



## Generalist Species Have a Central Role In a Highly Diverse Plant–Frugivore Network

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### ABSTRACT

Analysis of plant–frugivore interactions provides a quantitative framework for integrating community structure and ecosystem function in terms of how the roles and attributes of individual species contribute to network structure and resilience. In this study, we used centrality metrics to rank and detect the most important species in a mutualistic network of fruit-eating birds and plants in a cloud forest in the Colombian Andes. We identified a central core of ten bird and seven plant species in a network of 135 species that perform dual roles as local hubs and connectors. The birds were mostly large forest frugivores, such as cracids, cotingas, and toucans, which consume fruits of all sizes. The plants were species of intermediate successional stages with small- to medium-sized seeds that persist in mature forest or forest borders (e.g., *Miconia*, *Cecropia*, *Ficus*). We found the resilience of our network depends on super-generalist species, because their elimination makes the network more prone to disassemble than random extinctions, potentially disrupting seed-dispersal processes. At our study site, extirpation of large frugivores has already been documented, and if this continues, the network might collapse despite its high diversity. Our results suggest that generalist species play critical roles in ecosystem function and should be incorporated into conservation and monitoring programs.

Abstract in Spanish is available with online material.

**Key words:** Andean forests; community ecology; seed dispersal.

IN MUTUALISTIC NETWORKS, TWO SETS OF SPECIES DERIVE MUTUAL BENEFITS FROM THEIR INTERACTION (Bascompte & Jordano 2014). An important mutualistic network is exemplified by plant–frugivore interactions in tropical forests, where fruit-eating vertebrates disperse the seeds of up to 90 percent of plants (Howe & Smallwood 1982). In these networks, a set of frugivore species obtain food by consuming the fruits of a set of plant species, in turn acting as seed dispersers. Each species from one set, known as a node, may interact with one or more species from the other set, with interactions constituting links between the two sets. Mutualistic networks are characterized by a skewed distribution of links, with a majority of species having few links and a few species being highly connected (Vázquez *et al.* 2009). The topology and distribution of the number of links among interacting species generate different network configurations (Thébault & Fontaine 2010). Most networks have a nested structure, in which specialist species only interact with subsets of generalist species (Bascompte *et al.* 2003). In addition, they present a modular structure, such that species within a cluster have more interactions among the cluster than with species of other clusters (Olesen *et al.* 2007).

In highly diversified mutualistic assemblages, a few central species strongly influence the dynamics and shape the ecology of the entire community (Guimarães *et al.* 2011). Because species

vary in their ecological attributes and perform different roles in networks (Stouffer *et al.* 2012), centrality metrics are a useful tool for assessing the relative importance of each species at different levels of network organization, especially at the local scale of immediately interacting partners and at meso-scale and network-scale chains of interactions that consider indirect relationship spreading across the network (Estrada 2007, Jordán 2009). For instance, some species might be local hubs in their own modules, whereas others play a role as connectors to other parts of the network (Olesen *et al.* 2007). Furthermore, species may be ranked according to each of these measures to choose targets for conservation efforts. Such target species may also serve as proxies to evaluate changes occurring in ecosystems such as habitat loss, fragmentation, and climate change (Tylianakis *et al.* 2008).

We studied the mutualistic interaction network of fruit-eating birds and plants in a cloud forest in the Andes of Colombia, where species richness of frugivorous birds and fleshy-fruited plants are at a global maximum (Kissling *et al.* 2009). We identified central species that act both as local hubs and global connectors, forming the core of generalists in the network, or super-generalists. These highly connected species are essential for network cohesion, because their elimination may lead to cascades of secondary extinctions, with an impact on the integrity of the entire network (Memmott *et al.* 2004, Kaiser-Bunbury *et al.* 2010). Hence, our study identifies a group of species in a highly diverse community that may have a strong impact on the entire

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bird and plant assemblage of interacting species. We describe the nature and vulnerability of super-generalists and the potentially far-reaching consequences their loss may have for such a critical ecosystem function as seed dispersal.

