



The role of the endemic and critically endangered Colorful Puffleg *Eriocnemis mirabilis* in plant-hummingbird networks of the Colombian Andes

Mónica B. Ramírez-Burbano^{1,2,3,8,*} , F. Gary Stiles¹, Catalina González⁴, Felipe W. Amorim⁵, Bo Dalsgaard⁶, and Pietro K. Maruyama^{7,*}

¹ Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7495, Bogotá, Colombia

² Programa de doctorado en Ciencias- Biología, Departamento de Biología, Facultad de Ciencias Naturales y Exactas, Universidad del Valle, Calle 13 # 100-00, edificio 320, Cali, Colombia

³ Grupo de Estudios en Geología, Ecología y Conservación GECO, Departamento de Biología. Facultad de Ciencias Naturales, Exactas y de la Educación, Carrera 2 # 3N- 111, oficina 112, Sector de Tulcán, Popayán, Colombia

⁴ Departamento de Ciencias Biológicas, Universidad de Los Andes, Cra 1A # 18A-10 Universidad de los Andes. Edificio J - Laboratorio 103, Oficina A-304, Bogotá, Colombia

⁵ Departamento de Botânica, UNESP – Campus de Botucatu, Instituto de Biociências, Rua Prof. Dr. Antonio Celso Wagner Zanin, s/n° CEP: 18618-689, Botucatu, Brazil

⁶ Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, Universitetsparken 15, DK-2100, Copenhagen, Denmark

⁷ Departamento de Biología Vegetal, Instituto de Biología, Universidade Estadual de Campinas (Unicamp), Rua Monteiro Lobato 255, Cidade Universitária “Zeferino Vaz” Barão Geraldo, Campinas, SP, CEP 13.083-970, Brazil

ABSTRACT

Ecological network approaches may contribute to conservation practices by quantifying within-community importance of species. In mutualistic plant-pollinator systems, such networks reflect potential pollination of the plants and a considerable portion of the energy consumption by the pollinators, two key components for each party. Here, we used two different sampling approaches to describe mutualistic plant-hummingbird networks from a cloud forest in the Colombian Western Andes, home to the Colorful Puffleg *Eriocnemis mirabilis*, an endemic and critically endangered hummingbird. We contrast networks between two localities (a protected area inside a National park vs. its buffer zone) and across sampling methods (floral visitation vs. pollen loads) to assess how the network structure and the importance of each hummingbird species within the networks may change. Visitation networks were characterized as having higher sampling completeness, yet pollen load network recorded more pollen types than plant species recorded by visitation. Irrespective of the sampling methods, the Colorful Puffleg was one of the most important hummingbird species in the network within the protected area inside the National park, but not in the buffer zone. Moreover, most species-level network indices were related to hummingbirds' abundance. This suggests that conservation initiatives aimed at the endangered Colorful Puffleg may both help on the survival of this endangered hummingbird, as well as on maintaining its key role in the mutualistic interaction network inside the National Park. Our study illustrates how conservation practitioners could assess the local importance of endangered species using interaction network approaches.

Abstract in Spanish is available with online material.

Key words: Colombia; generalization; interaction diversity; Munchique National Park; network sampling; pollen load; pollination.

SPECIES ARE ENTANGLED IN NETWORKS OF INTERACTIONS. In these networks, each species plays distinct roles and contributes differently to the dynamics and stability of the system (Bascompte & Jordano 2007, Martín González *et al.* 2010, Saavedra *et al.* 2011, Schleuning *et al.* 2014, Mello *et al.* 2015). In this sense, many studies have investigated and compared the potential consequences of species losses on the robustness of the networks, mostly through simulations of coextinctions (*e.g.*, Solé & Montoya

2001, Memmott *et al.* 2004, Saavedra *et al.* 2011, but see Brosi & Briggs 2013 for an experimental approach). Such simulations have shown, for instance, that extirpating generalized species with numerous interactions have greater potential to affect the structure of the entire community than removing specialized species (*e.g.*, Solé & Montoya 2001, Memmott *et al.* 2004). Although most generalist species in the networks are often also the most abundant ones and, thus, unlikely to go locally extinct first (Winfree *et al.* 2014, Fort *et al.* 2016), these results indicate that core network generalists are important to consider when setting up conservation priorities for endangered species (Martín González *et al.* 2010). Notably, Vidal *et al.* (2014) recently reported that

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*These authors contributed equally to this study.

⁸Corresponding author; e-mail: monicab.ramirez@gmail.com

endangered frugivore birds in the Atlantic rain forest of South-east Brazil have disproportionately larger topological importance in plant-frugivore bird networks. This indicates that these ecological networks are extremely fragile because core components in the system face high risk of extinction. In this sense, conservation practices may benefit from using network approaches to evaluate the importance of each species in a given community (Bascompte & Jordano 2007, Martín González *et al.* 2010, Kaiser-Bunbury & Blüthgen 2015, Maruyama *et al.* 2016, Palacio *et al.* 2016).

