Frugivores at higher risk of extinction are the key elements of a mutualistic network

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Abstract. Most tree species rely on vertebrates for seed dispersal, and many vertebrates use fruits as food resources in tropical forests. Therefore, plant–frugivore interactions affect population dynamics and persistence in ecological communities. Plant–frugivore interactions often involve many species, forming networks of interacting plants and animals that play different roles in determining network organization. The network organization is the way interactions are structured in the community, which may have consequences for its ecological and evolutionary dynamics. Some species have greater influences on network organization and may be particularly important to species persistence. We identified the frugivores most important to the organization of networks of plants and frugivorous birds in three contiguous Atlantic forest sites in southeastern Brazil. We found that the species that contributed most to network organization were at higher risk of extinction. Among the main contributors to network organization were two cotingas and a toucan, large-bodied species that disperse seeds from many plants and are particularly vulnerable to habitat loss and hunting. As a consequence, ongoing extinctions may significantly affect the organization of plant–frugivore interactions in the studied system. We hypothesize that the crucial role of some threatened frugivores may occur in other seed dispersal systems in tropical communities, although the association between structural importance and degree of threat may be contingent on peculiarities of local communities and disturbances.

Key words: *Atlantic forest; extinction risk; frugivory; fruit-eating birds; interaction networks; modularity; mutualisms; nestedness; seed dispersal; southeastern Brazil; species roles; tropical rain forest.*

INTRODUCTION

In tropical ecosystems, seed dispersal by vertebrates is crucial. In fact, vertebrates disperse seeds from 70% to 94% of all woody species in tropical rain forests (Jordano 2000). The ongoing biodiversity loss may disrupt seed dispersal interactions (Hansen and Galetti 2009), and local extinctions of fruit-eating birds and mammals are major threats to the persistence of tropical tree populations (Silva and Tabarelli 2000). Declining plant populations may, in turn, negatively affect the populations of other seed dispersers, because fleshy fruits are critical food resources for many vertebrates (Jordano 2000). Therefore, the consequences of species extinction depend on the organization of interacting

assemblages (Tylianakis et al. 2010; but see Carlo and Yang 2011). In this context, it is a major challenge for conservation biology to infer the relative importance of endangered species to species-rich interacting assemblages.

Patterns of interaction are mediated by biological factors of both interacting organisms. For example, abundance affects the occurrence and frequency of interactions, so that abundant species will interact more frequently and with more species than do rare species (Vázquez et al. 2009). However, other factors are important in determining the organization of interacting assemblages, such as species' diets (Krishna et al. 2008) and phenological and morphological traits (Stang et al. 2006, González-Castro et al. 2012). In this way, species importance to the organization of frugivory systems may be related to biological attributes shaping interactions.

The network approach provides ways to characterize the patterns that emerge when pairwise interactions are considered together (Proulx et al. 2005). It is possible to describe the organization of networks of interacting species and the role of particular species in structuring these species-rich assemblages (Bascompte and Jordano 2007). For instance, plant–frugivore networks are often nested (Bascompte et al. 2003), a pattern in which species with few interactions interact with a subset of species that also interact with species with many interactions. Nestedness may improve species persistence in mutualistic networks (Thébault and Fontaine 2010; but see Allesina and Tang 2012). Some plant–frugivore networks are also modular, a pattern in which species are organized in semi-independent groups (Mello et al. 2011). Modularity is assumed to increase stability, because disturbances cascade more slowly through modular networks than through non-modular networks (Olesen et al. 2007, Tylianakis et al. 2010).

Nestedness and modularity represent network-level patterns to which each species may contribute differentially (Olesen et al. 2007, Almeida-Neto et al. 2008). These distinct structural roles are not only important to the organization of community-wide interactions, but also they may allow identification of the species that most affect species persistence in ecological networks (Saavedra et al. 2011, Stouffer et al. 2012). Thus, a central question in conservation biology is whether species important to the organization of ecological networks are at higher risk of extinction. We studied three networks of plants and fruit-eating birds in the Atlantic forest of southeastern Brazil, one of the most threatened biodiversity hotspots (Metzger 2009). We combine descriptors of interaction patterns at the species level in a single index, expressing the importance of each species to network organization. We use this index to identify the most important species, relating their structural contribution with biological traits. Finally, we report that the bird species contributing the most to network organization are at higher risk of extinction.

