

Linking structure and functionality in mutualistic networks: do core frugivores disperse more seeds than peripheral species?

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Seed dispersal networks are often organized in nested structures in a way that a few core species can disproportionately affect the remaining species in a network, in both the ecological and evolutionary sense. Yet, the relative importance of core and peripheral species has not been properly tested in seed dispersal network studies. We determined core species from 10 local seed dispersal networks composed by fleshy-fruited plants and frugivorous birds. Each of those local quantitative networks was characterized with a core quality value, a core score for each species and a threshold value between core and peripheral species. From a total of 52 bird and 69 plant species that interacted in the study area, only 8 and 15, respectively, were identified as core. Each local network had a core that comprised a small number of birds and plants, always lower than 30% of the interacting species. There was no difference in the quantitative component of seed dispersal effectiveness (QC) provided by the frugivorous bird assemblage to plant functional groups clustered according to their growth form and fruit characteristics. Core birds dispersed seeds from each of these plant functional groups with a higher QC than peripheral species. Thus, we empirically demonstrate for the first time that seed dispersal networks at a regional scale have a small core set of fruit-eating birds, upon which heavily rely most fleshy-fruited plants for their seed removal. Hence, the activity of just a few core frugivores could deeply impact the demography of an entire assemblage of fleshy-fruited plants.

Seed dispersal interactions are essential for the life cycle of most plants, and thus for the maintenance of vegetation and animal communities. Simultaneously, animals obtain nutrients from plants, which are important for survival and breeding. In this way, plants and animals are linked in mutualistic interactions that are often considered a biodiversity generator through co-evolutionary processes (Ehrlich and Raven 1964, Thompson 1999). These mutualistic interactions are often organized in networks with a nested structure, in which a few core species interact with most of the available partners, being able to influence on the ecological and evolutionary dynamic of the whole network (Bascompte et al. 2003, Díaz-Castelazo et al. 2010; but see Staniczenko et al. 2013, who associate nestedness to an analytical artifact more than a structure generated by biological processes). At the ecological level, core species are expected to deeply impact on the demography of their partners and, therefore, they serve as critical sources of selection on both sides of the mutualism. At the evolutionary level, a greater importance on fitness components of core species compared to peripheral ones would result in the convergence and complementarity of morphological traits. This would favor the addition of species into the network through co-evolutionary vortices (Thompson 2006).

The knowledge of core species identity and the links they establish is important because they provide cohesion to the network (Bascompte et al. 2003, Jordano et al. 2003, Bascompte and Jordano 2006, Vázquez et al. 2009). The extinction of core species may impact this 'cohesive' effect, and cause the fragmentation and eventual collapse of the entire network (Loiselle and Blake 2002, Thompson 2006). Given this key relevance of a network core for seed dispersal mutualisms, some studies have tried to determine the most influential species in a network using indices based on binary data, that is the presence/absence of interactions established by a given species and its partners (Vidal et al. 2014). These studies found that the most generalist species, i.e. species that interact with many different partners, usually interact closely with most other species connecting sub-networks otherwise unconnected, thus staying in the center of the network topology (Mello et al. 2013; for similar results in pollination networks, see also Martín González et al. 2010, Olesen et al. 2007). One weakness of indices using binary data is that the links between species do not consider interaction frequency, which reflects the biological effect of one species on its partners more accurately (Vázquez et al. 2005, 2012). Inclusion of interaction frequency can drastically change whether a species is classified as central or peripheral

in the network, and it makes network indices more accurate and informative than when using binary data (Blüthgen et al. 2008). Moreover, studies that considered interaction frequency found that the identity of central species temporally varies in pollination networks (Alarcón et al. 2008) and remains spatially constant in ant–plant networks (Dáttilo et al. 2013). All these studies estimated the species relevance in networks using topological centrality indices and generalism measurements (see also Jordano et al. 2006). However, centrality is not a synonym of coreness. Then, the differential importance of core versus peripheral species for essential aspects related to their partner's survival and reproductive success in ecological, mutualistic networks remains unclear. All nodes in a core are topologically central in a network, but the opposite is not necessarily true. One main difference between coreness and centrality is that the former enlighten on the pattern of links in the network as a whole, while the latter is interpreted regardless of the network structure (see Borgatti and Everett 1999 for a deeper discussion on this issue). To our knowledge, there is no study of mutualistic interactions using an objective method to determine the coreness of a network (such as those implemented in social networks, Borgatti and Everett 1999, Csermely et al. 2013, Rombach et al. 2014) and thus, establishing the relative importance of core and peripheral species for the persistence of their interaction counterparts.

Interaction frequency of an animal species with mutualistic plant species appears to be a good surrogate of the quantitative component (QC) of seed dispersal effectiveness (Vázquez et al. 2005; see Vázquez et al. 2012 for the reciprocal effects of plants on animals), which is defined as the number of seeds dispersed by a dispersal agent (Schupp et al. 2010). This conclusion was based on a meta-analysis of studies in which interactions were mostly recorded on one or few plants (Vázquez et al. 2005). This approach did not take into account the context dependence of the QC of seed dispersal effectiveness. This means that the total number of fruits consumed and, consequently, the relative number of seeds dispersed away from the maternal plant by the same frugivore can differ depending on the fruit species consumed and on the local occurrence of other partners (i.e. fruit species) (Schupp et al. 2010). Here, we propose that an interaction network framework combined with natural history data, such as fruit handling techniques, are essential to determine if generalists with relatively high interaction frequencies – such as core species – provide the highest QC of effectiveness for the plant species with which they interact.

Differences in seed dispersal effectiveness between core and peripheral frugivores can be assessed in a per species basis or considering functional groups of plants that share features related to the seed dispersal process. The last approach is interesting given that several studies have shown that some fruit characteristics could have evolved in association to certain types of fruit-eating animals that dispersed their seeds (van der Pijl 1972, Gautier-Hion et al. 1985, Lomáscolo and Schaefer 2010). Functional assessment has the potential to reveal differences in the seed dispersal services made by core and peripheral frugivores to particular plant growth forms (canopy trees, shrubs, epiphytes) and microhabitats (primary and secondary forest, gaps, edges) (Schleuning et al. 2011).

Besides, it can be useful from a conservation perspective since it provides insight of how endangered can be considered the persistence of a plant group, whether it depends on core and/or on peripheral frugivores for its seed dispersal (Mokany et al. 2014).

In this article we studied the interaction network structure between birds and plants with fleshy fruits at 10 sites of a subtropical mountain forest in northwestern Argentina, to answer the following two questions: 1) which bird and plant species make up the network core at each site? To address this question we analyzed the core–periphery structure of networks using methods developed in social network studies. 2) How does the importance for partners' dispersal varies between core and peripheral bird species? To tackle this question we compared the QC of the effectiveness in seed dispersal (Schupp et al. 2010) provided to functional groups of plants performed by core and peripheral bird species.

Methods

Study area

Austral Yungas forests extend from the Andean elbow in Bolivia (18°S) to Catamarca province (29°S) in northwestern Argentina. These montane forests are developed as a long and narrow discontinuous strip (ca 50–70 × 1200 km) on the eastern lower slopes of the Andes (Supplementary material Appendix 1). The climate is subtropical with a marked dry season from May to September, and rains are concentrated from November to March. The average annual rainfall varies between 1000 and 2000 mm depending on the elevation and latitude (Brown et al. 2001). Three altitudinal forest types can be recognized: piedmont forests (400–600 m a.s.l.); montane forests, which can be subdivided into 'basal' montane forests (600–1000 m a.s.l.) and 'Mirtaceous' montane forests (1000–1500 m a.s.l.); and cloud forests (1500–2800 m a.s.l.) (Brown et al. 2001).

Field work was carried out at 10 sites in northwestern Argentina, evenly distributed in latitude and altitude (Supplementary material Appendix 1), except for piedmont forests which were excluded given that they have been extensively disturbed by human activities. Sites were monitored between November 2008 and February 2012, during rainy seasons when most plant species have ripe fruits (Boletta et al. 1995, Malizia 2001). Each site was sampled twice over the whole duration of the study, to record interactions of fruit-eating birds with different plant species, because most of them have a brief peak of fruit ripening. A first sampling was made at the beginning of the rainy season (November or December) and the other at the end (January or February). Four sites had the two visits in the same rainy season, whereas the remaining six sites were visited in different rainy seasons. We made eight visits in the first rainy season, seven in the second, one in the third and four in the fourth. For every analysis we combined data – number of interactions, birds and fruit abundance – from both sampling periods of a given site. Therefore, interaction frequency, in this study, corresponds to the sum of the number of interactions recorded in both visits to a given field site. Besides, we used the term 'link' to denote the presence/absence of a given fruit–frugivore

interaction, irrespective of the frequency or strength with which the tie occurs.