In conservation, it is important to be able to sample interaction networks in a cost-effective manner with an appropriate method (Hegland *et al.* 2010). For plant–animal mutualistic interactions, including pollination, one may use either an animal- or a plant-centered approach (Bosch *et al.* 2009, Jordano 2016). Specifically, one can either observe floral visitors on plants and use these visitation frequencies to construct plant-centered interaction networks, or catch animals and use the pollen load as evidence of interactions to construct animal-centered interaction networks (also referred as phyto- and zoo-centric approaches respectively; Bosch *et al.* 2009, Jordano 2016). Examples of both approaches can be found in the literature, with plant-centered sampling being more common in plant-pollinator network literature (Jordano 2016). However, not many studies had simultaneously assessed the effect of these distinct methodologies on the description of network structure and the network topological importance of species. Moreover, all such studies were conducted in temperate or subtropical insect-pollinated systems (*e.g.*, Bosch *et al.* 2009, Alarcón 2010, Dorado *et al.* 2011). This scarcity calls for more studies, as distinct methods to quantify interactions may lead to changes in the description of the networks (Bosch *et al.* 2009, Alarcón 2010, Dorado *et al.* 2011).

Here, we describe a plant-hummingbird mutualistic network in a cloud forest of Munchique Natural National Park and surrounding buffer zone in the Colombian Western Andes, which is home of the Colorful Puffleg *Eriocnemis mirabilis*, an endemic and critically endangered hummingbird species (Fig. 1). A recent study

showed that hummingbird communities comprising smaller ranged species form specialized interaction networks with their nectar-food plants and, thus, may be more vulnerable to secondary extinctions than those communities dominated by large-ranged species (Sonne *et al.* 2016). Hence, characterizing the role of endemic hummingbirds in interaction networks could be relevant for conservation of hummingbird communities and their pollination services. In the literature, plant-hummingbird networks, as for other pollinator groups, are usually built using a plant-centered approach (see Martín González *et al.* 2015 for a recent compilation), although one previous study has used an animal-centered approach by capturing birds and using pollen samples (Maglianesi *et al.* 2015). Nevertheless, for hummingbird-plant networks, comparison of the two approaches from simultaneously collected data is lacking. Here, we build plant-centered visitation networks to describe the topological importance of *E. mirabilis* in the only two localities where this species is known to occur (López-Ordóñez *et al.* 2008): one locality inside a protected National Park where this species is commonly found, and another locality from the surrounding buffer zone. Previous observations have indicated that this hummingbird interacts with fewer plant species in the buffer zone than in the protected area inside the National Park (Ramírez-Burbano 2013). Here, we take a network approach to better contrast such differences. Then, for the locality inside the National Park, we contrast the visitation network and the animal-centered pollen network to determine whether the network structure and the topological role of each hummingbird species change according to sampling methodology.

METHODS

STUDY SITE AND DATA COLLECTION.—Data collection on hummingbird visitation to flowers was carried out at two localities: within and around the Munchique Natural National Park (MNNP) in the state of Cauca, Colombia. In the first site inside the park, Changuayaco (2°40'N; 76°57'W, hereafter 'protected area'), observations were conducted from February to September 2001, with monthly samples of three days each. In the second site, Veinte de Julio (2°31'N; 76°59'W, hereafter 'buffer zone'), which is located in the buffer zone of the MNNP and belongs to Mirabilis Swarovski Nature Reserve (Fundación ProAves), field observations were conducted from April to September 2006, with monthly expeditions of 4 days each. Observations were conducted along transects of 300 × 5 m in each of the sites, three at the protected area (total of 4500 m²) and six at the buffer zone (total of 9000 m²). These localities are *ca.* 20 km apart, have somewhat similar cloud forest habitats and are located at similar elevations ranging from *ca.* 2200 to 2500 m asl. Climate in the region is characterized by temperature varying between 10 and 15°C and with a mean annual rainfall above 3000 mm (Ramírez-Burbano *et al.* 2007). Interactions were sampled along transects by recording all legitimate visits of hummingbirds to flowers, *i.e.*, birds probed flowers from the corolla opening, touching the reproductive structure of flowers. Thus, flowers were included regardless of whether these showed the traditional ornithophilous syndrome or not.

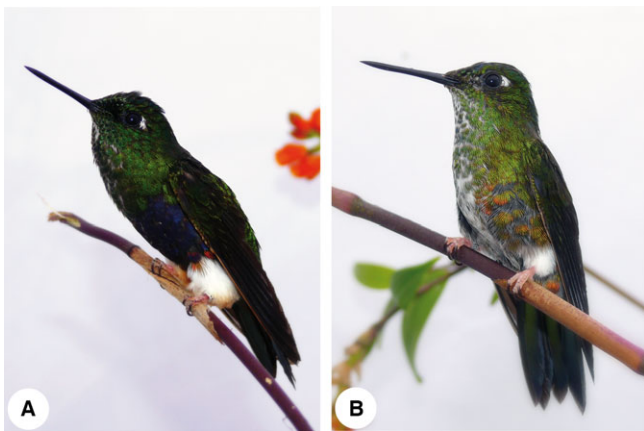


FIGURE 1. Colorful puffleg, *Eriocnemis mirabilis*, is one of the most threatened bird species in the world, found only at specific localities in the Colombian Andes. (A) male and (B) female. (Photo credit: Juan Pablo López O.)

