

## POLLINATION NETWORK OF A HERMIT HUMMINGBIRD COMMUNITY (TROCHILIDAE, PHAETHORNITHINAE) AND THEIR NECTAR RESOURCES IN THE COLOMBIAN AMAZON

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**Resumen.** – Red de polinización de una comunidad de colibríes ermitaños (Trochilidae: Phaethornithinae) y sus recursos de néctar en la amazonia colombiana. – Los colibríes (Aves: Trochilidae) y sus recursos de néctar interactúan construyendo redes de polinización de diferentes grados de complejidad, donde una especie de colibrí puede estar conectada con una o más especies de plantas (o viceversa). En este trabajo evaluamos la estructura del ensamblaje de una comunidad de colibríes ermitaños (Subfamilia Phaethornithinae) y las plantas de las que se alimentan, en bosques de la amazonia colombiana. La composición de especies de colibríes se estableció a partir de capturas con redes de niebla y observaciones directas, mientras que el ensamblaje de plantas visitadas por estos se determinó a partir de cargas de polen y observaciones directas. Esta red de polinización está compuesta por siete especies de colibríes y 44 especies de plantas; presenta una estructura asimétrica y está fuertemente anidada. Cuatro de las especies de colibríes fueron altamente generalistas y se alimentaron de un gran número de especies de plantas, mientras que las especies más especialistas de colibríes interactuaron a su vez tanto con especies de plantas tanto generalistas como especialistas. Las interacciones más fuertes entre grupos de colibríes con ciertos grupos de plantas, apoyaron la hipótesis de la coevolución difusa como mecanismo modelador de las interacciones en esta comunidad.

**Abstract.** – Pollination network of a hermit hummingbird community (Trochilidae, Phaethornithinae) and their nectar resources in the Colombian Amazon. – Hummingbirds (Aves: Trochilidae) and their nectar resources interact building pollination networks that differs in complexity because co-occurring hummingbirds species visit the same and different plant species. In this work we evaluated the network structure of a hermit hummingbird community (Subfamily Phaethornithinae) and their food resources in a Colombian Amazon forest. We studied the hummingbird community using mist nets and direct observations, and the plant community with pollen loads and direct observations. This pollination network is composed of seven hummingbird species and 44 plant species. It has an asymmetric structure and is strongly nested. Four hummingbird species were extremely generalist. Each visited many plant species, while the more specialist hummingbird species interacted with generalist and specialist's plant species. The strongest interactions between hummingbird's species groups and some plant's species groups supports the hypothesis of diffuse co-evolution, where some hummingbirds interact more strongly with some plant species, like modeler of the interactions in this community.

**Key words:** Amazonas, community organization, diffuse co-evolution, Colombia, hermit hummingbird-flower interaction, mutualistic networks, Phaethornithinae, Trochilidae.

## INTRODUCTION

Ecological communities are formed by interactions that include predation, competition and mutualisms such as pollination. They create a complex network of interacting species that vary in their connections and the strength of their interactions. (Verdú & Valiente-Banuet 2008, Thompson & Medel 2010). Mutualistic interactions needed for pollination and seed dispersal involve many species that form complex networks of interdependences (Bascompte & Jordano 2007). In the highly biodiverse neotropics, more than 90% of tropical plants depend on animals for seed dispersal (Jordano 2000) and pollination (Bawa 1990). Hence these interactions are considered key drivers of biodiversity.

Early studies of mutualistic interactions between plants and animals focused on pairwise interactions (for a revision see Bascompte & Jordano 2007, Verdú & Valiente-Banuet 2008). With the development of modern network analysis, recent studies view, explore and analyze interactions by multiple species in complex assemblages (Jordano 1987, Atmar & Patterson 1993, Bascompte *et al.* 2003, Almeida-Neto *et al.* 2008, Verdú & Valiente-Banuet 2008, Jordano 2010), even from a geographical and evolutionary point of view (Dalsgaard *et al.* 2011). From these studies, networks of plant-animal mutualisms tend to have diffuse and nested mutualistic interactions, where the interactions among different species (that can or can not share an evolutionary origin) are mostly facultative, of low specialization and variable in time and space, with most of connections concentrated in few core species (Jordano 1987; Bascompte & Jordano 2007, Castaño Salazar 2009).

Hummingbirds (Aves: Trochilidae) live only in Americas with more than 320 described species, mainly in the Neotropical region (Stiles 1981). These birds feed on nectar and are pollinators of a large number of American

plants (Schuchmann 1999, Arizmendi & Rodríguez-Flores 2012). Hermit hummingbirds (Subfamily Phaethornithinae) have long and curved bills, are mostly understory trapliners (Stiles & Wolf 1979, Stiles 1981, 1985, Cotton 1998b, Hilty & Brown 2001), and reach their higher dominance and diversity in humid lowland forests (lower than 1000 m.a.s.l.) in the Amazon region (Stiles 1981). These hummingbirds are known as pollinators of monocot plants especially of the genus *Heliconia*, in which they share distributional patterns (Stiles 1978, 1981).