METHODS

We studied the networks of interacting plants and frugivorous birds in three different sites in the Atlantic rain forest, collecting data between 1999 and 2002. All sites are at Parque Estadual Intervales (PEI), a 41 704-ha protected area surrounded by reserves that together encompass more than 120 000 ha of continuous forests in southeastern Brazil (FF/SMA-SP 2008). The three studied sites are at 980 m, 847 m, and 597 m altitude (Hasui 2003), hereafter identified as "hilltop," "middle slope," and "bottom of valley," respectively. The three sampled sites are in mature forest, exhibiting high avian species diversity, with species (especially frugivorous birds) typical of undisturbed areas (Vielliard and Silva 2001).

We characterized traits of interacting bird and plant species. By placing mist nets in the three study sites, one of us (EH) captured birds and measured their body mass and bill dimensions, besides collecting fecal material (see methods details in Appendix A). To estimate plant abundance and phenology, EH placed plots where all endozoochorous plants were marked and monitored for one year. Bird-dispersed plant species were characterized for seed morphology. We used information on abundance of bird species from our "bottom-of-valley" site (Vielliard and Silva 2001), where exhaustive bioacoustics sampling provided an abundance index for a number of bird species (details in Appendix A). We also classified all bird species regarding their degree of frugivory (high and low) based on the frequency of fruits/seeds in fecal samples.

Interaction data were obtained by direct observation of the foraging behavior of canopy and understory birds: EH walked along trails and recorded every time a bird was observed feeding on fruits as a feeding bout. Sampling area was similar in each site, where we collected interaction data for one year, with sampling performed for about two hours, five days per month, totaling 120 h of sampling effort per site. From the recorded feeding bouts, we built plant–frugivorous bird networks for each site. We included in the networks only bird species observed feeding on fruits. Accordingly, only plant species whose fruits were consumed by birds were included in the networks.

For the three interaction networks, we explored two patterns: nestedness and modularity. We assessed nestedness by computing NODF (Almeida-Neto et al. 2008), a metric that also permits the contribution of each species to nestedness (n_i) to be estimated, based on overlap and decreasing fill. Modularity (M) was estimated using a simulated annealing optimization procedure (Guimerà and Amaral 2005). We recorded the species' roles in modularity by computing (1) the standardized within-module degree (z_i), which is a measure of the extent to which each species is connected to the other species in its module, and (2) the among-module connectivity (c_i), which describes how evenly distributed are the interactions of a given species across modules (Appendix B). We performed null model analyses to assess whether heterogeneity in the number of interactions could generate the observed patterns of nestedness and modularity. The null model generates networks in which the probability that two species will interact depends on the number of interactions of both species in the real network (Bascompte et al. 2003). The null model also allows control of the effects of bipartivity on modularity index, which was originally designed for one-mode networks, by generating theoretical networks with the same bipartite structure (Pires et al. 2011). We described the role of each species in the network using n_i, z_i, c_i, and the number of interactions (k_i). To allow pooling of the

TABLE 1. Descriptors of the three interaction networks (hilltop, middle slope, and bottom of valley) between plants and frugivorous birds in a well-preserved Atlantic forest remnant in southeastern Brazil.

Descriptor	Hilltop	Middle slope	Bottom of valley
Species richness			
Birds	37	31	44
Plants	32	30	42
Mean no. interactions			
Birds	2.54	3.06	3.68
Plants	2.94	3.17	3.86
Connectance	0.08	0.10	0.09
Nestedness, NODF			
Birds	23.69	22.11	19.42
Plants	17.66	19.44	14.65
Total (observed)	21.12	20.82	17.15
Total (null model)	12.66	15.08	12.65
Modularity, M			
Observed	0.55	0.48	0.45
Null model	0.55	0.50	0.48

Note: NODF is a nestedness metric based on overlap and decreasing fill.

information from the three sites, we standardized the data by calculating the z scores for each value of k_i, n_i, c_i, and z_i, subtracting from these variables the mean value of each group (birds or plants) at each site, and dividing the result by the standard deviation. Whenever a species was recorded at a different site, we used the average of the standard values calculated. Each metric estimates the importance of the species to one particular aspect of network organization; however, they are correlated, indicating that the species have similar importance in distinct aspects. We performed a principal component analysis (PCA) on the correlation matrix among k_i, n_i, z_i, and c_i values, for birds and plants separately. We used the first principal component to synthesize the species' contributions to connectivity, nestedness, and modularity in one descriptor of its structural role (Sazima et al. 2010). Further, we explored the biological correlates of species' contribution to network structure. We performed linear regression analyses between species' contribution to network structure and bird traits (body mass, bill dimensions, degree of frugivory, and local abundance) and plant traits (seed size, fruit size, length of fruiting period, and local abundance). We also evaluated the relationship between bird taxonomy and species' contribution to network organization (Appendix A), by performing randomization tests (1000 randomizations; Manly 1997).