## METHODS

**STUDY SITE.**—We conducted the study in the cloud forest of San Antonio-km 18, on the Western Cordillera of the Colombian Andes on the Cali-Buenaventura road. The total area was approximately 700 ha at elevations of 1800–2200 asl (Fig S1). Mean annual temperature is 16°C. The rainfall regime is bimodal with a mean annual precipitation of 1967 mm and peaks of precipitation occurring in April–May and October–November. The site is an Important Bird Area according to BirdLife International (IBA – CO100) and is a forest reserve that protects an important watershed for the city of Cali. The forest in this region was subjected to strong fragmentation in the first half of the previous century (Kattan *et al.* 1994) but thanks to ongoing conservation efforts, forest vegetation has recovered and at present, the area is a relatively well-connected mosaic of successional stages from early second growth to mature forest, with clearings created by small farms and suburban houses.

**DATA COLLECTION.**—To record plant–bird interactions, we walked at a slow pace on pre-existing trails from 0.5 km to 3.7 km long, covering both edge and forest interior, as well as different successional stages and disturbances representative of the area. We noted fruit consumption events with spot censuses, as birds were encountered along the trails. We aimed to maximize the number of interactions recorded in the study area. At the spatial scale of our study, the forest can be considered a homogeneous unit in terms of species composition, structure, and functional properties, with the natural mosaic variation typical of a tropical forest.

Our sampling method is appropriate for areas of high species diversity, where most plants have low visitation rates and the use of focal observations is impractical. This method maximizes the chance of detecting rare consumption events (P. Jordano pers. comm.). It also indirectly incorporates information on species abundances, which is proportional to the number of interactions (Vázquez *et al.* 2009). Thus, the results represent the ‘real’ network structure, *i.e.*, a structure not biased by sampling artifacts (Vázquez *et al.* 2009, Gibson *et al.* 2011). We conducted observations during June–November 2013, encompassing both a dry and wet season, for a total of 16 wk and at a sampling intensity of 512 h. We performed two daily monitoring sessions (0600–1100 and 1500–1800 h), alternating sessions in trails each week. We included all bird species eating fruits, considering them to be potential seed dispersers (Schupp *et al.* 2010).

We characterized bird species according to their ecological and morphological traits, classifying them according to their degree of diet specialization as obligate, partial, and opportunistic frugivores (Kissling *et al.* 2009). Obligate frugivores eat fruits most of the time (>50% of diet, Fleming *et al.* 1987), partial frugivores have fruits as an important component of their diet

and opportunistic frugivores consume fruits only occasionally (*i.e.*, insectivores, nectarivores, granivores). We compiled information about bird body mass from published sources (*e.g.*, Dunning 2008). We selected body mass because it is highly correlated with bill gape, which influences the sizes of fruits that may be eaten by each species (Wheelwright 1985) and allows results for mutualistic networks to be generalized.

We characterized plant species with the following ecological and morphological attributes: life-form, successional stage, and fruit diameter (mm). We measured the diameter of 5–10 fruits from 2 to 10 plants of each species and calculated the weighted average. The complete data set for both plants and birds can be found in Appendix S2.

**DATA ANALYSIS.**—To analyze network structure, we compiled a binary (presence–absence) adjacency matrix  $A_{ij}$ , where birds are arranged in  $i$  rows and plants in  $j$  columns. A fruit consumption interaction between a plant and bird species received a value of 1, while a value of 0 indicates no interaction. To assess the sampling completeness of the network, we computed an accumulation curve with the number of interactions as a function of sampling effort, using 100 iterations with EstimateS 9.1 (Colwell 2013). We then used the non-parametric estimator Chao 2 to calculate the percent asymptotic interaction richness following Chacoff *et al.* (2012):

$$\%S_o = 100 \frac{S_o}{S_E}$$

Where  $S_o$  are the observed interactions and  $S_E$  is the richness estimated with Chao 2.