The purpose of this work was to study the structure of the mutualistic network of plants and hermit hummingbirds in the Colombian Amazon, using like a model a hermit-plant community previously studied but from an ecomorphological perspective (Rodríguez-Flores & Stiles 2005). Due to the tight correspondence among Hermits and Heliconias, we predict that the network will be: 1) highly heterogeneous because most hummingbird species visits few plant species; 2) nested because specialists interact with subsets of the species in which generalists interact; 3) asymmetric with weak dependencies among species because few generalists provide most of the pollinator services; and 4) some nodes interact more strongly among them that with other species of different nodes (Bascompte & Jordano 2007, Vázquez *et al.* 2009, Jordano 2010).

## METHODS

*Study Area.* Field work was done between November 2001 and July 2002 in the southern part of the Parque Nacional Natural Amacayacu (PNNA) (Colombia, Amazonas; between 3°02' and 3°47'S, 69°54' and 70°25'W (Rudas 1996)) (Fig. 1). Mean annual temperature was 25.9°C, and mean annual rainfall 3377 mm with one rainy season (Amaya-Márquez 1991). In the study area three vegetation types can be distinguished: riverside, meadow and mainland (Amaya- Márquez



FIG. 1. Location of Parque Nacional Natural Amacayacu, Amazonas, Colombia. Map courtesy of Parques Nacionales Naturales de Colombia (2011).

*et al.* 2001). Field work concentrated in mainland because this forest is the most extensive in the area, and has the highest diversity of nectar resources for hermit hummingbirds (Cotton 1998a). In mainland forest five sites were selected and visited twice during study period for a total of 20 continuous days, separating visitation times by at least 3 months among them.

*Bird and plant composition.* To determine hermit hummingbird's species and their nectar resources, direct observation to focal plant

species were done in 8 hour periods (beginning at 5:30 h) for 10 out of the 20 days in each visit. During the observation period we registered all the visits to the flowers, recording the time, the hummingbird species that visited the flowers, and the plant species visited by them. Plant specimen was collected, identified and deposited in the Herbario Nacional Colombiano (COL) from the Instituto de Ciencias Naturales (ICN) of the Universidad Nacional de Colombia.

Hummingbirds were captured using 5 mist nets opened during 8 days per site from 06:00 to 12:00 h and from 14:00 to 17:00 h, alternating with observation days. Nets were placed in the same place where direct observations were done, varying the placement of the nets between visits. From each captured hermit, pollen was obtained from bill, gorget and head using a stained jelly to make a permanent slide for each individual (Amaya-Márquez 1991). Pollen loads were analyzed in the Palynology Laboratory of the ICN.

*Network structure.* To study the structure of plant-hummingbird interactions, a quantitative and qualitative matrix were constructed, with hummingbirds placed in columns (H) and plants in rows (F). For the qualitative matrix,  $r_{ij} = 1$  if the plant  $i$  was visited by the hummingbird  $j$ , and  $r_{ij} = 0$  if no interaction was registered. For the quantitative matrix, the total number of visitations was recorded. To do this, observations and pollen loads were taken together assuming that: 1) For each pollen load, independently of the number of pollen grains of each species on it, we assumed only one visit of the hummingbird to each of these species; 2) each time a hummingbird visited a flower, independently of the number of flowers that the hummingbird visited in the same bout, only one visit was counted.

Using the information of the presence-absence (qualitative) matrix, the cumulative frequency distribution  $P(k)$  of the number of interactions per node ( $k$ ) was calculated. Probability was fitted to three different distributions: 1) exponential  $P(k) \sim \exp(-\gamma^k)$ , 2) power law  $P(k) \sim k^{-\gamma}$ , and 3) truncated power law  $P(k) \sim k^{-\gamma} \exp(-k/k_x)$ , where  $\gamma$  is a fixed constant (degree of exponent) and  $k_x$  is the truncated value (Jordano *et al.* 2003, Bascompte & Jordano 2007, Olesen *et al.* 2008, Castaño Salazar 2009). For each distribution, an Aikake information criterion (AIC) was calculated considering that the distribution with the lowest value is the one that better represents the

original distribution of the data (Olesen *et al.* 2008). Statistical tests for distributions and AIC values were done using function `brainwaver` of R (R Development Core Team 2011).