We classified all bird species by IUCN (2012) conservation status. We combined endangered, vulnerable, and near-threatened species into a single "higher risk" category, because it includes species at high risk of extinction in the wild or species that could become threatened in the near future. All species classified as "least concern" were treated as "lower risk," because this classification includes widespread and abundant taxa (IUCN 2012). We also used an alternative classification of bird sensitivity to human disturbances, based on Stotz et al. (1996); see Appendix C. We explored the relationship between bird extinction risk and species' contribution to network organization by performing a two-sample randomization test (Manly 1997). We randomized the species' contribution to network organization between the two categories of extinction risk (1000 randomizations) and calculated the proportion of the differences of means that were equal to or greater than the observed difference of means. We performed similar randomization tests to investigate if higher- and lower-risk threat categories differed in mean traits of species (body mass, bill dimensions, local abundance, and degree of frugivory) and to investigate how evenly distributed was the extinction risk across bird families. We computed the probability that a given family would have so many (or so few) species threatened by chance (Appendix A).

RESULTS

The number of frugivorous bird species was slightly higher than the number of plant species at all three sampled sites (hilltop = 37 bird and 32 plant species; middle slope = 31 bird and 30 plant species; bottom of valley = 44 bird and 42 plant species). As observed in other species-rich networks, the proportion of all possible interactions that were actually observed (i.e., connectance) was markedly low in all sites (hilltop = 0.08, middle slope = 0.10, bottom of valley = 0.09). In fact, each plant species, on average, interacted with 3.28 ± 3.41 bird species (mean ± SD), and each bird species interacted with 2.95 ± 1.90 plant species. Rarefaction analysis showed that network structure was robust to sampling intensity (Appendix D).