We evaluated nestedness using the NODF metric based on overlaps and decreasing fill (Almeida-Neto *et al.* 2008) implemented in the program ANINHADO 3.0 (Guimarães & Guimarães 2006). NODF values may vary from 0 to 100, where values close to 100 indicate highly nested matrices. We calculated statistical significance by comparison to a null model, generating 1000 random matrices of the same size in our network, where the probability of interaction between a bird and a plant species is proportional to their total number of interactions (Bascompte *et al.* 2003). To assign a cutoff value and to separate generalists from peripheral species, we used the formula proposed by Dáttilo *et al.* (2013) to find the generalist core of species with more interactions in our network:  $G_c = (\bar{k}_i - \bar{k}_{\text{mean}})/\sigma_k$ , where  $\bar{k}_i$  = mean number of links for a given bird or plant species,  $\bar{k}_{\text{mean}}$  = mean number of links for all bird or plant species in the network, and  $\sigma_k$  = standard deviation of the number of links for bird or plant species.  $G_c > 1$  are species of the generalist core, and  $G_c < 1$  are peripheral species. We also computed an adjusted boxplot that better represents the skewed distribution of the species degrees (Hubert & Vandervieren 2008).

We detected modularity with the program MODULAR (Marquitti *et al.* 2014). We performed 1000 iterations with a simulated annealing algorithm that uses a global optimization procedure to maximize the modularity function  $M_B$  proposed by

Barber (2007). Traditionally, module detection has relied on functions developed for one-mode networks (Guimera & Amaral 2005) and their performance on bipartite configurations may not be the most appropriate. By contrast, the function  $M_B$  is designed specifically for bipartite networks and better detects modularities in presence-absence matrices (Thébault 2013). This function is calculated as:

$$M_B = \sum_{i=1}^{N_m} \frac{L_i}{L} - \left( \frac{k_i^C - k_i^R}{L^2} \right)$$

Where  $N_m$  is the number of modules,  $L$  the number interactions in the whole network,  $L_i$  the sum of interaction in the module  $i$ ,  $k_i^C$  the sum of interactions in the module  $i$  that belong to the plant set  $C$  and  $k_i^R$  the sum of interactions in the module  $i$  that belong to the bird set  $R$ .

We estimated the significance of  $M$  by generating 1000 random matrices using the same null model as in nestedness. Due to its heuristic nature, the algorithm exhibits degenerate solutions when classifying nodes in different groups. Therefore, we ran the algorithm 25 times and combined information from the different partitions generated to assign species to a specific module (Good *et al.* 2010). We found species that clustered together in different partitions, called cores, to augment confidence in the generated modules. For this, we used the program Coral (Filippova *et al.* 2012), which allows different partitions to be compared both visually and quantitatively. The program works by calculating the cores using a dynamic algorithm and generating a co-clustering matrix to visualize the results. We performed a Kruskal–Wallis test to compare median body mass and fruit diameter among species modules.

We assessed the functional role of bird and plant species using three centrality metrics (Degree, Betweenness, and Closeness) that are ecological surrogates of each species' importance in the community (Martín González *et al.* 2010). Degree centrality (DC) is a measure of the number of interactions of a given species, reflecting its degree of generalization *vs.* specialization. Betweenness centrality (BC) measures the extent to which a species acts as a connector on the lowest number of direct or indirect interactions among other pairs of species. A species with high BC connects modules of interacting species that otherwise would be highly unconnected. Closeness centrality (CC) is the mean of the lowest number of direct or indirect interactions from one species to every other species in the network, with higher numbers yielding lower CC scores. Species with high CC scores act as local hubs and are responsible for cohesiveness within networks. DC works at the local level, while BC and CC are meso-scale measures that consider indirect relationships that spread across the network (Jordán 2009). We computed the indices using Pajek 3.14 (Batagelj & Mrvar 2013, for calculation details, see de Nooy *et al.* 2011).