Field work

We accomplished 40 h of observations of bird-fruit interactions at each visit, during 3–4 days and across a ~50 ha area. We walked along human-and-cattle-made trails during the first 5 h after dawn, crossing primary and secondary forests, gaps and riparian areas. We followed any fruit-eating bird until fruit consumption was recorded. We defined ‘interaction’ as an individual bird eating one or more fruits from an individual plant. Consumption of more than one fruit on one individual plant by the same individual bird was considered as a single interaction. If an individual bird consumed fruits from more than one individual plant, we recorded as many interactions as plants visited. Likewise, we recorded as many interactions as individual birds from a flock observed consuming fruits in an individual plant. Most times, interaction records corresponded to one individual bird eating fruits on one individual plant (82%, $n = 3401$ interactions recorded during walks). For each interaction we recorded the bird and fruit species involved, as well as observations about how the bird processed the fruit. When the fruit was not completely swallowed (‘mash’ and ‘bite’ methods, sensu Foster 1987), we determined if seeds were either swallowed or discarded. We intentionally excluded fruit consumption events made by parrots from all analyses, since they are largely recognized as seed predators (Collar 1997). The remaining bird species included, most of them small to medium-sized passerines (Supplementary material Appendix 2 Table A1), were assumed to have the potential to disperse seeds from fleshy fruits.

We set 5–7 mist nets (12×4 m, 36-mm mesh) at each visit, in order to record interactions not detected during the walks. Sampling effort with mist nets was not standardized (range = 57.91–337.26 h net⁻¹, where 1 h net⁻¹ is 1 net opened during 1 h). Caught birds were placed in plastic containers lined with filter paper during 10–15 min, to collect fecal samples with seeds (Loiselle and Blake 1990). Samples were kept in paper envelopes and then analyzed in the lab with a magnifying glass. Seeds were identified using a reference material collected during this study. We added one interaction per seed species regardless the amount of each seed species in that fecal sample. Interactions recorded with this method represented only 5% of the total number of interactions and were always smaller than 10% of the interactions recorded at each site (range = 0–33 interactions per site). They represented 5.9% of core bird interactions, 3.8% of peripheral birds interactions, 4.2% of core plant interactions and 6.1% of peripheral plant interactions (see below methodology for core and peripheral species determination). Moreover, 75% of the interactions coming from seeds in feces were links already seen during walks at each site. Thus, bias due to differences in sample effort regarding the time in which mist nets were opened would seem negligible and almost equally distributed between core and peripheral species.

During the walks we determined the abundance of fruit-eating birds by counting every individual seen or heard as far away as 30 m on both sides of the trails. We considered this approach to be a reasonable estimate of the relative

abundance of fruit-eating bird species at each visit, because the sampling effort during the rainy season was always 40 h per visit. Also, even when bird abundance and interaction frequency data are not strictly independent in statistical terms, we still think that our analysis has a strong biological meaning. Indeed, many individual birds seen or heard were not observed consuming fruits, and some individual birds contributes with more than one interaction. Blending et al. (2012) applied a similar methodology and found that co-variation between bird abundance and the frequency of fruit consumption depended on the bird species considered; deviations of this relationship can be partially explained by frugivory level of bird’s diet. Bird scientific names follow those recommended by the South American Classification Committee of the American Ornithologist Union (<www.museum.lsu.edu/~Remsen/SACCBaseline.html>).

To determine the abundance of ripe, fleshy fruits (i.e. every kind of fleshy diaspora, such as berries, drupes, arillated seeds and syncarps) we established transects in the same area where performed the interaction observations. Transect length was 50 m and width varied between 20 m for trees, epiphytes and vines, and 4 m for herbs and shrubs (Blake et al. 1990). We estimated the amount of ripe fleshy fruits in every individual plant inside the transects, using binoculars. The number of transects sampled per visit varied from 7 to 18 and it was determined by a plot of the cumulative number of plant species with ripe fruits. When this number reached a plateau (no new species with ripe fruits added in five consecutive transects) we assumed that the given number of transects was an adequate sample size. Fruit number was converted to dry pulp weight per area (g m^{-2}) (P. G. Blending and N. P. Giannini unpubl.). For a more detailed description of fruit sampling methods, see Ruggera et al. (2014). Scientific plant names follow the Instituto de Botánica Darwinion (<www.darwin.edu.ar/Proyectos/FloraArgentina/Especies.asp>). Bird–fleshy fruit interactions were arranged in matrices with bird species in rows and plant species in columns. Cell values represented the interaction frequency between bird and fruit species. These matrices were then used to draw the bipartite, quantitative networks with Pajek Software (Batagelj and Mrvar 1998).

Detection of core–periphery structure and core species determination

We delimited the core of each network by identifying those nodes that were well connected to the entire network, and differentiated from the periphery, i.e. nodes that are well-connected to the core but sparsely to each other. To identify core species at each of our sites we used bipartite quantitative networks that captured the frequency of interactions between birds and plants. To each of these networks, we applied the method developed by Rombach et al. (2014). We summarize the important features here. Each node i was assigned a core score C_i (range = 0 [peripheral node] – 1 [core node]) that depended on two parameters, α and β . We first specified the n possible scores, where n is the size of the network. The scores are a ranking from 0 to 1 where nodes with the highest scores are those most likely to be found in the network’s core and lowest scores are those most likely in the network’s periphery. Given these possible scores, we assigned precisely

one to each node so that the core quality, $R_{\alpha,\beta}$, was maximized. The core quality captures the heuristic that a core will be well-connected, while the periphery sparsely so. The core quality was determined by the same two parameters α and β , both ranging from 0 to 1. The former is a relaxation parameter that determines the flexibility of the scoring distribution; $\alpha = 1$ requires core nodes to all have score 1 and periphery nodes a score of 0. Decreasing α relaxes this differential between core and periphery in addition to ranking nodes in terms of their core position. The latter parameter β determines the proportion of nodes that will be counted as core. Since these parameters prescribed a fairly constrained core-periphery structure onto the network, the scores were then averaged over all possible α and β , and weighted by the core quality $R_{\alpha,\beta}$. The higher the core quality, the more weight the core scores of α and β will receive. This average for a node is called the aggregate core score $CS(i)$ (see Rombach et al. 2014 for a full discussion of core quality). Specifically, the aggregate core score is given by:

$$CS(i) = Z \sum_{\alpha,\beta} C_i(\alpha,\beta) R_{\alpha,\beta}$$

where $C_i(\alpha,\beta)$ is the core score and Z normalizes all core scores so that $0 \leq CS(i) \leq 1$.

We computed the aggregate core scores for all species, at each of the 10 sites. We then determined a threshold for these scores to delimitate a core-periphery division. Specifically, if $\{i_1, i_2, \dots, i_n\}$ are the ranked nodes and $CS(i_1) \geq CS(i_2) \geq \dots \geq CS(i_n)$, we considered that core and periphery are given by $X_C = \{i_1, \dots, i_{core}\}$ and $X_P = \{i_{core+1}, \dots, i_n\}$, respectively. Assuming that both core and periphery had at least size 2, the core-periphery division was obtained by:

$$\hat{i}_{core} = \arg \max_{i_{core} \in \{i_3, \dots, i_{n-2}\}} \frac{2E(X_C, X_C)}{|X_C||X_{C-1}|} + \frac{E(X_C, X_P)}{|X_C||X_P|} - \frac{2E(X_P, X_P)}{|X_P||X_{P-1}|}$$

The first term above is the core's edge density to itself. The second term is the edge density between core and periphery. Both these densities are favorable in identifying core-periphery structure. The last is the periphery's edge density with itself, which we want to make as sparse as possible. Further details are given in Supplementary material Appendix 3. Routines for these analyses were implemented with MatLab 2012a student version and Python 2.7.9

Summarizing, the method seeks for species that have a strong influence on the network dynamics. This is achieved not only by finding nodes with strong links to many plant/bird species, but also with connections to such plant/bird species that themselves play strong roles. For example, if a given frugivore only visits plants that are infrequently visited by the rest of the frugivorous assemblage, such frugivore will not be part of the core. This means that it is not enough for a species to be considered as core to have a high degree (i.e. to interact with many species).

We additionally calculated several measurements commonly included in studies of mutualistic networks, such as the nestedness and connectance of networks, as well as the centrality, generalism and functional indices of

species, to allow comparisons with previous studies. These measurements were estimated with 'Bipartite' package for R (< www.r-project.org >).

Plant functional groups

Fruit species consumed were pooled into groups from a dendrogram based on a cluster analysis, in agreement with plant growth form and fruit characteristics relative to size, weight, color, pulp and seeds (Supplementary material Appendix 4), obtained from P. G. Blendinger and N. P. Giannini (unpubl.). Analyses were performed with the 'Cluster' package of R. We called 'plant functional groups' clusters of plant species that shared similar suites of characteristics, and assumed that plant functional groups determined by this analysis could potentially be an evolutionary consequence (at least partially) of the seed dispersal process and more specifically, of their relationship with frugivorous partners.

Estimation of the quantitative component (QC) of seed dispersal effectiveness

Seed dispersal effectiveness of frugivores can be determined through the estimation of quantitative and qualitative components (Schupp et al. 2010). Here we assess the quantitative component (QC), given that the dense vegetation in most sites prevented us from following birds and detecting the microhabitats where they dropped their feces or regurgitate seeds. Besides, information of the effect of gut passage on the seed viability is unknown for most of the fruit-eating birds in our study area.