Nestedness was calculated using two parameters (based on the qualitative matrix): Nested Temperature (NT, Atmar & Patterson 1993) and Nestedness metric based on Overlap and Decreasing Filling (NODF, Almeida-Neto *et al.* 2008). Matrix temperature ( $T^\circ$ ) is a measure of disorder, where  $T^\circ=0$  means a perfect nested matrix and  $T^\circ = 100$  a perfect not nested one (Atmar & Patterson 1993). NT is defined as  $NT = (100-T^\circ)/100$  and varies between 0 and 1; matrix with  $NT = 1$  present a maximum nestedness,  $NT = 0.5$  matrixes with random structure and  $NT = 0$  matrix with compartments (Bascompte *et al.* 2003). NODF has been proposed as a better parameter because: 1) it can calculate the nestedness between rows and columns independently, 2) allows the evaluation of nestedness between one or more rows or columns with respect to others, and 3) is dependent on the arrangement of columns and rows, and so hypothesis can be tested regarding species order (Almeida-Neto *et al.* 2008). High values of NODF indicate that the matrix: 1) is high nestedness, 2) has a perfect 1's overlap from right to left and from up to down, and 3) has a decreasing marginal totals between all pairs of columns and rows (Almeida-Neto *et al.* 2008). To test the significance of the level of nestedness in the matrix, the values of  $T^\circ$  and NODF were compared with two types of null models: 1) ER: 1's in the matrix were assigned randomly to different cells in the matrix, 2) CE: the probability of having a 1 in the  $r_{ij}$  cell was  $\left(\frac{P_i}{C} \cdot \frac{P_j}{F}\right)^{1/2}$ , where  $P_i$  is the number of presences in the row  $i$ ,  $P_j$  is the number of presences in the column  $j$ ,  $C$  is the number of columns, and  $F$  is the number of rows (Guimarães & Guimarães 2006). This later model means that the probability of having an interaction in the simulated matrix is proportional to the generalization of plants and animals in the original matrix

(Bascompte *et al.* 2003). 4000 random nets were generated, 2000 for each model and inside that 1000 were used to calculate mean  $T^o$  and the other 1000 mean NODF. Null models,  $T^o$  and NODF were calculated using ANHIDADO (Guimarães & Guimarães 2006).

The asymmetry and evenness of the matrix were calculated according to Vázquez *et al.* (2009). Asymmetry index was defined as  $A = \frac{\sum_i d_i}{k}$ , where  $k_i$  was the number of species that interacted with species  $i$  and  $d_{ij}$  is a measure of the strength of the interaction between  $i$  and  $j$  (Vázquez *et al.* 2009). When one species has an asymmetry index close to 1 means that these affected strongly the species that interacted with it but received low effects of the others; a value closet to -1 means that a species is influenced strongly by others but has little influence over them (Vázquez *et al.* 2007). Interaction evenness index was defined as Shannon index  $H = -\frac{p_i \cdot \log_2 p_i}{\log_2 F}$  where  $p_{ij}$  is the proportion of interactions that involved  $i$  and  $j$ , and  $F$  was calculated from interactions observed in the matrix. An uneven network (values closet to 1) is one with high skewness in the 185 distribution of interaction frequencies (Vázquez *et al.* 2009). Parameters were calculated using functions “species level” and “network level” of the bipartite package of R (R Development Core Team 2011).

Resources's Importance Valuation Index (IVIR, Amaya-Márquez *et al.* 2001), was used to determine the importance of each resource used by hermits in the community. For plants, IVIR represents the rate between cumulated use intensities by hermit hummingbirds and number of hermit species. Higher IVIR values mean higher importance of the resource for hermits.

To test the effect of hummingbirds and plant species extinctions on the network, we simulated three different sequences of species extinction: 1) **Random**: In this case, random without replacement numbers were generated for the number of plants (44) and hummingbirds (7) species that are forming the network,

and following this order the elimination of specific nodes was done; this procedure was repeated 10 times. 2) **Generalists to specialists**: In this case we remove the species from the more (i.e. generalists) to the less connected (i.e. specialist) nodes. 3) **Specialist to generalists**: Here the less connected species were eliminated first, followed by the generalists. After each simulation, we observed which species left connected to the network, and one node was considered to be extinct when it lost all the interactions (Verdú & Valiente-Banuet 2008).

A Binary Correspondence Analysis (ACB) was done using “VEGAN” package in R (R Development Core Team 2011). This procedure allowed us to detect association between hummingbirds and plants based on similar resource use. The data used here was the visitation frequency, calculated as the ratio between the visits of one hummingbird species to a plant species and the total number of visits of this hummingbird species. This value is a good measure of the intensity of plant use by hummingbirds (Arizmendi 2001).

## RESULTS

Seven hermits species were identified: Rufous-breasted Hermit (*Glancis hirsutus*), Pale-tailed Barbthroat (*Threnetes leucurus*), Black-throated Hermit (*Phaethornis atrimentalis*), Reddish Hermit (*P. ruber*), White-bearded Hermit (*P. hispidus*), Straight-billed Hermit (*P. bourcierii*) and Great-billed Hermit (*P. malaris*) (Remsen *et al.* 2009). They visited 44 plant species with detection by direct observations (8 plant species), palynological evidence (26 plant species), and both methods (10 plant species). Families with highest number of visited species were Heliconiaceae (7 species), Gesneriaceae (7), Rubiaceae (6), Acanthaceae (4) and Costaceae (3). The total number of matrix entries was 281 from 407 direct observation hours and pollinological analysis of 50 slides (Table 1).