Binary data are appropriate for characterizing topological patterns through centrality measures, as opposed to quantitative approaches that weight each interaction based on the number of times it occurs (Gilarranz *et al.* 2012). Although weighting

interactions can affect node ranks, this effect is more important in other networks such as food webs. In mutualistic interactions, weighting does not produce a large difference in node centrality ranks, probably because these interactions are more evolutionarily stable (Scotti *et al.* 2007). In addition, the different metrics may be correlated, although they do not necessarily identify the same species as the most central ones (Estrada 2007). Hence, we tested for correlations among indices using Spearman's coefficient ( $\rho$ ) and then determined if the rankings provided by each centrality index were similar. For this, we calculated Kendall's coefficient of concordance ( $W$ ), whose values range from 0 to 1, with 1 representing total agreement between the indices and 0 indicating no consensus.

We evaluated the relationship between species generalization level and network robustness using a cumulative removal of species procedure to determine the number of secondary losses following primary extinctions. We removed species from each side of the network (plants and birds) using selective elimination, moving from super-generalist to least generalist species and running 1000 randomizations in each process. We then repeated the procedure with random elimination of species. We graphed an extinction curve, plotting the number of surviving species as a function of the cumulative number of species removed from the network. We calculated the area under the curve ( $R$ ) is an index of robustness explaining how fast the network collapses under cumulative removals (Burgos *et al.* 2007). The index ranges from 0 to 1, with values close to 1 indicating a network highly robust to secondary extinctions and values close to 0 corresponding to networks vulnerable to the removal of super-generalists. We performed the analyses using Bipartite 2.02 (Dormann *et al.* 2008) implemented in the statistical software package R 3.0.2 (R Core Team, 2013).

## RESULTS

We recorded a total of 75 bird species eating the fruits of 60 plant species, for a network size of 135 species. We estimate sampling completeness at 80.1 percent of the asymptotic interaction richness (Fig. S2) and on a taxonomic level, the plant and bird species included in the sample were representative of the diversity in our study area (Appendix S1).

The birds comprised 19 families and 59 genera, with a strong representation of tanagers in the genus *Tangara* (nine species). The species included forest specialists such as the golden-headed quetzal *Pharomachrus auriceps* and the crimson-rumped toucanet *Aulacorhynchus haematopygus* and more generalist species such as black-billed thrush *Turdus ignobilis* and streaked saltator *Saltator striatipectus*. Seventy species were permanent residents and represented 95.7 percent of interactions. The other five species were Nearctic–Neotropical migrants that consume fruits occasionally.

The plants belonged to 38 botanical families, with a strong representation of genera typical of Andean forests such as *Miconia*, *Palicourea*, *Cecropia*, *Solanum*, and *Ocotea*. The growth forms were as follows: trees (31 species), shrubs (15), palms (5), hemiparasites (3), epiphytes (3), and one vine (Supplement 2). Most species belonged to intermediate successional stages (31), followed by late successional (23) and early successional (4) species.

Structurally, the network was highly nested (NODF = 41.22,  $P < 0.001$ ) and significantly modular ( $M = 0.28$ ,  $P < 0.001$ ). Module number varied between four and seven in the 25 partitions generated. The consensus obtained in the co-clustering matrix was five modules. Testing for species-specific traits in the modular structure of our network revealed that bird body mass (Me) varied across modules ( $H = 19.22$ ,  $P < 0.001$ ,  $df = 4$ ), with significant differences among module 2 (Me = 142.35 g) to modules 4 (Me = 17.75 g) and 5 (Me = 23.0 g). The correlation between bird body mass and fruit diameter was positive and highly significant ( $r = 0.98$ ,  $P < 0.001$ ,  $df = 58$ ). Fruit diameter did not vary significantly among modules ( $H = 8.43$ ,  $P = 0.08$ ,  $df = 4$ ), which suggests that bird body mass is driving this network's modular structure.

