help us develop new ecological concepts of specialization for complex multispecies systems, focused either at each species or the whole network. Those new concepts could be used in the study of ecological networks, as most theory so far has focused on the organism and population levels (Devictor et al. 2010). In addition, there are other biological attributes that need consideration in future studies, especially those related to the abundance of frugivores and fruits, and to chemical and visual attraction of frugivores (Cazetta et al. 2009, Hodgkison et al. 2013). The variation among study sites in the relative importance of frugivore species in seed dispersal networks underlines the importance of conducting network studies of species at as many sites as possible. Finally, the closeness centrality and accessibility of specialized frugivores, combined with the greater extinction likelihood of specialist species (Şekercioğlu 2011), suggests that the disappearance of specialized frugivores can have disproportionate impacts on ecosystems worldwide.

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Supplementary material (available online as Appendix oik.01613 at <www.oikosjournal.org/readers/appendix>). Appendix 1–6.