TABLE 1. Interaction matrix of hermit hummingbirds and their nectar resources in PNNA. The interactions represent the data get during the direct observations and pollen loads. 1 = presence of interaction, 0 = lack of interaction. The species are arranged according to the NODF criteria for maximum nestedness. The area enclosed by the black line includes the most generalist species.

FAMILY	SPECIES	Abrev.	PM	PH	PB	GH	TL	PA	PR	TOTAL <sup>1</sup>
Rubiaceae	<i>Dauria hirsuta</i>	Du.hir	1	1	1	1	1	0	0	5
Costaceae	<i>Costus scaber</i>	Co.sca	1	1	1	1	0	0	1	5
Gesneriaceae	<i>Drymonia semicordata</i>	Dr.sem	1	1	1	1	1	0	0	5
Heliconiaceae	<i>Heliconia stricta</i>	He.str	1	1	1	1	1	0	0	5
Cucurbitaceae	<i>Gurania spinulosa</i>	Gu.spi	1	1	1	0	0	1	0	4
Heliconiaceae	<i>Heliconia aff.standleyi</i>	He.aff	1	1	0	1	1	0	0	4
Heliconiaceae	<i>Heliconia standleyi</i>	He.sta	1	1	0	1	1	0	0	4
Gesneriaceae	<i>Besleria aggregata</i>	Be.ag	1	1	1	0	0	0	1	4
Gesneriaceae	<i>Drymonia coccinea</i>	Dr.coc	1	1	1	0	1	0	0	4
Rubiaceae	<i>Pulicourea lasiantha</i>	Pa.las	1	1	0	1	1	0	0	4
Acantaceae	<i>Sanchezia peruviana</i>	Sa.per	1	1	0	1	1	0	0	4
Campanulaceae	<i>Centropogon cornutus</i>	Ce.cor	1	1	1	0	0	0	0	3
Rubiaceae	<i>Psychotria poeppigiana</i>	Psy.po	0	0	1	0	0	1	1	3
Gesneriaceae	<i>Drymonia anisophylla</i>	Drani	1	1	1	0	0	0	0	3
Passifloraceae	<i>Passiflora coccinea</i>	Pas.co	1	0	1	0	0	0	0	2
Lecythidaceae	<i>Bertholletia excelsa</i>	Be.ex	1	1	0	0	0	0	0	2
Gesneriaceae	<i>Columnea eriae</i>	Co.eri	1	1	0	0	0	0	0	2
Rubiaceae	<i>Psychotria bahiensis</i>	Psy.ba	0	0	0	1	1	0	0	2
Rubiaceae	<i>Psychotria platypoda</i>	Psy.pl	1	0	0	1	0	0	0	2
Loranthaceae	<i>Psittacanthus cupulifer</i>	Pyc.cup	1	0	1	0	0	0	0	2
Apocynaceae	<i>Tabernaemontana siphilita</i>	Ta.sip	1	0	1	0	0	0	0	2
Gesneriaceae	<i>Gasteranthus corallinus</i>	Ga.cor	1	1	0	0	0	0	0	2
Costaceae	<i>Costus longibractulatus</i>	Co.lon	1	0	0	0	0	0	0	1
Marantaceae	<i>Calathea altissima</i>	Ca.al	0	0	0	0	0	0	1	1

TABLE 1 (Continuation).

FAMILY	SPECIES	Abrev.	PM <i>Phaethornis</i> <i>malaris</i>	PH <i>Phaethornis</i> <i>bispidus</i>	PB <i>Phaethornis</i> <i>bourcieri</i>	GH <i>Glaucois</i> <i>hirsuta</i>	TL <i>Threnetes</i> <i>leucurus</i>	PA <i>Phaethornis</i> <i>atrimentalis</i>	PR <i>Phaethornis</i> <i>ruber</i>	TOTAL <sup>1</sup>
Marantaceae	<i>Calathea contrajefenestra</i>	Ca.con	0	0	0	0	0	1	0	1
Fabaceae	<i>Dioclea ucyalina</i>	Di.uc	0	0	0	0	0	1	0	1
Apocynaceae	<i>Tabernaemontana heterophylla</i>	Ta.het	0	0	0	0	0	1	0	1
Combretaceae	<i>Combretum lleveynii</i>	Co.lle	0	1	0	0	0	0	0	1
Rubiaceae	<i>Psychotria blephanophora</i>	Psy.bl	0	1	0	0	0	0	0	1
Gesneriaceae	<i>Drymonia serrulata</i>	Dr.ser	1	0	0	0	0	0	0	1
Acantaceae	<i>Mendocia lindavii</i>	Me.lin	1	0	0	0	0	0	0	1
Fabaceae	<i>Erythrina fusca</i>	Er.fus	1	0	0	0	0	0	0	1
Heliconiaceae	<i>Heliconia hirsuta</i>	He.hir	1	0	0	0	0	0	0	1
Marantaceae	<i>Ischnosiphon puberulus</i>	Is.pub	0	0	0	0	0	1	0	1
Heliconiaceae	<i>Heliconia julianii</i>	He.jul	1	0	0	0	0	0	0	1
Passifloraceae	<i>Passiflora nitifolia</i>	Pas.vi	1	0	0	0	0	0	0	1
Costaceae	<i>Costus erythrocorone</i>	Co.cry	0	1	0	0	0	0	0	1
Lyttracae	<i>Cuphea melvilla</i>	Cu.me	0	0	0	1	0	0	0	1
Heliconiaceae	<i>Heliconia juruana</i>	He.jur	1	0	0	0	0	0	0	1
Heliconiaceae	<i>Heliconia spatheocrinata</i>	He.spa	1	0	0	0	0	0	0	1
Acantaceae	<i>Ruellia chartacea</i>	Ru.cha	1	0	0	0	0	0	0	1
Myrtaceae	<i>Psidium guineense</i>	Ps.gui	0	0	1	0	0	0	0	1
Acantaceae	<i>Sambeszia putumayensis</i>	Sa.put	1	0	0	0	0	0	0	1
Malvaceae	<i>Pseudobombax</i> sp.	Pseu.	0	0	0	0	1	0	0	1
	TOTAL <sup>2</sup>		31	19	14	11	10	6	4	95