Transects were walked slowly by one observer from 0600 to 1200 h each day of sampling (total observation of 144 h in both sites). From both localities, voucher species of the plants interacting with hummingbirds were collected and deposited at CAUP herbarium of Universidad del Cauca, Colombia for identification.

At the protected area, we also sampled the interactions using an animal-centered approach, *i.e.*, using mist nets to capture hummingbirds and collecting pollen samples from the bird's body (bill, forehead, and throat). We placed six mist nets of 12×3 m with 15 mm mesh and five shelves, during two subsequent days after the observations in each sampling month, also from 0600 to 1200 h, totalizing 576 mist net hours of sampling (*sensu* Ralph 1976). Mist nets were located throughout the observation transects, sometimes near flowering plants to optimize capture. Each captured hummingbird was identified to species level, and then these birds were inspected carefully to collect pollen samples. For this purpose, we used small pieces of glycerin jelly which were rubbed on the hummingbirds, and then kept in plastic vials for posterior analysis in the laboratory. Pollen samples collected from the hummingbirds, as well as from flower buds of all potentially hummingbird-visited plants found at the study site, were treated using Erdtman acetolysis and mounted on glass slides (Erdtman 1969). Samples from flower buds were used for cross comparison and identification of the pollen samples found in the hummingbirds. We also compared the samples to reference pollen grain collections and pollen identification keys at the Palynology and Paleoecology Laboratory of Universidad de Los Andes in Bogotá, Colombia. In our study, the captured hummingbirds were not tagged, which means that hummingbird individuals could have been sampled in mist nets more than once. Although this potentially generates repeated sampling of some hummingbird individuals, the same may happen for interactions based on visitation to plants.

On the basis of these interaction data, we constructed hummingbird-plant networks with plant-centered (hereafter visitation network) and animal-centered (pollen network) approaches. We constructed the visitation networks defining each visit as the number of times a hummingbird was recorded in a plant individual. The pollen network was constructed from pollen load recorded on hummingbird species and using the number of hummingbird individuals captured carrying a given pollen morphotype as the interaction frequency. We used this approach instead of counting the pollen grains as different plant species vary greatly in the amounts of pollen produced, rendering such counts less meaningful (see also Maglianesi *et al.* 2015, Sazatornil *et al.* 2016). Taking into account only legitimate interactions, we consider the visitation networks to represent interactions with potential for pollination. Likewise, pollen transport network also at some extent indicate the capacity of pollinators to carry pollen from one flower to another (see a list of plant groups indicated as pollinated by hummingbirds in literature found in the pollen samples, Table S1). Nevertheless, we are aware that such currencies used here to build the networks do not necessarily translate into plant reproduction.

SAMPLING COMPLETENESS.—We estimated the sampling completeness of the networks following Chacoff *et al.* (2012), with

modifications from Vizentin-Bugoni *et al.* (2016). In this approach, each combination of a hummingbird and plant species is regarded as equivalent of 'species' and the frequency of each pairwise interaction as their 'abundances' (Vizentin-Bugoni *et al.* 2016). Using these data, we used the Chao 1 estimator of species richness (see Chao 1984, Colwell & Coddington 1994) to estimate the total number of hummingbird-plant interactions in the community, *i.e.*, interaction richness. Then, sampling completeness was calculated by dividing the observed by the estimated richness of interactions, giving the proportion of the estimated number of interactions that was actually observed (Chacoff *et al.* 2012). It should be noted that because some unrecorded links may actually be impossible in nature, *i.e.*, forbidden links, this estimate of sampling completeness is fairly conservative (Jordano 2016). The Chao 1 estimator was computed using the *iNEXT* package (Hsieh *et al.* 2014) in R (R Development Core Team 2014). Using the same package, for each one of the networks, we also evaluated the interaction richness by plotting individual-based rarefaction and extrapolation curves with Hill numbers (order of Hill number, $q = 0$; Chao *et al.* 2014, Hsieh *et al.* 2014).