All three networks were significantly nested ($P < 0.05$ in all cases; Table 1). On the other hand, the modularity of all networks was similar to the modularity expected from the observed heterogeneity in the number of interactions across species ($P > 0.50$ in all cases; Table 1). This latter result suggests that species' contribution to network modularity is strongly associated with the species' number of interactions. Indeed, k_i, n_i, z_i, and c_i were almost always positively correlated among themselves for both birds and plants (Pearson's $r > 0.47$, $P \leq 0.0001$ in all cases except the correlation between n_i and z_i in birds, which is $r = 0.256$ and $P = 0.0504$; Appendix B: Table B1). The positive relationship among those variables means that species with many links tend to establish interactions both within and among modules and to exhibit a greater contribution to nestedness. The first principal component (PC1) resulting from the PCA was positively associated with k_i, n_i, z_i, and c_i, retaining
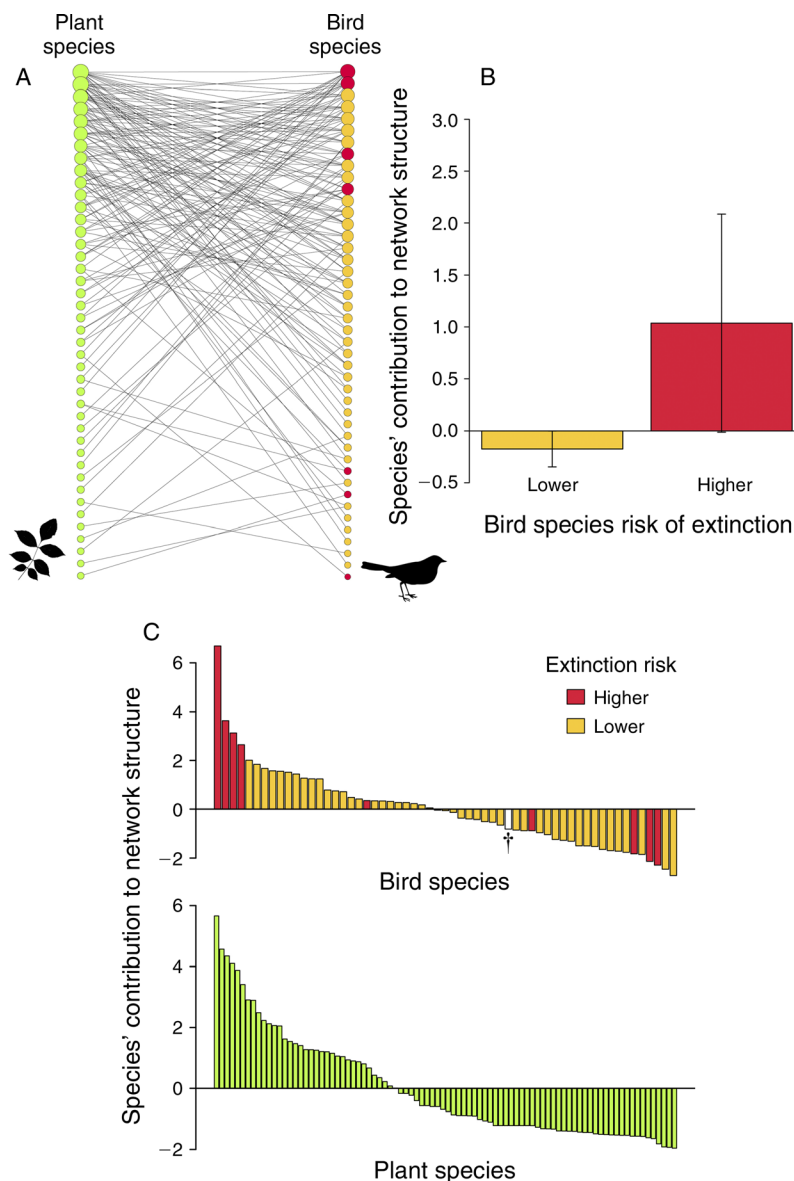
Fig. 1. (A) Plant–frugivore network from the bottom of valley site. Node sizes (circles) are proportional to species' contribution to network structure, which is composed by metrics that characterize the patterns of interaction of each species in the network (for details, see *Methods*). Green nodes depict plant species; orange and red nodes are lower-risk and higher-risk bird species, respectively. (B) Bird species' contributions to network organization (mean ± SE) by risk of extinction (lower vs. higher risk). (C) Bird and plant species' contribution to network organization, with values pooled from the three Atlantic rain forest sites (details in *Methods*). Species are arranged in order of decreasing contribution to network organization. In the top panel (birds), species are discriminated by their extinctions risk (higher vs. lower risk, according to IUCN). The dagger symbol (†) and open bar indicate a species identified only to the genus level; consequently, we were not able to classify its risk of extinction.

much of the information provided by network measurements for both birds (69.6%) and plants (76.6%). PC1 was used as a new variable summarizing species' contribution to network organization. The PC1 scores assigned to each species correspond to its contribution to network organization, such that higher scores indicate greater contributions to all analyzed structural aspects of network organization (Fig. 1A).

Combining data from the three networks, we found a total of 88 plant species and 59 bird species, nine of which were at higher risk of extinction (Appendix F: Table F1). Species' contributions to network organization were distributed more evenly among plants than among birds (Fig. 1C). The plants most important to network organization were *Miconia pusilliflora* (Melastomataceae), *Coussapoa microcarpa* (Urticaceae), *Myr-*

cia fallax (Myrtaceae), and *Miconia theaezans* (Melastomataceae). Four bird species, all of which are "near-threatened," exhibited markedly high values of contribution to network topology (Fig. 1C): *Carpornis cucullata* (Cotingidae) was the bird species with the greatest contribution, followed by *Lipaugus lanioides* (Cotingidae), *Thraupis cyanoptera* (Thraupidae), and *Pteroglossus bailloni* (Ramphastidae). On average, species that contributed more to network organization were at higher risk of extinction (Fig. 1B; $P = 0.025$), although some higher-risk species showed markedly smaller contributions to network structure (e.g., *Pipile jacutinga*, Cracidae). These results are consistent with similar analyses using another classification of birds' sensitivity to human disturbances (Appendix C).