<sup>1</sup> Number of total records for each plant species.<sup>2</sup> Number of total records for each hummingbird species.

The cumulative frequency distribution of the network ( $P(k)$ ) was heterogeneous. 90% of the total species forming the network had 6 or less connections (all plants and two hermits), while 5 species (all hermits) were more connected than expected by chance (having between 10 and 31 connections) (Fig. 2; Bascompte & Jordano 2007, Castaño Salazar 2009). This network had a better fit to power law ( $\gamma = 2.22$ ) than to exponential ( $\gamma = 0.27$ ) or truncated power law functions ( $\gamma = 1.15$ ,  $k_x = 3.24$ ; Fig. 2).

The network analyzed here was nested, with the level of nestedness variable according to the different parameters reviewed. The NT value indicated that this network was highly nested ( $T^o = 23.75$ ,  $NT = 0.76$ ) and significantly different from random matrixes ( $T^o$  model ER = 61.65,  $p > 0.01$ ;  $T^o$  model CE = 46.62,  $p < 0.01$ ). The NODF value showed a

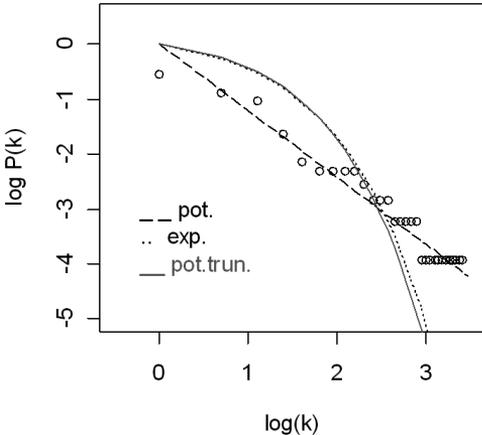


FIG. 2. Cumulative frequency distribution ( $P(k)$ ) of the number of links ( $k$ ) for a hermit hummingbird-plant mutualistic network in the Colombian Amazon. The graph in a log-log scale combine as plant as hummingbird interactions. The original data (circles) was adjusted to three distributions: 1) power-law function (pot.), 2) exponential (exp.) and 3) truncated power-law (pot.trun.). This network has a better fit to the power-law function ( $AIC_{exp.} = 238.150$ ,  $AIC_{pot.} = 167.659$ ,  $AIC_{pot.trun.} = 237.546$ ).

random structure (NODF = 47.64) but significantly nested with respect to null models (NODF ER model = 33.18,  $p < 0.01$ ; NODF CE model = 38.26,  $p < 0.01$ ).

The network was highly uneven ( $H = 0.90$ ) and asymmetrical (Fig. 3), indicating that the number and intensity of connections among species were not homogeneous. The seven hermit species affected importantly the 44 plant species used by them (values of  $A_i > 0$ ), while the plants had no significant effect over hummingbirds ( $A_i < 0$ ) (Fig. 3).

Hermits and the plant species that they visited formed a highly cohesive network, with a core group of generalist's hummingbirds that visited both generalist and specialist plants (Fig. 4). Most of the interactions were classified as weak (less than 5% of the plants had

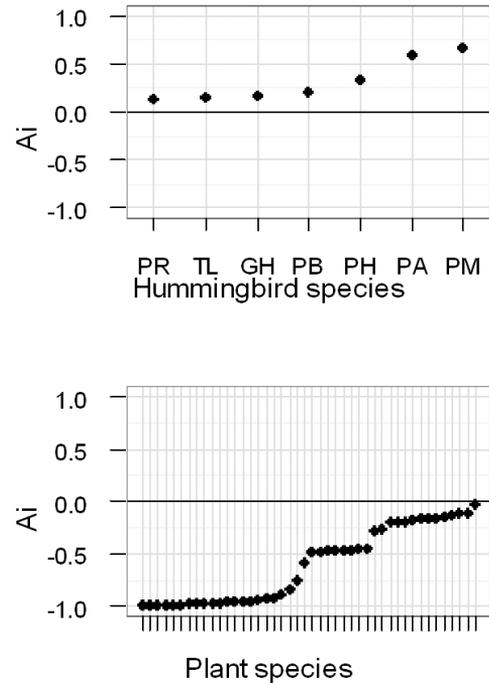


FIG. 3. Asymmetry Index ( $A_i$ ) of the seven hermit hummingbird species (top) and 44 plant species (bottom) visited by them in PNNA. For species' abbreviations see Table 1.