The QC of seed dispersal effectiveness corresponding to individual fruit-eating bird species was estimated for each plant functional group separately, by multiplying: 1) the dependence of the plant functional group on the frugivory made by a given fruit-eating bird species at every site (d_{ij}); and 2) the proportion of seeds from that plant functional group dispersed away from the maternal plant at the same site by the same bird species.

The dependence was calculated following Bascompte et al. (2006) as

$$d_{ij} = IF_b / IF_t$$

where IF_b is the interaction frequency of a bird species j with all fruit species of the plant functional group i at a given site, and IF_t is the total interaction frequency of the plant functional group i in that site.

The proportion of seeds dispersed for every bird-fruit species pair at each site was calculated as the fraction between the number of seeds swallowed or taken away from the maternal plant and the total seed number implied in the number of fruits consumed. We considered that birds dispersed all the seeds when a fruit was completely swallowed ("gulpers" sensu Foster 1987) or when birds plucked a fruit and flew off the maternal plant regardless of the feeding method used subsequently. When birds did not swallow fruits in the maternal plant, they used one of the following feeding methods: 'mashing', which means that fruits were plucked and processed with the bill, discarding the peel and some seeds below the maternal plant; or 'pecking', meaning that

fruits were not plucked but pecked from a perch, with birds occasionally being able to swallow some small seeds (Foster 1987, Levey 1987, Jordano and Schupp 2000). Since seed size in one-seeded fruits is often bigger than in multi-seeded fruits, the proportion of the former's seeds dispersed through mashing and pecking was considered to be zero. However, we assumed that birds using mashing and pecking methods dispersed the 50% and the 25% of seeds from multi-seeded fruits respectively. These assumptions were based on our own observations of fruits mashed and dropped below the maternal plant, and pecked fruits that remained attached to the plant. Sometimes a bird species used different methods to process the same fruit species. For example, let us consider a bird eating 10 fruits with 40 seeds each, implicating 400 seeds. If it swallowed the entire fruit three times, once plucked it and flew off, and used mashing six times, then it dispersed 280 seeds (70%). We made this calculation for the remaining fruit species from the same plant functional group, consumed by the same bird species, therefore obtaining the proportion of seeds of a given functional plant group dispersed by a specific bird species at a particular site.

We built a two-dimensional landscape to plot the QC of the seed dispersal effectiveness for each plant functional group (Schupp et al. 2010), where axes correspond to the dependence on the fruit consumption by individual bird species, and to the proportion of seeds dispersed by them, at each site. Isoclines represent different combinations of those components, which multiplication yields to the same QC of seed dispersal effectiveness. Values of the QC in isoclines and number of isoclines on each landscape were arbitrarily determined based on the range of QC values obtained, and on the number of frugivorous species, respectively.

Differences in the QC of seed dispersal effectiveness between core and peripheral species

We made a randomized factorial ANOVA to test for differences in the QC of the seed dispersal effectiveness shown by core and peripheral species. We considered the influence of two main factors (if it was a core or a peripheral species and the plant functional group) and their interaction, on the QC of the seed dispersal effectiveness provided by frugivores. Cases in which a whole plant functional group received fewer than five total interactions at a given site were not considered. We used a type II sum of squares and set the significance level at 0.05. Bonferroni corrections were applied when comparing the QC of seed dispersal effectiveness provided to each plant functional group separately. Analyses were run in R.

Results

We registered 9182 fruit-eating individual birds, and only 33.7% of them were observed eating fruits at least in one individual plant (2789 birds in one plant, 294 on two, and 8 on three). We recorded 3579 interactions (3401 during walks + 178 from seeds in feces) between 52 bird and 69 plant species connected by 452 links (Fig. 1). Non-passerine frugivores were relatively unimportant in our study system, involving seven species that consumed fruits and representing 0.8% of the total interaction number (Fig. 1,

Supplementary material Appendix 2 Table A1). We collected 281 feces from fruit-eating birds, 140 of which contained seeds. Most of feces with seeds (96%) belonged to species in the Turdidae, Tyraniidae, Thraupidae and Emberizidae families (Supplementary material Appendix 2 Table A1). Seeds in feces looked almost always intact (i.e. without mechanical damages visible with a magnifying glass). There were only two instances in which we found broken seeds in feces: *Leptotila megalura*, a medium-sized dove, had all the *Sambucus nigra* seeds broken (around 40) in one fez; and *Zonotrichia capensis*, a small-sized emberizid, had five of eight *S. nigra* seeds broken in one fez. Therefore, the QC of seed dispersal effectiveness of *L. megalura* when consuming *S. nigra* (which was only recorded in that fecal sample) was zero, while we considered that *Z. capensis* dispersed 38% of *S. nigra* seeds swallowed.

Seeds in feces added 45 links that were not registered during observation walks. These interactions implied 40 new local links (i.e. pairs that were not seen interacting during walks in the two visits to the site in which fecal samples were obtained) and 20 new regional links (i.e. pairs that were not seen interacting during walks in the whole study area).

There was a 1:1 trend in bird and fruit species richness per site (Table 1); a great disparity between bird and fruit species was found only in one site (Quebrada del Portugués), in which there were twice as many fruit-eating species as plant species with ripe fleshy fruits (Fig. 1).

Network structure in all sites was characterized by few species involved in most of the interactions, whereas many species had just a few links (Fig. 1). There were few specialized interactions; instead, species with few interactions were almost always linked to relatively generalist partners (Fig. 1). The relative interaction frequency was better explained ($r^2 = 0.28$, $F = 129.3$, $p < 0.001$) by the bird relative abundance ($b = 0.34$, $p < 0.001$) than by the fruit relative abundance ($b = 0.18$, $p < 0.001$).

Overall, the highest qualities of core-periphery structures in networks were obtained when cores involved 30% of species as much (Supplementary material Appendix 3 Fig. A1). Quebrada del Portugués was the site with the highest core-quality (Supplementary material Appendix 3 Fig. A1). When we computed the core-periphery division using the edge-density metric, this site, as expected, demonstrated the highest affinity for core-periphery structure (Table 1, Supplementary material Appendix 3 Fig. A2). Other features of local networks are summarized in Table 1.

Core species

Core species per site ranged from one to three in birds and from one to four in plants (Table 2, Fig. 2). Eight bird species, all of them passerines, were classified as core species (Table 2, Supplementary material Appendix 3 Fig. A1). These eight bird species combined accomplished 2912 interactions (81% of total interactions). Five of these core species served as core in at least two of the 10 sites, while the remaining two species were only core in a single site (Table 2, Fig. 2).

There was a total of 15 plant species making up the core across the 10 sites, which included big trees (e.g. *Podocarpus parlatorei*, *Ocotea puberula*, *Blepharocalix salicifolius*),