We found ten bird and seven plant species in the generalized core of network interactions ( $G_c > 1$ ) representing 12.6 percent of all species. Together, they accounted for 60.6 percent of all interactions in the network, and their number of interactions is in the long tail of the distribution (Fig. 1). The three centrality indices showed positive correlations ( $0.82 < \rho < 0.95$ ,  $P < 0.001$  in all cases,  $df = 133$ ) and high agreement between their rankings (Kendall  $W = 0.92$ ,  $P < 0.001$ ), where species in the generalist core function as local hubs and connectors and are super-generalist species. The top five super-generalist bird species belonged to module 2 and were obligate frugivores (Table 1); 8 of 12 (67%) obligate frugivores were included in this module. Among plants, the top super-generalist species were trees and shrubs from intermediate stages of succession and with small to medium fruit sizes. In our simulations (Fig. 2) network, robustness was high for random extinctions of plants ( $R = 0.87$ ) and birds ( $R = 0.86$ ). By contrast, selective elimination starting with super-generalist species more rapidly generated secondary extinctions in both the plant ( $R = 0.58$ ) and bird sets ( $R = 0.65$ ).

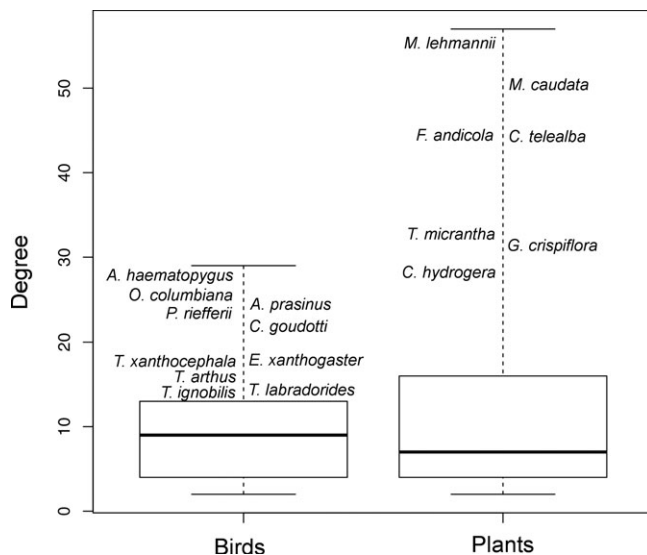


FIGURE 1. Adjusted boxplot for degree (number of links) in plant and bird sets. All super-generalist species ( $D > 17$ ) are above the upper quartile.

## DISCUSSION

We identified a generalist core of ten bird and seven plant species in a diverse assemblage of mutualists. These birds and plants are central species that interact with a large number of species of the other set, performing roles as both local hubs and connectors (*i.e.*, super-generalists). Even though we can expect a few more super-generalists to be identified in the future, such as plants that did not produce fruit during our study, we do not expect these additional species to change our overall results. Our survey of interactions was 80 percent complete, and the missing interactions likely correspond to infrequent consumption events from taxa that have little influence on network structure (Nielsen & Bascompte 2007).

The top five super-generalist bird species in our network are resident, large-bodied obligate frugivores, such as toucans and cracids. Their large gapes give them access to large-fruited species (such as laurels [*Nectandra*, *Ocotea*]) that they swallow whole, but they also feed on small fruits, such as those of *Miconia* spp. Hence, they have broad, generalist diets (Wheelwright 1985). Other large birds have more restricted diets, such as the crested quetzal *Pharomacrus auriceps*, which primarily eats laurels and palms and was not included as a super-generalist in our results. Most of the other five super-generalist birds are small-bodied *Tangara* spp., which as a group make an important contribution to network structure and should be more thoroughly investigated. Among plants, super-generalists are fast growing species of intermediate successional stages that persist inside mature forest or in forest borders. Species in genera such as *Cecropia*, *Miconia*, and *Ficus* have a high degree of connectedness in our network. These three plant genera are abundant in Andean cloud forests (Gentry 1995) and provide an important and continuously available source of food for a broad array of frugivorous birds (Rios 2005, Kessler-Rios & Kattan 2012, Kattan & Valenzuela 2013).