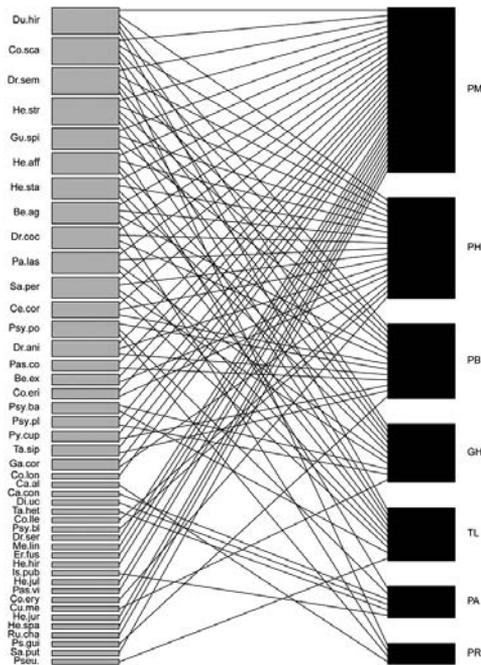


FIG. 4. Ecological network of hermit hummingbirds (black boxes) and plants (grey boxes) on the Colombian Amazon. The lines represent the 95 interactions registered, and the box size is proportional to the number of species with which each species is interacting. For species' abbreviations see Table 1.

IVIR > 0.1), while trophic dependence was different for each guild: 50% of plant species were highly dependent on one or two hummingbird species, while 5 out of the 7 hermit species used 10 or more plant species as nectar resources. Some species represented key nodes because they connected specialized species to the network (Castaño Salazar 2009). These key species were the Great-billed Hermit and the White-bearded Hermit. Great-billed Hermit was the main visitor of 15 plant species, 10 of which were visited exclusively by them; White-bearded Hermit visited 9 plant species, three of which were only visited by them (Appendix 1, Fig. 4).

The number of hummingbirds and plants species that remained connected to the net-

work changed according elimination order (Fig. 5). This network was more sensitive to the elimination of generalist than of specialist species, while random elimination had an intermediate effect on the number of species that remained connected to the network. The network resisted better the elimination of plants than of hummingbirds, because all hummingbird species remained attached to the network after losing 50% of the plants independently of the order of elimination (Fig. 5).

ACB explained 74% of data variance and divided the community in three associations (Fig. 6):

1. First association (Fig. 6A) was composed by the Black-throated Hermit and four plant species visited only by them. The flowers of this plants look like entomophilous species (Faegri & van der Pijl 1979) having short to medium corollas ( $22.66 \pm 12.56$  mm; Rodríguez-Flores & Stiles 2005).
2. Second association (Fig. 6A) was formed by Reddish Hermit, Straight-billed Hermit and seven plant species. The four species visited by Reddish Hermit belonged to this association, and three of them (with exception of *Calathea altissima*) were also visited by two more hermit species. Of the 14 plant species used by the Straight-billed Hermit, the five more intensively visited, belonged to this association. Flower morphologies and growth form of these species were very different, including vines, herbs and trees, and flowers with red, orange, yellow and white corollas (Rodríguez-Flores & Stiles 2005).
3. Third association (Fig. 6B) was formed by the heavier four hummingbird species (Great-billed Hermit, White-bearded Hermit, Rufous-breasted Hummingbird and Pale-tailed Barbthroat and 33 plant species (see Rodríguez-Flores & Stiles 2005 for morphological informa-

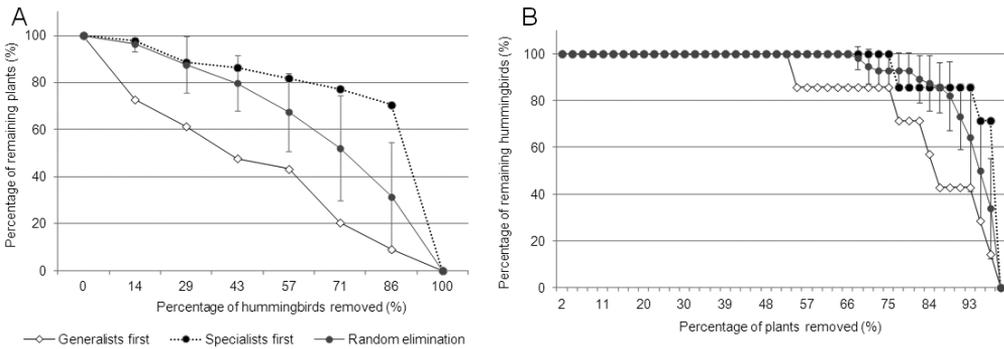


FIG. 5. Percentage of plants (A) and hummingbirds (B) that remain connected to the network after co-extinction simulations following three scenarios: generalist first, specialist first and random elimination (each point represents the mean value, and the line the standard deviation)