None of the bird traits that we investigated (body mass, bill dimensions, degree of frugivory, and local abundance) was significantly related to species' contribution to network structure (Fig. 2C, D; Appendix A: Table A1, Fig. A1). In contrast, seed size was negatively related to structural importance (for seed width, $R^2 = 0.067$, df = 1, 76, $F = 5.4$, $P = 0.022$; for seed length, $R^2 = 0.057$, df = 1, 76, $F = 4.6$, $P = 0.035$), whereas the fruiting period length was positively related to species' contribution to network structure ($R^2 = 0.106$, df = 1, 40, $F = 4.7$, $P = 0.036$; Fig. 2A, B; Appendix A: Table A1, Fig. A2). We found that higher-risk bird species are larger (log-transformed body mass) than lower-risk bird species ($P = 0.007$; Appendix A: Table A2). Accordingly, there is a tendency for higher-risk bird species to have wider bills, although the relationship was not significant ($P = 0.058$; Appendix A: Table A2). Bird families did not differ in their mean contribution to network organization (Appendix A: Table A3). However, we found that one family, Cotingidae, has more higher-risk species (four species) than would be expected by chance ($P = 0.004$; Appendix A: Table A4).

DISCUSSION

Theory associates nestedness with greater resilience to species loss (Bascompte and Jordano 2007, Thébault and Fontaine 2010) due to the core of generalist species that characterize nested networks. Thus, the nested pattern found in the three studied networks suggests that interactions among plants and fruit-eating birds in the Atlantic forest show some robustness to random species extinctions. We also found that highly connected species are the most important contributors to different aspects of network organization, linking different groups of species in the network and promoting nestedness (Olesen et al. 2007). Highly connected species in nested mutualistic networks may favor the long-term species persistence (Saavedra et al. 2011; but see Allesina and Tang 2012); however, nested networks may be very fragile if generalist species die out (Memmott et al. 2004). Highly connected species are also crucial components of modular organization, connecting distinct modules (Olesen et al. 2007). The loss of such network hubs may have important consequences for ecological and evolutionary dynamics. For instance, the extinction of highly connected species may lead to co-extinctions (Solé and Montoya 2001, Memmott et al. 2004) and possibly affect the evolutionary dynamics of the whole network (Guimarães et al. 2011). Nevertheless, empirical evidence associating nestedness and persistence or evolutionary dynamics of interacting populations is still lacking. Future studies integrating natural history with network analysis are necessary to assess whether predictions based on network organization hold when incorporating information on the biology of interacting species. For now, our results call attention to the relevance of highly connected species to network organization and, potentially, to network dynamics (González-Castro et al. 2012).

Our results indicate that plant species with smaller seeds and longer fruiting period tend to be more important to network organization. Indeed, the most important plant species (*Miconia pusilliflora*, *Coussapoa microcarpa*, *Myrcia fallax*, and *Miconia theaezans*; Appendix E) bear small fruits that do not constrain consumption by small-gaped birds (Hasui et al. 2009) and their fruiting phenology may favor their attractiveness to frugivorous birds. *C. microcarpa* and *M. fallax* have synchronic massive fruiting, with many individuals bearing ripe fruits for one or two months (Hasui 2003), increasing their attractiveness to frugivorous birds, whereas *M. pusilliflora*, as for other *Miconia* species, has a long and asynchronous fruiting period ensuring frugivore fidelity (Hasui 2003, Maruyama et al. 2007) and plant importance to frugivorous birds (Galetti and Stotz 1996). All of these species belong to plant families that are important to frugivorous birds throughout the neotropics (Snow 1981). Myrtaceae and Melastomataceae are two dominant families in the Atlantic rain forest (Pizo 2002) and are common in all studied sites. Additionally, Urticaceae species are common in forest understory and edges (Gaglioti 2010). Some species from these plant families are also dispersed by frugivores other than birds (Appendix E). Given their dominance and generalist interactions, the key plant species are likely to be resilient network components. The same is not true of birds.