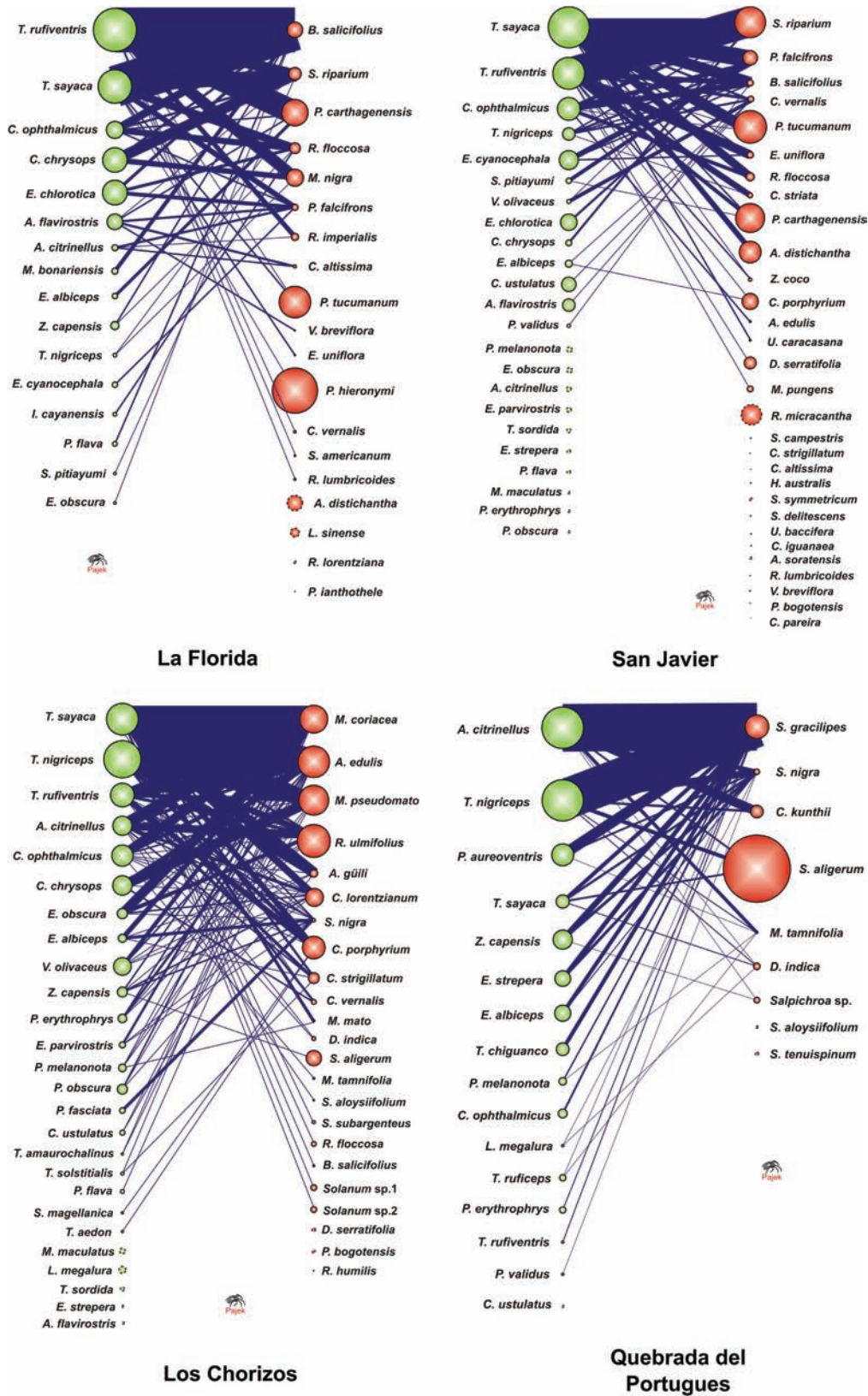
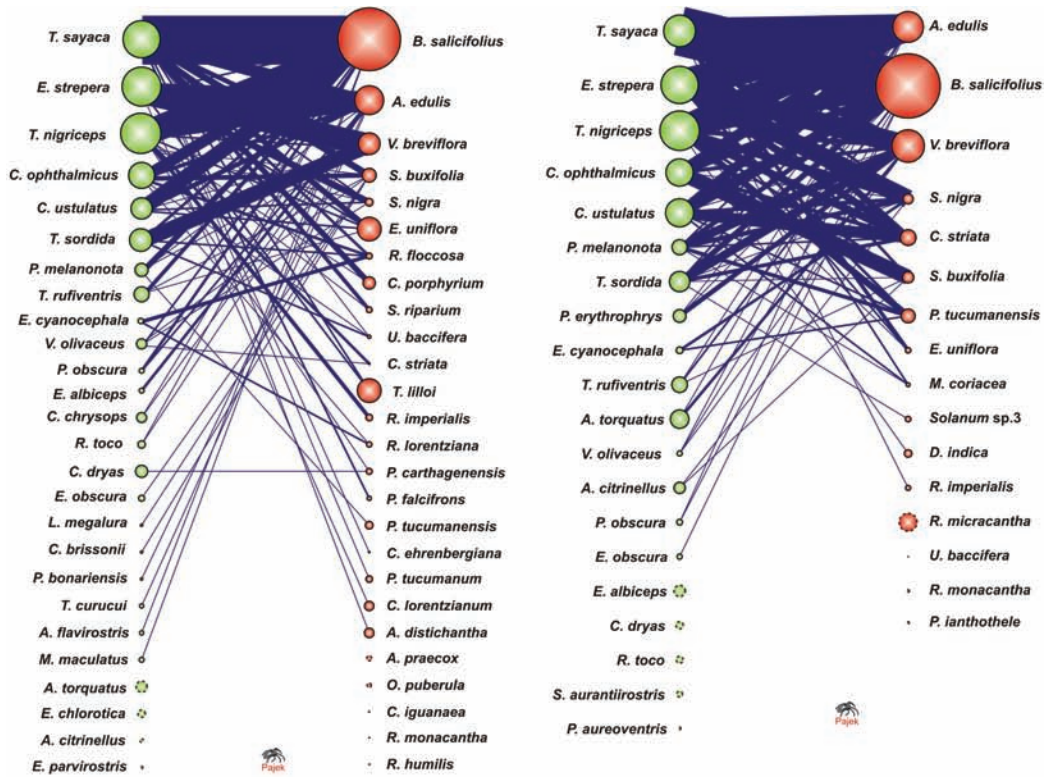
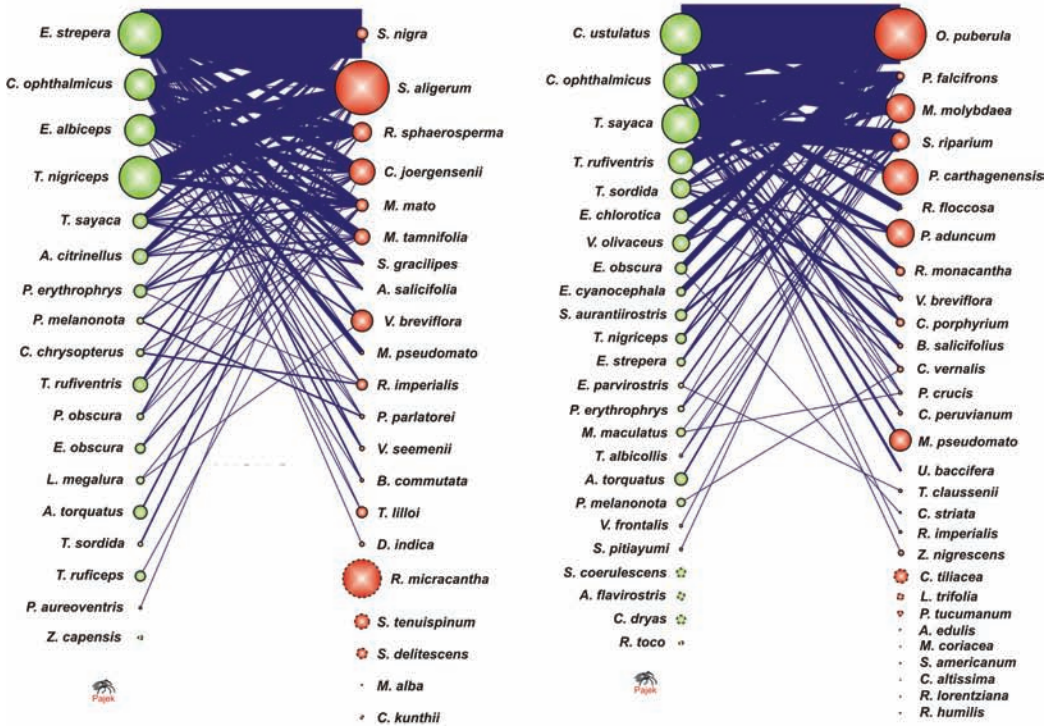


Figure 1. Topology of bird–fruit mutualistic interactions recorded at 10 sites of the Austral Yungas in northwestern Argentina, during the rainy seasons (November–February) of 2008–2012. Green circles correspond to fruit-eating bird species (left sides) and red circles denote plant species with fleshy fruits (right sides). Circle size is proportional to the relative abundance of the species, whereas width of lines linking bird and plant species is proportional to the interaction frequency recorded between two given species. Species are shown in decreasing order from top to bottom, according to their total interaction frequency. Fruit-eating birds and plants with ripe fleshy fruits occurring in a given site but for which we did not record interactions, are shown at the bottom without links and with dash-bordered circles.



Chorro de Loros

Pozo Verde



EcoPortal de Piedra

A. Tres Cruces

Figure 1. Continued.