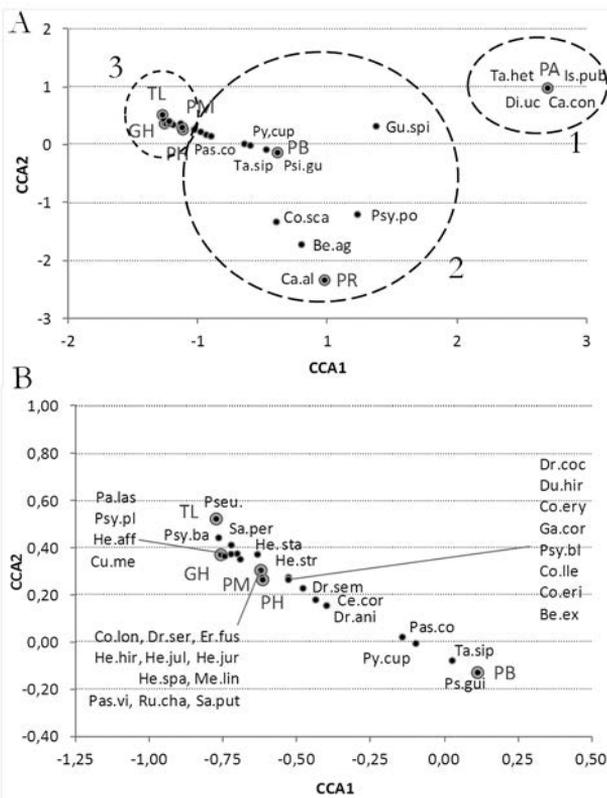


FIG. 6. Binary Correspondence Analysis for the seven hermit hummingbird species (gray points) and the 44 plant species (black points) visited by them in the PNNA. The numbers 1, 2 and 3 in the top figure (A) represent the principal associations formed by the analysis; B figure is a close up of the group 3 (see text for details). Species' abbreviations in Table 1.

tion). In this group is relevant: 1) The location close to the origin of the ordination on the graph, and 2) the overlap between plant species's positions on the graph, indicating that many of the plant shared their flower visitors.

## DISCUSSION

The community analyzed here can be described as a diverse guild of hermit hummingbirds (7 species, Cotton 1998a) and plants visited by them (44 species; Rodríguez-Flores & Stiles 2005). Hermits used resources with morphologies not typically classified as hummingbird species (less than 70% of the plant species being classified as ornitophylous; Rodríguez-Flores & Stiles 2005). However, bigger species tended to use more ornitophylous species (according to Faegri & van der Pijl 1979). This pattern has been found elsewhere (i.e. Amaya-Márquez *et al.* 2001), suggesting that in spite of the opportunistic behavior of hummingbirds, among Hermits selective pressures have maintained fidelity with ornitophylous flowers as those of the genus *Heliconia* (Stiles 1978, 1981).

Mutualistic network analyzed here was incomplete due mainly to 1) temporal incompleteness (only 9 months surveyed) and 2) the lack of all the Trochilinae members. However, the months included are the most diverse both in flowering plants as hummingbirds in the studied site (41 species flowering from November to July, 14 species from August to October; Cotton 1998b), and Trochilinae are more abundant in forest canopy and secondary vegetation (Cotton 1998b, Rodríguez-Flores & Stiles 2005). This spatial segregation between the two subfamilies had implications in the low overlap in resource use by the two groups (Amaya-Márquez *et al.* 2001). Moreover, during observation bouts no Trochilinae species was registered visiting flowers, and only 13.6% of the total net captures corresponded to this subfamily with only one registered species, the

Fork-tailed Woodnymph (*Thalurania furcata*), a resident and abundant species in the study area (Cotton 1998a). A possible network taking into consideration both groups of hummingbirds should show a clear separation between Trochilinae and Phaethornithinae interactions. Also, a complete year-round study may probably not add any hermit hummingbird to the network nor find huge changes in hummingbird's abundances according to what is found by other studies (e.g. Cotton 1998ab, Amaya-Márquez *et al.* 2001). With this in mind, is possible that when include more time, new plant species could be added to the network, acting like specialist nodes that will make the network more nested and cohesive (Bascompte & Jordano 2007).