NETWORK METRICS AND SPECIES ROLES.—Next, we calculated a number of distinct network metrics commonly used in the literature that characterize distinct aspects of the network structure: *Connectance* is calculated as the proportion of the possible links in the network that are actually realized. Assuming that these absent links are forbidden due to species traits, connectance is an estimate of how interactions are constrained within the community (Jordano 1987). It is sometimes also used as a measure of specialization/generalization in binary networks. *Complementary specialization*, H_2' , is an index designed to measure network-wide specialization for quantitative interaction matrices and describes how species restrict their interactions from those randomly expected based on partner's availability (Blüthgen *et al.* 2006). Thus, it is interpreted as a measure of the exclusiveness of interactions. *Nestedness* quantifies the degree to which interactions of specialized species are subsets of interactions of the more generalist species in the networks, and was calculated as the NODF index and its quantitative variation wNODF (Almeida-Neto *et al.* 2008, Almeida-Neto & Ulrich 2011). *Modularity* - Q quantifies how prevalent are the interactions structured within modules, *i.e.*, subunits, in relation to interactions occurring among modules and was estimated using the QuanBiMo algorithm (see Dormann & Strauss 2014). The organization of interactions into modules may reflect trait matching among species, thus it provides information on how the interactions are partitioned in the community of plants and hummingbirds (Maruyama *et al.* 2014, 2015). The QuanBiMo modularity algorithm uses an iterative approach to find the optimal final solution, thus the value of Q might vary slightly between runs (Dormann & Strauss 2014). It is therefore usually run several times before the optimal module conformation is accepted, choosing the solution with highest value of modularity (*e.g.*, Maruyama *et al.* 2014, Schleuning *et al.* 2014). Here, we ran the algorithm 20 times for each network. For the plant-centered matrices, we set the number of Markov Chain

Monte Carlo (MCMC) moves to 10^7 steps to yield no improvement before the algorithm stops. For the animal-centered network, this was set to 10^8 steps as the latter was a considerably larger matrix (see Results).

The network-level metrics were calculated mostly with the intent of contrasting the two sampling methodologies and to assess the significance of these network-level metrics, we compared the observed values to those generated by null models. For binary nestedness (NODF), we used the *r1* algorithm from the *vegan* package, which uses the row and column marginal frequencies as probabilities to distribute the presence of interactions (Oksanen *et al.* 2013). For quantitative indices, we used the *Patefield* algorithm (Patefield 1981) to generate simulated matrices with the same marginal totals as the original network, so that species interacting with highest frequencies (or least) in the observed matrices were the same in the simulated ones. We estimated the 95% confidence interval (CI) for each metric from the simulated values, and a metric value was considered significant if it did not overlap with the CI.

As we are interested in assessing the role of species within-networks, we calculated several species-level indices that capture distinct topological properties of a species: (1) *species strength* is the sum of the proportions of interactions performed by a given species across all its interaction partners, thus, it measures the extent to which the assemblage of plants depend on a specific hummingbird species (Bascompte *et al.* 2006); (2) *partner diversity* calculated as the exponential Shannon's diversity and interpreted as a measure of generality of interactions, with the advantage of down-weighting rare interactions (Dormann 2011); (3) species-level specialization d' , which quantifies how interaction frequencies of a given species deviate in relation to the availability of interaction partners in the network, defined by their marginal totals (Blüthgen *et al.* 2006); (4) *betweenness centrality* measures to what extent a species lies on the shortest paths among other pairs of species, quantifying its importance as a network connector (Martín González *et al.* 2010, Mello *et al.* 2015); and (5) *closeness centrality*, which measures the proximity of a species to all other species in the network (Martín González *et al.* 2010, Mello *et al.* 2015). Centrality indices are calculated through one-mode projections of bipartite networks, carried out by assigning a link to two species that share an interaction with a member of the other set, *i.e.*, plants in case of pollinators (Martín González *et al.* 2010). Higher values of *diversity* and *strength* indicate that hummingbirds are more generalized and more plants depend on them, respectively, while high values for d' indicate high exclusiveness on the interaction with plants. For the two *centrality* measures, the higher the values, the more species are located at central positions in the networks. Calculations of all network-related indices were conducted with the *bipartite* package version 2.05 (Dormann *et al.* 2008) in R (R Core Team 2014).

We are here interested on quantifying the species roles of hummingbirds, especially the endangered *E. mirabilis* in the protected area inside the park and its buffer zone. Moreover, within the protected area, we also contrast the hummingbirds' roles between networks built using different approaches to sample the interactions (*i.e.*, visitation and pollen load). We are aware that

species-level network indices can be strongly dependent on the context of the community, *e.g.*, the number of partner plants for hummingbirds is likely constrained by the number of available plants in the network. In this sense, we standardized the species indices within each network by subtracting the mean value for all hummingbirds within the network and dividing the result by the standard deviation, *i.e.*, z-scores. Moreover, to assess the consistency across distinct sampling approaches to quantify the interactions in the protected area, we used Spearman rank correlations to assess the relationship of the indices. Finally, to evaluate how abundances of hummingbirds associate to their roles in the networks, we calculated the relative abundance of hummingbird species by standardizing, within each community, the number of captured birds in mist nets for each species, *i.e.*, we calculated z-scores as for network indices. For the protected area, the same data on captures used to build the pollen network was used to estimate abundances. For the buffer zone, we additionally used 15 mist nets of 12×3 m with 15 mm mesh and five shelves, which were placed in trails during 6 days each month, from April to September of 2006, between 0600 and 1200 h, totalizing 3240 mist net hours of sampling (*sensu* Ralph 1976). Then, for each standardized species-level network indices, we fitted a linear model with the standardized abundance as the predictor variable across all networks. Using a standardized value, our measure does not express the abundance *per se*, but it reflects how each species is abundant in relation to all other species in the same community. All statistical analysis were conducted in R (R Development Core Team, R 2014).