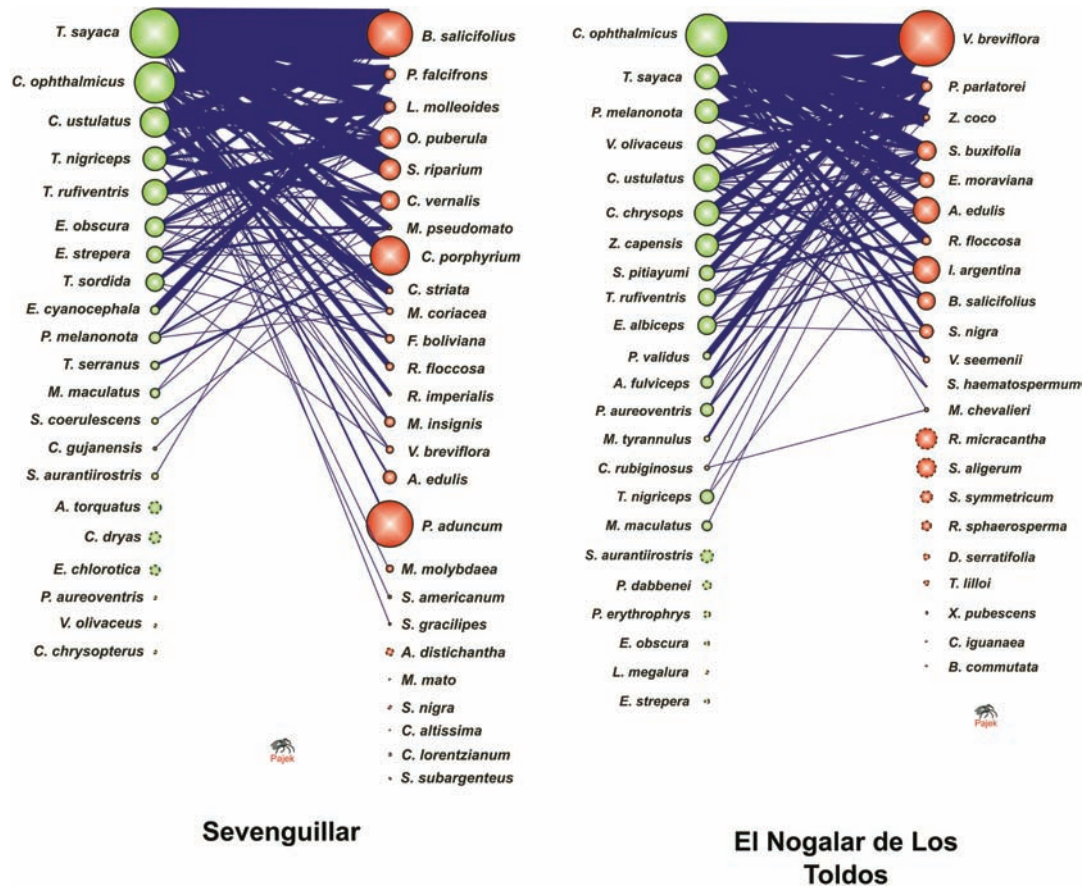


Figure 1. Continued.

medium and small trees (e.g. *Allophylus edulis*, *Solanum riparium*, *Sambucus nigra*), shrubs (e.g. *Solanum aligerum*, *Vassobia breviflora*) and hemiparasitic plants (*Phoradendron falcifrons*) (Table 2, Supplementary material Appendix 2 Table A2). Core plant species concentrated 2638 interactions (74% of total interactions). *Blepharocalix salicifolius* was a core species in almost all montane forest sites (both

basal and Myrtaceae); *A. edulis* was important in Mirtaceous montane forests, and *S. nigra* in cloud forests (Fig. 2).

QC of the seed dispersal effectiveness of core and peripheral species

We found six plant functional groups (Supplementary material Appendix 4, Fig. A1), which will hereinafter be referred to as the ‘epiphytes’, ‘purple-fruited shrubs’, ‘light-seeded trees’, ‘Piper’, ‘Morus-like’ and ‘heavy-seeded trees’ groups (Table 3). Seven of the core plant species belonged to the ‘light-seeded trees’ group, whereas the other core plant species were in the ‘purple-fruited shrubs’ (three species), ‘heavy-seeded trees’ (three species), ‘Morus-like’ (one species) and ‘epiphytes’ (one species) groups.

Comparison of the QC of effectiveness between core and peripheral species when consuming fruits of the ‘Piper’ group was not assessed due to the low interaction number recorded. From a total of 32 records involving fruit consumption of the ‘Piper’ group, 30 were made by core species: *Thraupis sayaca* (27 interactions), *Turdus rufiventris* (2) and *Chlorospingus ophthalmicus* (1); the two remaining interactions were performed by one peripheral species. Seeds from the remaining five plant functional groups were dispersed with a similar QC of effectiveness ($F_{obs} = 1.55$; $p = 0.18$). Although birds had a slightly higher mean QC of seed dispersal effectiveness when consuming fruits of the ‘epiphytes’ and ‘Morus-like’ groups, than when eating the ‘purple-fruited

Table 1. General characteristics of the bird–fleshy fruit interaction networks from 10 sites of the Austral Yungas in northwestern Argentina, recorded between November and February from 2008 to 2012. F = number of plant species with fleshy fruits recorded with interactions; B = number of fruit-eating bird species recorded with interactions; I = number of interactions recorded; CQ = core quality given by the edge density metric (Supplementary material Appendix 3); WNODF = weighted nestedness based on overlap and decreasing fill (range = 0 [no nested] – 100 [completely nested]; Almeida-Neto and Ulrich 2011); Cn = connectance (i.e. realized links/possible links).

Site	F	B	I	CQ	WNODF	Cn
La Florida	15	16	321	0.45	33.84	0.19
San Javier	16	13	263	0.40	41.90	0.23
Los Chorizos	20	21	444	0.44	42.06	0.23
Qda. del Portugués	7	15	370	0.67	55.30	0.36
Chorro de Loros	21	22	345	0.37	35.58	0.16
Pozo Verde	12	15	439	0.47	56.01	0.39
EcoPortal de Piedra	16	17	363	0.53	49.84	0.31
A. Tres Cruces	20	20	348	0.33	27.19	0.17
Sevenguillar	20	15	348	0.43	34.93	0.26
El Nogalar de los Toldos	13	17	334	0.41	37.04	0.33

Table 2. Core species from the fruit-eating bird – fleshy fruit mutualistic networks, recorded at 10 sites in the Austral Yungas, northwestern Argentina, during the rainy seasons of 2008–2012. Means were obtained with values recorded at those sites in which species were identified as core. CS = aggregate core score; BC = betweenness centrality; CC = closeness centrality; d' = specialization index; A = species interaction asymmetry; QC (only for bird species): quantitative component of the seed dispersal effectiveness (for a detailed definition and formulae of these indices, Supplementary material Appendix 3). For bird species: M = ‘mashers’; G = ‘gulpers’. For plant species: H = hemiparasitic; U = understory; S = subcanopy; C = canopy.

	No. of sites as core	Mean CS	Mean BC ¹	Mean CC ²	Mean d' ³	Mean A ⁴	Mean QC
Bird species							
<i>Thraupis sayaca</i> (M)	7	0.89	0.53	0.10	0.19	0.40	0.24
<i>Turdus nigricaps</i> (G)	4	0.69	0.15	0.10	0.12	0.13	0.14
<i>Chlorospingus ophthalmicus</i> (M)	2	0.79	0.78	0.15	0.20	0.45	0.13
<i>Turdus rufiventris</i> (G)	2	0.95	0.40	0.10	0.32	0.52	0.15
<i>Catharus ustulatus</i> (G)	2	0.73	0.12	0.08	0.30	0.14	0.11
<i>Elaenia strepera</i> (G)	2	0.86	0.59	0.15	0.14	0.21	0.16
<i>Elaenia albiceps</i> (G)	1	0.56	0.06	0.10	0.09	0.10	0.06
<i>Atlapetes citrinellus</i> (M)	1	0.87	0.71	0.20	0.06	0.27	0.09
Plant species							
<i>Blepharocalix salicifolius</i> (C)	5	0.88	0.54	0.14	0.16	0.30	
<i>Solanum riparium</i> (S)	3	0.72	0.25	0.12	0.22	0.05	
<i>Allophylus edulis</i> (S)	3	0.86	0.18	0.12	0.11	0.27	
<i>Phoradendron falcifrons</i> (H)	2	0.58	0.19	0.12	0.30	0.34	
<i>Sambucus nigra</i> (S)	2	0.71	0.49	0.25	0.11	0.22	
<i>Vassobia breviflora</i> (U)	1	0.89	0.87	0.29	0.13	0.27	
<i>Ocotea puberula</i> (S)	1	1.00	0.62	0.09	0.30	0.43	
<i>Lithraea molleoides</i> (S)	1	0.58	0.06	0.11	0.23	0.12	
<i>Podocarpus parlatorei</i> (C)	1	0.62	0.13	0.14	0.23	0.33	
<i>Solanum aligerum</i> (U)	1	0.76	0.12	0.18	0.19	0.34	
<i>Schinus molle</i> (U)	1	1.00	0.81	0.78	0.05	0.69	
<i>Psychotria carthagenensis</i> (U)	1	0.51	0.03	0.07	0.35	0.20	
<i>Zanthoxylum coco</i> (S)	1	0.70	0	0.15	0.24	0.02	
<i>Myrcianthes pseudomato</i> (C)	1	0.62	0	0.06	0.19	0.11	
<i>Myrsine coriacea</i> (S)	1	0.96	0.82	0.08	0.10	0.34	

¹Centrality based on how critical a species is for the network cohesion, linking network areas otherwise scarcely or not connected at all. Spans between 0 (peripheral) and 1 (central).

²Centrality based on the minimum number of species needed to link a focal species with all the other species in the network. It measures how close a species is from the rest of the species in the network. Spans between 0 (peripheral) and 1 (central).

³It is the deviation of the actual interaction frequencies from a null model assuming that all partners are used in proportion to their availability. Spans between 0 (the most generalist) and 1 (the most specialist).