We were able to identify super-generalists in a straightforward manner using degree (the number of links per species), because the centrality measures are correlated and rank species in a similar manner. Our findings are in agreement with other studies that also link degree to the importance of individual species and to community persistence (Dunne *et al.* 2002, James *et al.* 2012). Specifically, the elimination of super-generalists has a potentially profound effect on the stability of the network, because a cascade of secondary extinctions may occur and induce important changes, especially in seed-dispersal processes (Restrepo *et al.* 1997). If the forest is disturbed, due to their fragile nature, some species of high conservation priority, such as endemics and those involved in specialized interactions, may be lost earlier than super-generalists. However, networks as a whole are robust to the extinction of these less-connected species, presumably because they do not influence the global network structure (Bascompte & Jordano 2014). The importance of super-generalists, therefore, lies in the potential impact that their loss may have across entire plant and bird assemblages.



TABLE 1. Central species in the San Antonio seed dispersal network and their ecological and morphological traits. Species listed here are network hubs in the generalized core of interactions with  $G_c > 1$  and are ranked according to their degree centrality. Frugivore level: OF = obligate, PF = partial. Successional stage: IS = intermediate, LS = late. Life-form: T = tree, S = shrub.

|    | Bird species and rank (degree)          | Body mass (g) | Frugivory level | Plant species (degree)            | Fruit size (mm) | Life-form | Successional stage |
|----|---|---------------|-----------------|-----------------------------------|-----------------|-----------|--------------------|
| 1  | <i>Aulacorhynchus haematopygus</i> (29) | 208           | OF              | <i>Miconia lebmanni</i> (57)      | 15.3            | S         | IS                 |
| 2  | <i>Ortalis columbiana</i> (28)          | 600           | OF              | <i>Miconia candata</i> (47)       | 17.6            | S         | IS                 |
| 3  | <i>Aulacorhynchus prasinus</i> (25)     | 189.7         | OF              | <i>Cecropia telealba</i> (43)     | 3.5             | T         | IS                 |
| 4  | <i>Pipreola riefferii</i> (23)          | 62            | OF              | <i>Ficus andicola</i> (43)        | 3.6             | T         | IS                 |
| 5  | <i>Chamaepetes goudotii</i> (21)        | 685           | OF              | <i>Trema micrantha</i> (31)       | 3.6             | T         | IS                 |
| 6  | <i>Euphonia xanthogaster</i> (19)       | 13            | OF              | <i>Guettarda crispiflora</i> (30) | 7.9             | S         | IS                 |
| 7  | <i>Tangara xanthocephala</i> (19)       | 22            | PF              | <i>Clusia hydrogera</i> (28)      | 9               | T         | LS                 |
| 8  | <i>Tangara arthus</i> (19)              | 19            | PF              | —                                 | —               | —         | —                  |
| 9  | <i>Tangara labradorides</i> (17)        | 15            | PF              | —                                 | —               | —         | —                  |
| 10 | <i>Turdus ignobilis</i> (17)            | 85            | PF              | —                                 | —               | —         | —                  |