Among birds, species widely regarded as important frugivores are important in structuring the networks. The cotingas *Carpornis cucullata* and *Lipaugus lanioides* heavily rely on fruits in their diets, dispersing a variety of plant species (Pizo et al. 2002), as does *Pteroglossus bailloni* (Galetti et al. 2000). In the studied sites, these three species consume a wide variety of fruits, primarily large-seeded fruits (Hasui et al. 2012), playing an important role in seed dispersal for these plant species. In addition, *Thraupis cyanoptera*, the species with the

third-greatest contribution to network organization, consumes fruits of very different sizes (Hasui et al. 2012). Despite its smaller gape width, *T. cyanoptera* can crush fruits externally (Levey 1987) to consume fruits that are larger than its bill. The importance of *T. cyanoptera* corroborates the role of thraupid birds as important seed dispersers in plant–frugivore networks (Schleuning et al. 2014). All of these species are considered near-threatened because populations are declining due to habitat loss, degradation, and/or hunting and capture (IUCN 2012). Therefore, the four bird species that contribute most to the organization of the studied plant–frugivore networks are those threatened by human activities, which is surprising, given the fact that only 15.5% of all recorded birds are at higher risk of extinction. These four threatened species drove the differences between the mean contribution to network organization of higher-risk and lower-risk species, as shown by the two-sample randomization test.

An important question is what makes these species strong contributors to network organization? We have not detected consistent effects of body mass, bill dimensions, abundance, or of the degree of frugivory on network contribution, suggesting that species-specific traits of the birds may explain their key position in the network. For example, some of these near-threatened species, such as *Carpornis cucullata* and *Lipaugus lanioides*, are still locally abundant in the study area and may be important contributors due to numerical effects (Vázquez et al. 2009). In contrast, we hypothesize that the strong contribution of some locally rare, threatened species such as *P. bailloni* and *T. cyanoptera* may be related to their highly frugivorous diet. The degree of frugivory is known to mold the numerical effects of relative abundances on network organization (Krishna et al. 2008). Finally, it is worth noting that some birds at higher risk of extinction have a low contribution to network organization. For example, *Pipile jacutinga*, despite being highly frugivorous, is now reduced to very low densities (Galetti et al. 1997).

Large-bodied birds, such as *C. cucullata*, *L. lanioides*, and *P. bailloni*, are especially vulnerable to hunting and land use change (Wright 2007). Indeed, higher-risk species in the studied networks tend to be larger and have wider bills than lower-risk species. In addition to the greater range of seed sizes that they can ingest, large birds can also provide long-distance dispersal (Wotton and Kelly 2012), being functionally important in seed dispersal networks (Vidal et al. 2013). Widespread habitat loss and fragmentation, hunting, and other anthropogenic pressures in the Atlantic rain forest may lead to significant declines in bird populations, with important shifts in community composition (Banks-Leite et al. 2012). Such changes can lead to major changes in the structure and dynamics of plant populations through the disruption of processes such
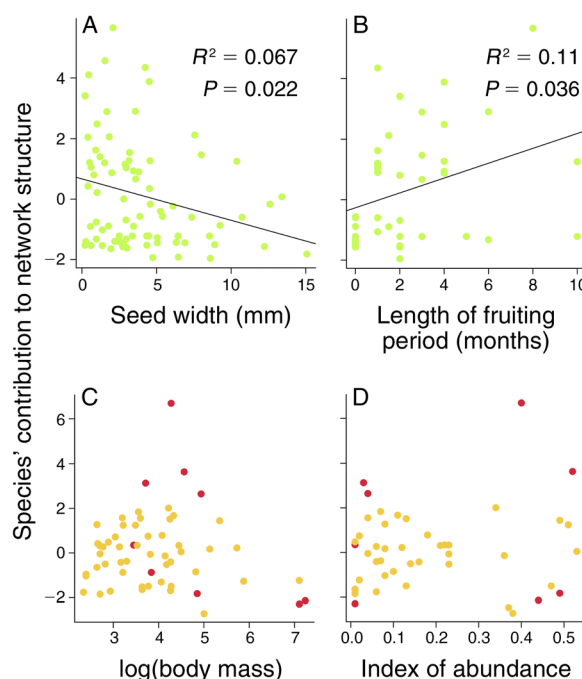

FIG. 2. Effects of biological traits of (A, B) plants and (C, D) birds on species' contribution to network structure. (A) Seed width and (B) length of fruiting period are significantly associated with plant species' contribution to network structure. In contrast, (C) body mass and (D) abundance are not related to bird contribution to network structure; red dots depict higher-risk bird species and orange dots represent lower-risk bird species.

as seed dispersal (Silva and Tabarelli 2000). Moreover, the observed relationship between the importance of a given species to network organization and its extinction risk, although contingent on particular traits of both the site and the plant–frugivore assemblages, may be found in other natural communities. Conservation practices should consider the network of interactions that underpins plant and animal communities, giving special consideration to endangered species that are key to network structuring.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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