⁴Sum of mismatches between the strength of the focal species and the strength of its partners, divided by the number of links established by the focal species. Varies between 1 (focal species strongly affects to its partners) and -1 (focal species is strongly affected by its partners).

shrubs’, ‘light-seeded trees’ and ‘heavy-seeded trees’ groups, these differences were not statistically significant (pairwise comparisons with Bonferroni-corrected p -values > 0.05 ; Fig. 3A). Core species had a QC of effectiveness significantly higher than peripheral species ($F_{\text{obs}} = 106.06$; $p < 0.001$); this differential QC of effectiveness provided by core species was seen in the five plant functional groups (interaction of main factors was statistically non significant: $F_{\text{obs}} = 0.33$; $p = 0.86$) (Fig. 3B).

Within each plant functional group, most fruit-eating birds had a relatively low QC of seed dispersal effectiveness, mainly due to low values of dependence; just one or two core bird species, both gulpers and mashers, had a QC of effectiveness higher than 0.5 (Fig. 4). The relatively low QC's of the seed dispersal effectiveness when consuming fruits of the ‘light-seeded trees’ and ‘heavy-seeded trees’ groups (Fig. 3A) were also caused by a low proportion of seeds dispersed; specifically, 55% of the peripheral bird species dispersed only 50% or less of seeds (Fig. 4). Core bird species on which plant functional groups were highly dependent for their fruit removal always dispersed a relatively high proportion of the seeds; in other words, lower right corners of

QC landscapes were invariably empty (Fig. 4). The highest QC of seed dispersal effectiveness provided by peripheral birds was to fruits of the ‘epiphytes’ group, which was mainly due to the fruit removal made by *Euphonia cyanocephala* and *E. chlorotica* (arrows in Fig. 4).

Discussion

Our study linked for the first time the species coreness in a network with the quantitative component (QC) of the seed dispersal effectiveness provided through their interactions. Our results empirically show what has been extensively claimed for seed dispersal and pollination interactions but never numerically assessed, namely, that ecological, mutualistic networks have a clearly distinctive core of relatively few species linked to a high number of peripheral species. Networks monitored in this study along a great extension of a subtropical montane forest had only eight core bird species that were decisive for the fruit removal of fleshy-fruited plants, and the frugivorous diet of fruit-eating birds was mainly comprised by only 15 fleshy-fruited plant species.

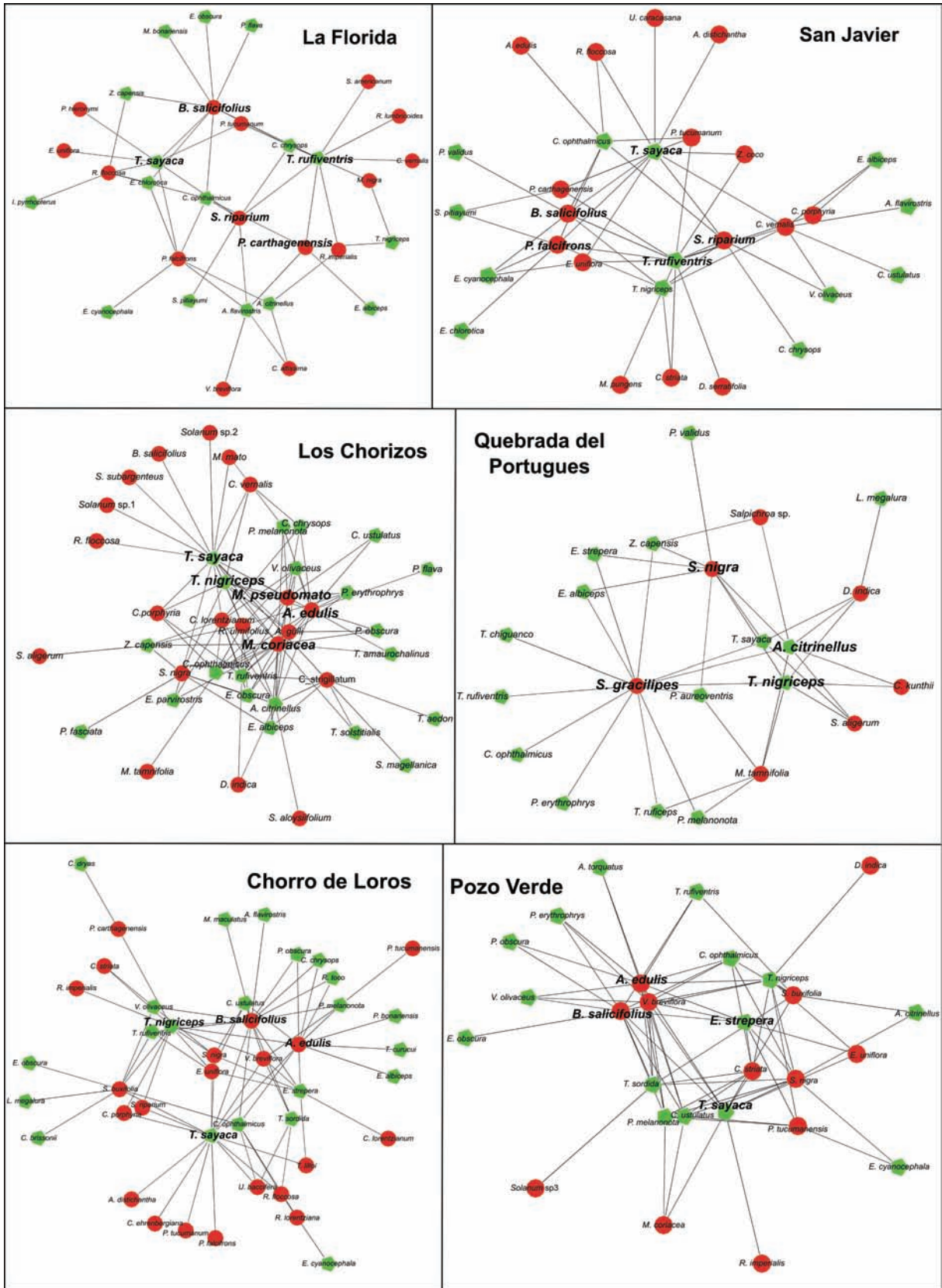


Figure 2. Core species in bird–fruit mutualistic networks in 10 sites of the Austral Yungas, northwestern Argentina, during the rainy seasons (November–February) between 2008 and 2012. Red circles = fleshy-fruited plant species; green pentagons = fruit-eating bird species. Core species are shown with a bigger bolded font size. Networks were layout with the Fruchterman–Reingold algorithm, which relocate the nodes (i.e. species) in such a way that an equilibrium state is reached when all the edges (i.e. interactions) have about the same length, and there is as less edges crossing over nodes as possible. By doing this, species with many interactions or connecting different parts of the network, will be placed near of the graph center.