RESULTS

The visitation network from the protected area comprised eight hummingbird species and 27 species of plants, while for the buffer zone a total of 14 hummingbird species and 19 plants were

TABLE 1. Network characteristics and metrics for visitation and pollen networks in the Munchique National Park (protected area) and its buffer zone, Colombian Andes.

Network	Visitation networks		Pollen network
	Protected area	Buffer zone	Protected area
Hummingbird richness	8	14	13
Plant richness	27	19	98 [†]
Interaction diversity	55	55	173
Chao1 (\pm SE; 95%CI)	134.5 \pm 44.1	126.6 \pm 36.3	523.8 \pm 96.2
Sampling completeness (%)	40.9	43.4	33.0
Connectance	0.25	0.21	0.13
NODF	43.3	49.9*	25.7
wNODF	33.6	44.3	23.6
H_2'	0.46*	0.26*	0.33*
QuanBiMo	0.43*	0.37*	0.21

*Metric values that did not overlap with the 95% CI of the null values generated by randomizations.

[†]Pollen morphotypes.

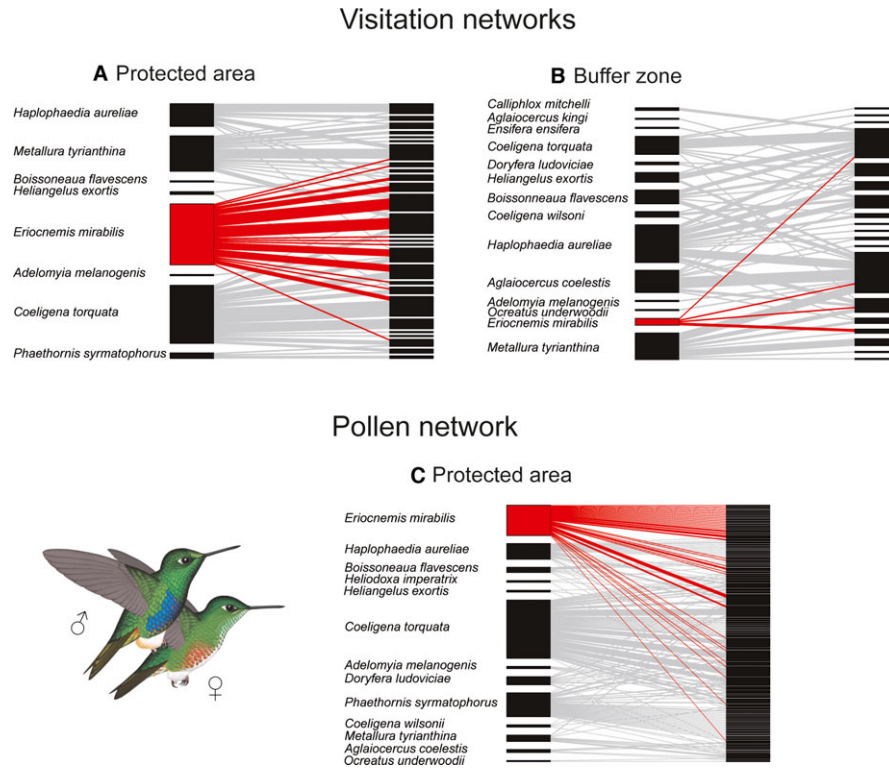


FIGURE 2. Bipartite graphs of the plant-hummingbird networks from Munchique Natural National Park and its buffer zone in Colombia. Visitation networks in (A) protected area, (B) buffer zone; and Pollen network from (C) protected area. Bar thickness represent the total number of interactions for each species. In red, the interactions involving *Eriocnemis mirabilis*. The illustration depicts a male (top) and female (bottom) of *E. mirabilis* (Credit: Fernando Ayerbe-Quiñones). Detailed information on the interaction matrix can be found in the Supplementary material.

recorded (Table 1, Fig. 2; Tables S2–S3). Most frequently interacting hummingbirds in the protected area were *E. mirabilis* and the Collared Inca, *Coeligena torquata*. In the buffer zone, the Greenish Puffleg, *Haplophaedia aureliae*, the Tyrian Metaltail, *Metallura tyrianthina*, and the Violet-tailed Sylph, *Aglaiocercus coelestis*, were most frequent. In the pollen network from the protected area, 13 hummingbird species and 98 pollen types were identified, with *C. torquata* and *E. mirabilis* again as the most frequently interacting hummingbird species (Table 1, Fig. 2; Table S4). Only a fraction of pollen samples could be confidently identified to genera and species (40.2% and 9.3%, respectively; Tables S4 and S5). Moreover, only 7.4 percent (2) of species and 87.5 percent (14) of genera recorded in the visitation network were confirmed in the pollen network from the protected area (Tables S2, S4 and S5). Sampling completeness for the visitation networks were 40.9 percent and 43.4 percent for the protected area and buffer zone, respectively (Table 1). In comparison, pollen network had lower sampling completeness, with 33.0 percent of estimated pairwise combinations recorded (Table 1). Interaction richness estimated based on extrapolations with Hill numbers show that both visitation networks have roughly the same number of estimated plant-hummingbird pairwise combinations, while both observed and estimated richness in the pollen network are higher (Table 1; Fig. 3).