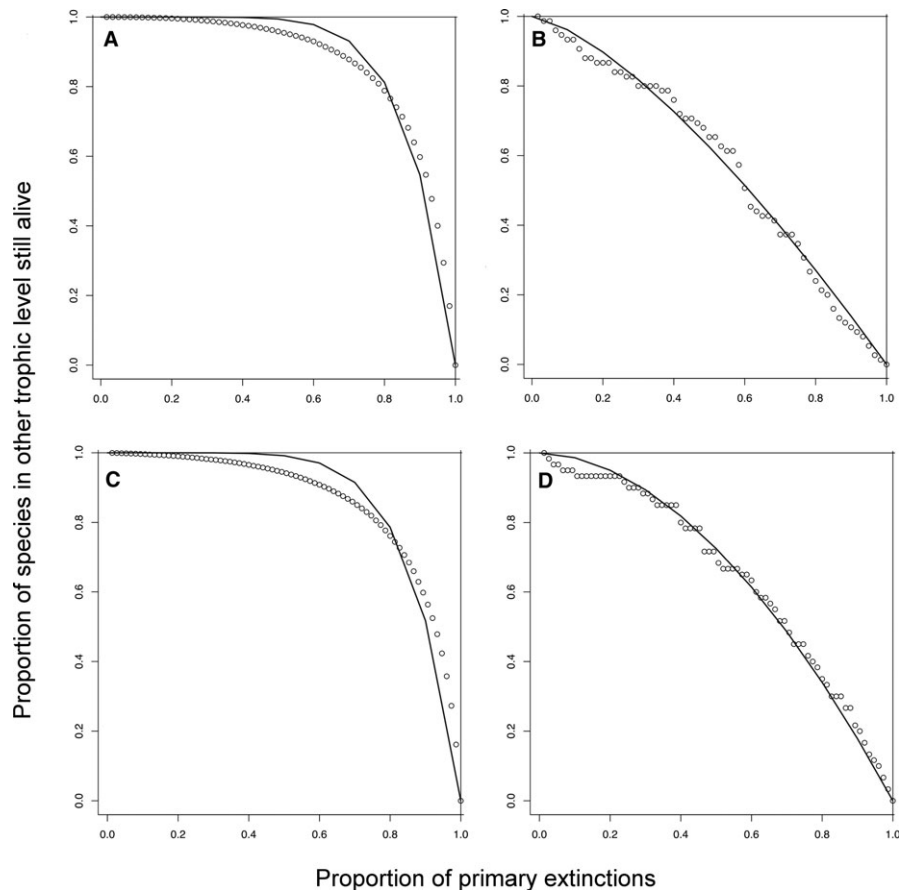


FIGURE 2. Network robustness to cumulative extinctions following two different simulation procedures. (A) Random plant species removal. (B) Generalist plant species removal. (C) Random bird species removal. (D) Generalist bird species removal. The simulation in (D) is more likely to occur, as four large frugivores with broad diets have already disappeared from our study area (Kattan *et al.* 1994).

Both at our study site and at a nearby location in the Colombian Andes, local extinctions of birds have been documented in relation to forest fragmentation (Kattan *et al.* 1994, Renjifo 1999). These studies identified large-bodied frugivores as particularly vul-

nerable to tropical montane forest fragmentation, and this vulnerability is compounded by other threats such as illegal hunting and the live bird trade. Four species of large frugivores, including the black-billed mountain-toucan *Andigena nigrirostris*, the toucan barbet

*Semnornis ramphastinus*, the Cauca guan *Penelope perspicax*, and the red-ruffed fruit-crow *Pyroderus scutatus*, were extirpated from our site coincident with forest fragmentation during the first half of the past century (Kattan *et al.* 1994). These birds have broad diets (Remsen *et al.* 1993, Serrano 1994, Restrepo & Mondragón 1998, Muñoz *et al.* 2007) and were likely super-generalists. The consequences of their local extinctions for forest function are unknown. Although the plants they consume are still present in our study site, long-term negative population trends may be occurring in some plant species, especially those that produce large seeds.

There are two facets to the mutualistic network documented in this study. On one hand, the high diversity of plant and bird species makes this network resilient to the loss of random species. On the other hand, some of the most connected species (such as large frugivores) are highly vulnerable, and if their loss continues, the network may collapse. In the Atlantic forest of Brazil, the most important species for network organization also include large frugivorous birds that are at high risk of extinction (Vidal *et al.* 2014). Whether the paradox of simultaneous resilience and vulnerability occurs in other diverse mutualistic networks depends on the ecological properties of central species. Here, we show that ranking species by their generalization level enables identification of these central species, providing important information for decision-making in conservation and monitoring programs. In particular, for similar communities in tropical forests, the conservation of generalist frugivores that promote fruit supply depends on maintaining a connected forest landscape with a mosaic of plants at different successional stages.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

APPENDIX S1. Presence-absence matrix.

APPENDIX S2. Species ecological and morphological traits, degree, and module assigned.

FIGURE S1. Map of the San Antonio cloud forest showing the trails where we conducted our survey.

FIGURE S2. Accumulation curve for unique interactions with increasing sampling effort.

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