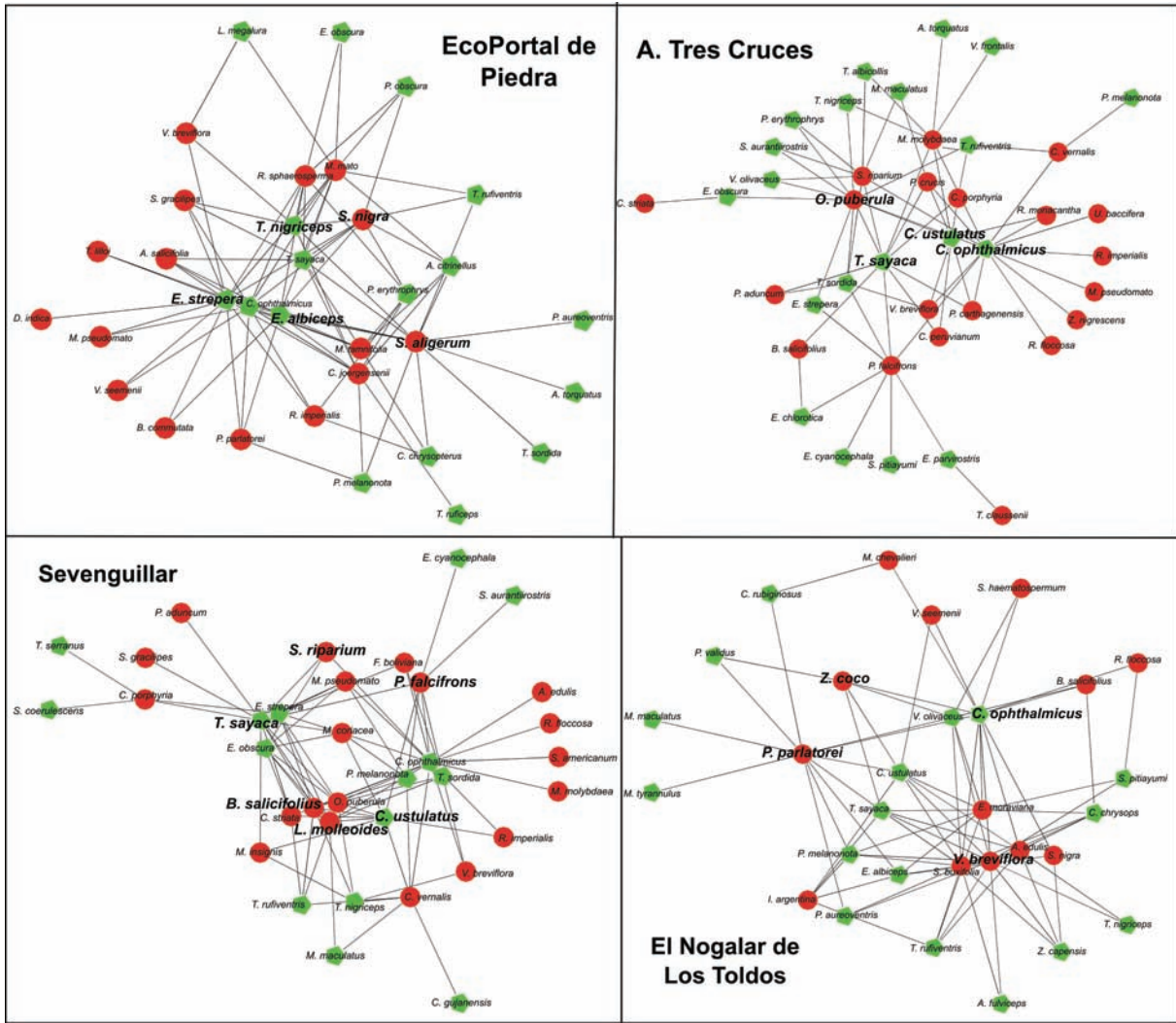


Figure 2. Continued.

It is often hypothesized that core species would greatly determine the co-evolutionary pattern in mutualistic networks due to their huge impact on the remaining species in the system (Bascompte et al. 2003, Bascompte and Jordano 2006). For fleshy-fruited plant species in particular, this impact could be attributable to the higher seed dispersal effectiveness provided by core rather than peripheral frugivores. We found that core bird species had a higher quantitative component of that effectiveness than peripheral bird species. Future studies should elucidate if this difference in the quantitative component is also found in the qualitative component, which would include considering the seed treatment inside the mouth and gut of dispersers and the sites of seed deposition (Schupp et al. 2010). Only then, we will be able to conclude that core dispersers can be considered as one of the major factors influencing the diversification of the fleshy-fruited plant traits involved in these interactions.

Some of the plant species that were dispersed with a higher QC of seed dispersal effectiveness by core species make up the main structural matrix of the forest, given that they are understory shrubs, as well as subcanopy and canopy trees. The highest QC of seed dispersal effectiveness provided

by peripheral bird species was to fruits of the ‘epiphytes’ group, and corresponded to relatively specialized interactions. Particularly, peripheral species of the genus *Euphonia* had a relatively high QC of seed dispersal effectiveness when consuming fruits of the mistletoe species *Phoradendron falcifrons*. The *Euphonia*–*Phoradendron* relationship is a well-known specialized interaction (Wetmore 1914, Aukema and Martínez del Río 2002, Restrepo et al. 2002). It is increasingly being recognized that mistletoe-specialized birds have lower qualitative effectiveness than generalist birds, because they tend to deposit mistletoe seeds in host trees already parasitized, which increase the density-dependent competition and decrease the likelihood of mistletoe recruitment (Watson and Rawsthorne 2013, Mellado and Zamora 2014). On the other hand, core generalist species in this study, such as *T. sayaca* and *C. ophthalmicus*, dispersed a great amount of hemiparasitic and epiphytic cacti seeds. Thus, not only the quality of seed dispersal that specialists provide to hemiparasitic and epiphytic fruits could be lower than that given by generalists, but also the quantitative effectiveness in the seed dispersal of these fruits may be sometimes quite different.

Table 3. Characteristics of the six fleshy-fruited plant functional groups from the Austral Yungas in northwestern Argentina, obtained in a hierarchical clustering analysis. For categorical variables (i.e. 'Plant growth form' and 'Fruit color') is indicated the more representative state of the variable, and its frequency inside the group is in parentheses. For quantitative variables is shown the average value \pm the standard deviation, and the range is in parentheses.

	Group					
	'Epiphytes'	'Purple-fruited shrubs'	'Light-seeded trees'	'Piper'	'Morus-like'	'Heavy-seeded trees'
No. of species	10	16	17	3	5	14
Plant growth form	epiphytes (6) and herbs (3)	shrubs (11)	subcanopy (11) and canopy (3) trees	shrubs (3)	shrubs (3) and subcanopy trees (2)	subcanopy (10) and canopy (2) trees
Fruit colour	white (6)	dark purple-black (14)	dark purple-black (9) orange-red (6)	brown-yellow (3)	dark purple-black (5)	dark purple-black (7) orange-red (4)
Fruit weight (mg)	410 \pm 350 (80–1330)	180 \pm 90 (30–320)	140 \pm 100 (10–320)	2700 \pm 600 (2390–3350)	1430 \pm 500 (960–2150)	1000 \pm 600 (500–2800)
Fruit length (mm)	9 \pm 4.39 (5.1–20.6)	7.3 \pm 2.4 (4–12.8)	6.6 \pm 1.8 (3.5–10.2)	112.9 \pm 33.7 (84.1–150)	17.1 \pm 5.6 (11.5–25)	13.1 \pm 2.8 (9.1–17.5)
Fruit width (mm)	8.4 \pm 1.8 (5.5–10.9)	6.7 \pm 1.9 (4.1–12.3)	5.8 \pm 1.6 (3.1–8.3)	7.3 \pm 1.2 (6.3–8.6)	11.7 \pm 2.1 (8.5–14)	11.4 \pm 2.2 (8–16.9)
Seed number per fruit	52 \pm 56 (1–151.8)	16.8 \pm 21 (1–58.1)	2 \pm 1.9 (1–8.4)	423.3 \pm 166.7 (256.5–590)	128 \pm 69.7 (42.5–220.5)	9.5 \pm 29.7 (1–112.7)
Individual weight of seeds (mg)	7 \pm 17 (0.2–60)	5 \pm 6 (0.1–20)	26 \pm 19 (2–60)	1 \pm 2 (0.2–3)	1 \pm 1 (0.3–2)	276 \pm 212 (1–670)
Seed load per fruit (mg)	35 \pm 51 (3–170)	18 \pm 15 (3–50)	40 \pm 20 (2–80)	615 \pm 291 (280–800)	95 \pm 38 (60–150)	321 \pm 193 (100–670)
Water content of pulp (%)	89.2 \pm 2 (85.6–92.5)	84.4 \pm 6.9 (70.1–92.9)	60.3 \pm 22.5 (7.8–81.4)	67.8 \pm 13.2 (54.5–81)	86.7 \pm 5.7 (77.6–93.5)	72.7 \pm 9.5 (58.5–85.4)
Dry pulp weight per fruit (mg)	380 \pm 350 (100–1300)	160 \pm 100 (30–300)	100 \pm 80 (3–270)	2100 \pm 460 (1630–2550)	1330 \pm 460 (880–2000)	690 \pm 490 (230–2280)
Pulp/seed ratio	29.2 \pm 18.7 (2–63)	13.2 \pm 12.6 (3.2–53)	2.8 \pm 1.8 (0.2–6.4)	4.3 \pm 2.9 (2.1–7.5)	14.6 \pm 3.7 (11–20.8)	3 \pm 2.2 (0.5–7.8)
Amount of pulp per seed (mg)	40 \pm 40 (2–110)	30 \pm 30 (2–110)	60 \pm 60 (3–240)	10 \pm 4 (4–10)	10 \pm 5 (5–20)	500 \pm 400 (10–1580)

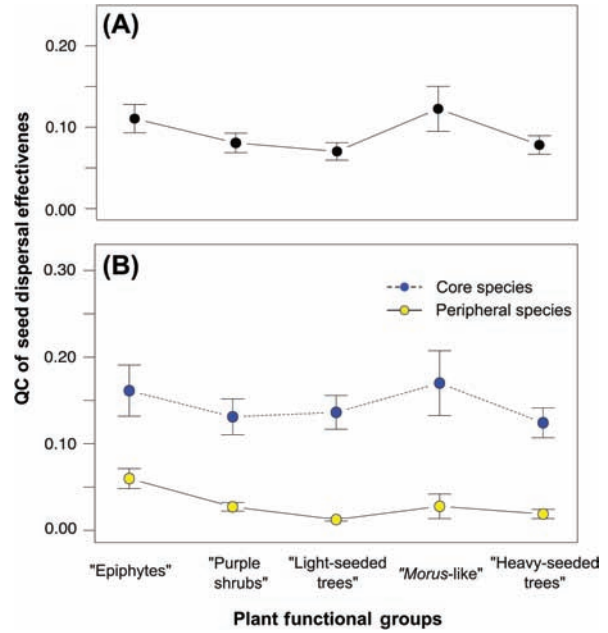


Figure 3. Quantitative component (QC) of the seed dispersal effectiveness for five of the six fleshy-fruited plant functional groups (Table 3) from the Austral Yungas, northwestern Argentina, provided by (A) the entire frugivorous bird assemblage, and (B) differentiated by core (blue) and peripheral (yellow) bird species. Circles and vertical black lines show the mean and standard errors of the QC of effectiveness.