Connectance, nestedness, and modularity were lower in the pollen than visitation network from the protected area (Table 1). Specifically, modularity—which is significant in the visitation network—was non-significant in the pollen network and the H_2' value was lower in the pollen network as well (Table 1). Nevertheless, H_2' was the only index significant across all networks, thus species partition their interactions more than what is expected by chance (Table 1). In general, metrics varied as much between localities as between methods within the same site. Regardless of the sampling method, *E. mirabilis* is one of the most important hummingbird species in the network inside the park, but not in the buffer zone (Figs. 2 and 4). Although different methods agreed on the importance of our focal species, results varied for other hummingbird species. Thus, while for species strength ($r_s = 0.72$, $P < 0.01$) we observed a reasonable correlation of species-level indices between sampling methods in the protected area, partner diversity ($r_s = 0.48$, $P > 0.05$), d' ($r_s = -0.38$, $P > 0.05$), betweenness ($r_s = 0.37$, $P > 0.05$), and closeness centrality ($r_s = 0.38$, $P > 0.05$) showed no significant correlation between sampling methods. Finally, hummingbird abundance is related to all species-level indices, with the exception of d' (Table 2). This relationship was especially strong for species strength ($R^2 = 0.69$; $P < 0.001$).

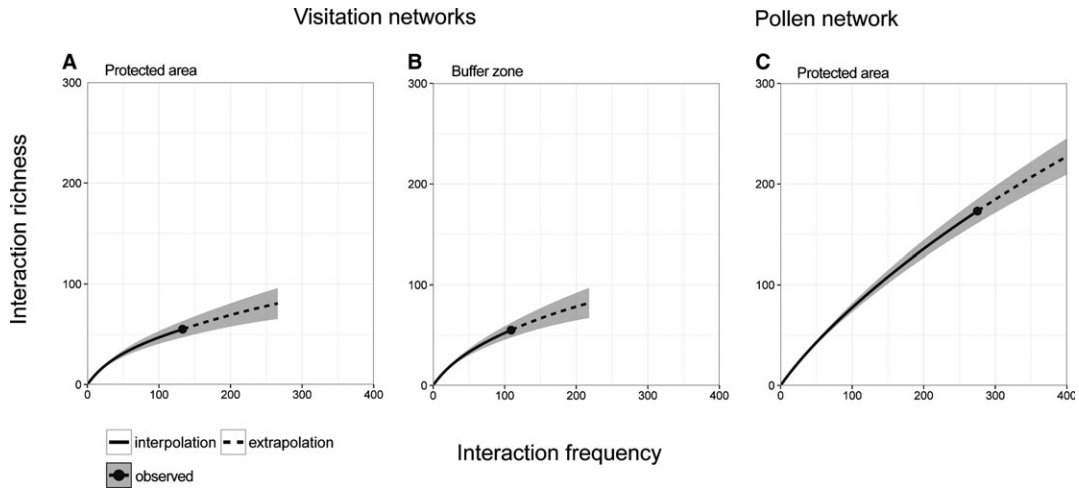


FIGURE 3. Rarefactions and extrapolations with Hill numbers ($q = 0$) for each of the networks. The extrapolations are estimated for up to twice the reference sample size, which is considered reliable for richness estimations (Chao *et al.* 2014). Visitation networks from protected area (A) and buffer zone (B); and pollen network (C).