The QC of seed dispersal effectiveness provided by *T. sayaca* to fruits in the *Piper* group represents an important link from the structural perspective of the network. Bats are the main dispersers of *Piper* spp. fruits in the Neotropics (Giannini 1999, Thies and Kalko 2004, Sánchez et al. 2012), and so, *T. sayaca* 'connects' the ornithochorous and the chiropterochorous modules of the seed-dispersal network. Frugivorous bird and bat species with large number of interactions connecting different modules in seed dispersal networks were also seen in the Peruvian Amazon (Mello et al. 2011) and in the Brazilian Atlantic Forest (Sarmiento et al. 2014). Multi-modular networks include a few 'supergeneralist' species or 'network hubs', which are important not only in their own module, but they also have a fundamental role in linking different network modules (Olesen et al. 2007). Given this cohesive function, supergeneralist species are of high priority conservation.

Core bird species of Austral Yungas include frugivores classified as mashers (Foster 1987). These have been considered poor dispersers because some seeds might be discarded below the maternal plant during feeding. This is especially true when fruits have one or a few big seeds (Levey 1987, Jordano and Schupp 2000). However, if fruits and/or seeds are small and the pulp is 'watery', such as most fruits occurring at Austral Yungas (Table 3), mashers can be as effective as gulpers in seed dispersal. Moreover, the existence of continuous differences in the QC of the seed dispersal effectiveness, which can be seen in the landscapes both for gulpers and mashers (Fig. 4), implies that fruit–frugivore interactions should be seen as a mutualism–antagonism gradient, and not as a discrete dichotomy (Wheelwright and

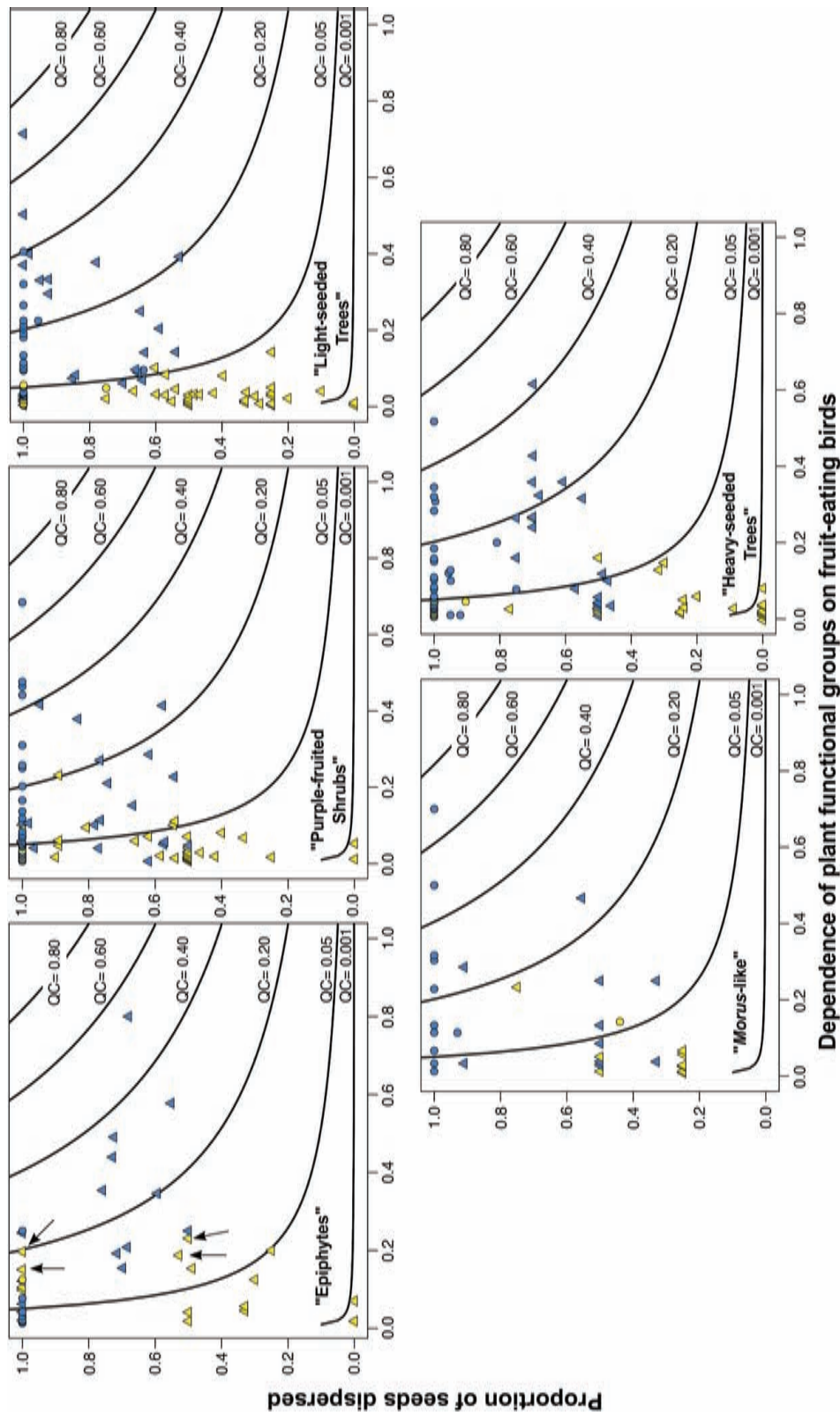


Figure 4. Landscapes of the quantitative component (QC) of seed dispersal effectiveness provided to fleshy-fruited plant functional groups from the Austral Yungas, northwestern Argentina. Isoclines represent spaces with an equivalent QC, based on the product of the dependence of the plant functional group on the seed dispersal provided by fruit-eating bird species and the proportion of seeds dispersed by those bird species, at each site. Colors denote core (blue) and peripheral (yellow) bird species; shapes depict the fruit-handling method most used by a bird species: 'gulpers' (circles) and 'mashers' (triangles). Arrows in the 'epiphytes' group point at the QC of seed dispersal effectiveness provided by *Eiphonia* species (*E. cyanocephalus* up and *E. chloritica* down).

Orians 1982, Hulme 2002, Heleno et al. 2011). The understanding of this gradient can be complex because the QC of seed dispersal effectiveness provided by a given bird species can vary in space and time, depending on the local context of ripe fruit species. Thus, the QC of the seed dispersal effectiveness or the frugivorous role needs to be viewed with caution when based only on the feeding methods more often used by a frugivorous species, and the importance of mashers needs to be re-assessed across geographic space and context. At the same time, our results highlight the importance of considering a network framework to address robust conclusions about the role of a given frugivorous species in the seed dispersal of plants in local communities.

Core plant species belonged to five different functional groups. This means that core plant species enclosed a wide spectrum of life forms, fruit colors, seed number and size, pulp mass, water content, etc. Therefore, considering the morphological characteristics used in this study, there seems to be no particular traits of plants that could be associated to their role as core species in the network. On the other hand, core bird species were part of a relatively homogeneous assemblage, at least in terms of body size and bill morphology (R. A. Ruggera unpubl.). This is, despite the occurrence of a few big-sized frugivores – such as toucans, trogons, guans, doves and woodpeckers – frugivore diversity and interactions mainly involved small to medium-sized passerines (Supplementary material Appendix 2 Table A1). Thus, even though our study system has been extensively explored, we are still not able to determine which biological traits make a plant or bird species as part of the network core.

Temporal variation in fruit resources and seasonal migration of bird species can lead to changes in the core species identity and/or in the interaction frequency and links between plants and birds (Alarcón et al. 2008, Blendinger et al. 2008, Carlo and Morales 2008, Carnicer et al. 2009). Our results are only from the rainy season, when most plants have their fruiting peak (Boletta et al. 1995). Other fruit-eating bird species (and of course, other fruiting plant species too) may become core species during the dry season. Some of the birds identified as core species here have migratory movements (Malizia 2001, Capllonch and Lobo 2005). Despite this, we do not expect drastic changes in the identity of core species in successive years (Jordano and Schupp 2000, Burns 2006), as those observed in mutualisms with insects (Alarcón et al. 2008, Petanidou et al. 2008), given the deep differences in their population dynamics. Instead, cyclic and almost repetitive replacements in the core species identity are likely to occur throughout the years.

The importance of a detailed knowledge of interaction networks for species conservation and environmental restoration programs has been increasingly recognized (Bascompte and Jordano 2006, Cadotte et al. 2011, Montoya et al. 2012). The knowledge not only of core species identity, but also of which species are the most effective seed dispersers, as well as the environmental contexts in which this happens, would economize effort and resources for conservation. It allows focus of conservation and restoration actions on a few species and their interactions, which will also favorably impact the remaining species building up local and regional networks.

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Supplementary material (available online as Appendix oik-02204 at <www.oikosjournal.org/appendix/oik-02204>). Appendix 1–4.