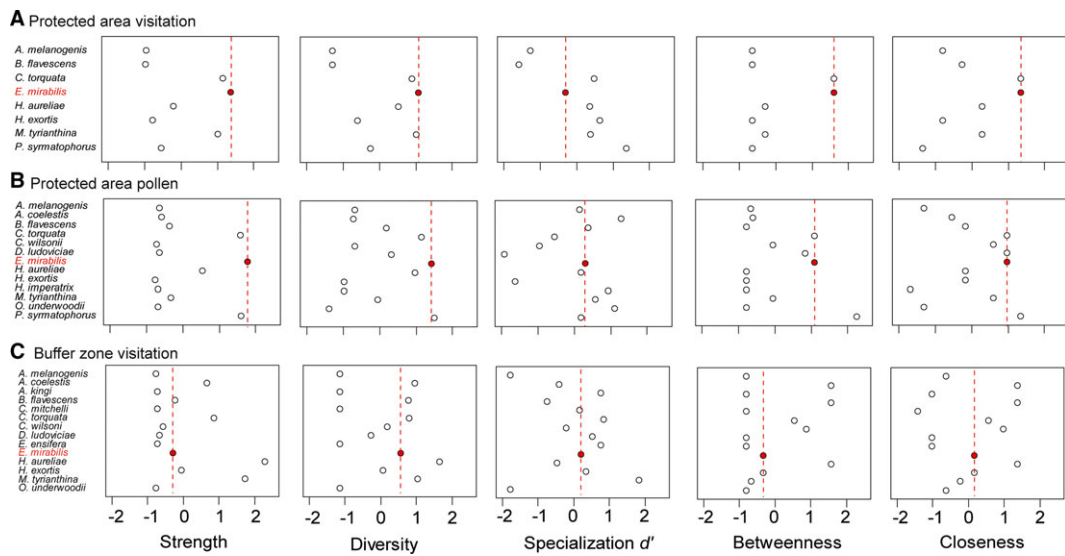


FIGURE 4. Species-level network indices: species strength, partner diversity, complementary specialization d' , betweenness and closeness centrality of hummingbirds in three plant-hummingbird networks from Colombian Andes. (A) Visitation and (B) pollen networks from protected area; and (C) visitation network from the buffer zone. Network indices were standardized using z-scores, which are calculated by subtracting the value of each species by the mean of all hummingbirds within the community, and then dividing by the standard deviation. In red, the values for *Eriocnemis mirabilis*.

DISCUSSION

The critically endangered and endemic Colorful Puffleg, *E. mirabilis*, is a core hummingbird species in the plant-hummingbird network at the protected area in the MNNP—Munchique Natural National Park of the Colombian Andes, one of the only places in the world where this species is known to occur. The key role of *E. mirabilis* in the protected area was clear irrespective of the method used to build the networks. Simulation studies suggest

that the extinction of such core species in networks have a great consequence on network dynamics (Solé & Montoya 2001, Memmott *et al.* 2004). Thus, if endangered species play such roles, then the system may face a higher risk of being disrupted (*e.g.*, Vidal *et al.* 2014). Moreover, recent experiments show that the loss of even a single dominant pollinator may affect the ecosystem functioning of plant-pollinator communities owed to changes in floral fidelity of remaining pollinators (Brosi & Briggs 2013). In this sense, even if the interactions of *E. mirabilis* were to be replaced by

TABLE 2. The relationship between hummingbird relative abundances and species-level network indices across protected area and buffer zone networks. Both the abundance and network indices were standardized (i.e., z-scores) within each community/network before fitting the linear models with relative abundance as the predictor variable.

Network index	R ²	P-value
Species strength	0.69	<0.001
Partner diversity	0.57	<0.001
Specialization (<i>d'</i>)	0.01	0.989
Betweenness centrality	0.49	<0.001
Closeness centrality	0.45	<0.001

other functionally similar hummingbirds, community-wide pollination may be compromised by the loss of this endangered species. Finally, the high importance of *E. mirabilis* in the network is probably owed to its high abundance in the protected area, in contrast to the buffer zone where it is less abundant.

Overall, 213 bird species are classified as critically endangered in the world, including nine other species of hummingbirds that, together with *E. mirabilis*, constitute ca. 5 percent of all bird species placed in this risk category (Ayerbe-Quiñones 2015, BirdLife International 2015). Whether these endangered species act as locally important components of networks is an interesting question to be addressed, especially concerning conservation practices in countries such as Colombia where many species have restricted distributions, making them vulnerable to extinctions (Kattan 1992). If these species are locally abundant, they may also be generalist core species (Fort *et al.* 2016) and, thus potentially important contributors to local network dynamics (Vidal *et al.* 2014). Network indices, such as partner diversity and complementary specialization *d'*, do suggest *E. mirabilis* to be rather generalist in resource use (Fig. 4). This ecological generalization extends to use of plants exhibiting both traditional ornithophilous as well as non-ornithophilous flowers, i.e., there is a considerable variation in floral phenotypes (Ramírez-Burbano *et al.* 2007). With a bill length of ca. 17 mm (Ramírez-Burbano, unpublished), such generalization is consistent to what is reported for many short-billed hummingbirds (e.g., Dalsgaard *et al.* 2009). Although important inside the MNNP, *E. mirabilis* was not so in the buffer zone where it was also less abundant, which may indicate its preference for certain habitat conditions in more preserved areas. This suggests that the habitat and protection measures inside the National Park favors *E. mirabilis*, and reinforces the need to better characterize factors responsible for the lower abundance at the buffer zone. One possibility is that higher richness of hummingbirds in the buffer zone, including many short-billed generalist hummingbirds similar to *E. mirabilis*, increases competition experienced by *E. mirabilis*. Such hypothesis could be further pursued in the future.

Because distinct interaction patterns are detected in the visitation and pollen data, these two approaches complement each other in describing the “true” network structure (Bosch *et al.* 2009, Alarcón 2010, Dorado *et al.* 2011). Previous studies adding

animal-centered approaches to visitation data showed that pollen loads provide information that helps to better describe pollination networks, unraveling a clearer pattern of the partition of the interactions (Bosch *et al.* 2009, Alarcón 2010). Conversely, for the plant-hummingbird network studied here, both modularity and network specialization decreased for the pollen network. One possible reason may be the considerably higher proportion of interactions recorded only once, i.e., singletons, by the pollen load approach. While in the visitation network 56.3 percent of the interactions were recorded only once, this proportion was 75.1 percent for the pollen network. The overabundance of these rare or ‘weak’ interactions probably relate to less clear pattern of partitioning of the interactions observed. This was the case even for quantitative network metrics that have been shown to be reasonably robust to sampling effort in a Brazilian plant-hummingbird network (Vizentin-Bugoni *et al.* 2016). Hence, sampling methodology may have important consequences on network metric values, albeit describing the same network. The high number of rare interactions is also responsible for the considerably higher estimated richness of the interactions for the pollen network, since the number of singletons and doubletons are used to calculate such estimates (Chao 1984, Colwell & Coddington 1994). Similarly, in the study by Bosch *et al.* (2009), the pollen based sampling approach also led to a relatively higher value of estimated interaction richness.

Potential reasons on why more interactions are detected is related to some hummingbirds having daily travel distances of hundreds to thousands of meters (Betts *et al.* 2015), meaning that the spatial scales from which floral visitation data is sampled are most likely considerably smaller than what is associated to pollen load data. Thus, interactions are unrecorded by visitation not only because they are missed in the field, but also because sampling is spatially broader for pollen load data. Nevertheless, the exact spatial scale sampled in animal-centered approach is unclear and also likely species specific (Freitas *et al.* 2014, Betts *et al.* 2015, Jordano 2016). This difference in scale should also apply for other systems involving long-distance flying animals such as hawkmoths (Amorim *et al.* 2014, Sazatornil *et al.* 2016) or flying frugivores (Vidal *et al.* 2014, Mello *et al.* 2015).

One point that should be considered in pollen based networks, though, is the potential difficulty of identifying pollen types. In contrast to previous studies conducted in less diverse scrubland, grassland, and desert-like systems (Bosch *et al.* 2009, Alarcón 2010, Dorado *et al.* 2011), attribution of identity to pollen types in highly diverse tropical forests is difficult owed to the local rarity of plants as well as similar pollen morphology among species in groups important for pollinators in these areas (e.g., Bromeliaceae, Ericaceae, Campanulaceae, Gesneriaceae, and Rubiaceae, see Table S1). In fact, distinct species may be lumped together as “morphotypes” (Tables S4–S5, Maglianesi *et al.* 2015, Sazatornil *et al.* 2016). In this sense, pollen data may not be the best approach for specific identification of important food sources for pollinators. Considering the practical side of the two approaches, the advantage of the pollen load lays on the fact that it can be sampled along other data from the captured

hummingbirds, such as demographic trends (*e.g.*, Rodrigues *et al.* 2013). Moreover, for some animal groups for which direct interactions are hard to record, such as nocturnal visitors, this may be the best suited approach (*e.g.*, Amorim *et al.* 2014, Sazatornil *et al.* 2016). Nevertheless, it also requires specialized training and later work in the laboratory in opposition of the visitation data, which may be entirely collected during the fieldwork. Ideally, both approaches should be jointly employed (Bosch *et al.* 2009, Jordano 2016), but if not, the choice of the appropriate method to sample the interactions must take in account the researcher's primary interest.

Network approaches have been proposed as promising tools for conservation planning (Hegland *et al.* 2010, Kaiser-Bunbury & Blüthgen 2015) by allowing characterization of within-community roles of species (*e.g.*, Martín González *et al.* 2010, Vidal *et al.* 2014, Maruyama *et al.* 2016, Palacio *et al.* 2016). In this sense, the fact that only one (species strength) of the five metrics considered showed significant correlation between plant- and animal-centered approaches could be concerning. This seemed to be caused by some species that appeared as peripheral in the visitation network that became central species in the pollen network (*e.g.*, the trap-lining forager Tawny-bellied Hermit, *Phaethornis syrmatorphorus*). Although these differences did not affect the assessment of the role of our focal species (*E. mirabilis*), it indicates that different methods should ideally be employed when one wishes to have a better characterization of interaction networks, especially in diverse tropical communities (Vizentin-Bugoni *et al.* 2016). Importantly, different sampling methods could improve our understanding of large-scale patterns in plant-hummingbird and other interaction networks (*e.g.*, Martín González *et al.* 2015). For *E. mirabilis*, the marked difference in the importance of this species between protected area and buffer zone networks seems to be related to differences in its abundance. Whether habitat preferences or competition with other hummingbirds are responsible for such differences would be essential to investigate for conservation of this critically endangered species.

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DATA AVAILABILITY

Data deposited in the Dryad Repository: <http://doi.org/10.5061/dryad.2jv81> (Ramírez-Burbano *et al.* 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. List of studies indicating hummingbird pollination of some genera included in pollen samples.

TABLE S2. Plant–hummingbird interaction matrix based on frequency of visitation data in the protected area of Munchique National Park in Colombia.

TABLE S3. Plant–hummingbird interaction matrix based on frequency of visitation data in the buffer zone, Veinte de Julio in Colombia.

TABLE S4. Plant–hummingbird interaction matrix from pollen loads data of Changuayaco, the protected area.

TABLE S5. Reference list of pollen types identification.

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