The fit of the cumulative frequency distribution to the power law function, imply that this network follow a preferential attachment mechanisms (Bascompte & Jordano 2007), in other words, this means that in evolutionary time, generalist species become more generalists because (by probability) new nodes tend to interact preferentially with the most-connected nodes (Vázquez & Aizen 2003, Bascompte & Jordano 2007). Nestedness in ecological nets arises when generalist interacting with other generalist, specialist interact with a particular subset of generalist, and interactions between specialist are very rare (Bascompte *et al.* 2003, Verdú & Valiente-Banuet. 2008). Plant-hummingbird mutualistic networks are specialized (Dalsgaard *et al.* 2012), just like the network analyzed here, however the NT value was lower than those found for other pollination ( $NT = 0.85 \pm 0.05$ ), dispersion ( $NT = 0.84 \pm 0.04$ ) and facilitation ( $NT = 0.89 \pm 0.03$ ) networks (Bascompte *et al.* 2003, Verdú & Valiente-Banuet. 2008, Castaño Salazar 2009). The NODF parameter got (NODF = 47.64) indicated that the net had a random structure but more nested than other positive interaction networks (NODF = 26, Verdú & Valiente-Banuet 2011). This reflects the fact that the plants in

the network (in opposition to the hummingbirds) broke the decreasing fill condition of the index (Table 1) (Almeida-Neto *et al.* 2008). In other words, this means that the hummingbirds were responsible of the nested structure observed, because the generalist hermits incorporated generalist and specialist plant species to the network and concentrated the most part of the links, whereas the specialist hermits connected to the generalist plant species.

One of the principal hypothesis proposed to explain causes of nestedness on ecological networks is the abundance of the species (Levinsohn *et al.* 2006), and the more connected hermit species in this network (the Great-billed Hermit and the White-bearded Hermit) were the more captured in the mist-nets (76% of all captured hummingbirds) and also the more observed species (39.83%). For the plants the relation was not so clear, because most of them were only connected with one hummingbird species and their abundance was not related to number of connections (Rodríguez Flores 2004).

A second explanation for nestedness in mutualistic networks is the phenotypic convergence and complementarity between groups (Santamaría & Rodríguez-Gironés 2007). Complementarity has been defined as the functional match between phenotypic traits in the interacting species, traits that can directly affect the reproductive success of the species connected. Once the pairwise interaction is established, other species can be added to the network by convergence to these traits (Bascompte & Jordano 2007, Rezende *et al.* 2007). In the context of hummingbird-plant interaction, has been established that the morphological traits that are determining the food patterns, diversity and specificity between these birds and their nectar resources are weight, beak's length and curvature, and corolla's length and curvature (Stiles 1981, 1995, Kodric-Brown *et al.* 1984, Brown & Bowers 1985, Cotton 1998b, Gutierrez & Rojas 2001, Rosero 2003, Temeles & Kress 2003, Rodríguez-Flores & Stiles 2005). In our case, no hummingbird species were con-

nected to the network by convergence, because hermits represent a monophyletic group in Trochilidae (McGuire *et al.* 2009), and where the specialized diet had resulted in a common general structure, with particular morphological, physiological and behavioral adaptations (Brown & Bowers 1985, Rosero 2003). In other side, plants visited by hermits belonged to diverse phylogenetic groups, with basal groups represented by Zingiberales (genus *Heliconia*, *Calathea*, *Costus*) and terminal groups by Asterales species (genus *Centropogon*) (Stevens 2001). Probably plant species had been connected to the net by convergence/complementarity. Interactions between hermits and *Heliconia* plants in the community are a good example of complementarity, mainly in the co adaptation shown by bills and corollas that results in a high pollination specialization (Stiles 1975, Temeles & Kress 2003). Convergence is not so easily shown in the community. However, the presence of resources as *Psidium guineense* or *Tabernaemontana heterophylla* that have flowers not adapted for hummingbird visitation, suggest that these hummingbirds are generalist and could be selecting other traits different to length and corolla's curvature. The connection of these resources to the net through the visitation of key hummingbird species, can lead to evolution of convergent traits in those plants (Thompson 2010).

Interactions between hummingbirds and plants were asymmetrical and weak, with the importance (measured like the dependence between species) concentrated among hummingbirds whose formed a core node to which other species can join the net (Jordano 2010) (Fig. 3). This showed that in spite of all morphological and behavioral restrictions, these hermit hummingbirds behave as generalist visiting a high diversity of resources (Buzato 1995, Cotton 1998b, Gutierrez & Rojas 2001, Rosero 2003, Borges & Machado de Almeida 2011, Gómez & Quintana 2011). For the plants we found very contrasting examples. *Passiflora vitifolia* depended almost completely

on the Great-billed Hermit for its connection to the net, but for these hummingbird *P. vitifolia* was a low importance resource used in low intensity (IVIR = 0,002). The other extreme, was *Costus scaber*, a generalist plant species visited by 5 hummingbird species, but used very intensively for a specialist hummingbird species, the Reddish Hermit (Appendix 1, Fig. 3).

Like other mutualistic networks, the one studied here was formed by multiple modules that act as the basic blocks of the network (Bascompte & Jordano 2007, Jordano 2010; Fig. 4). Species inside these modules interact more strongly among them than with others (Fig. 4), and groups were joined by generalist species as the Rufous-breasted Hermit and the Great-billed Hermit through non specific interactions (Bascompte & Jordano 2007). In ecological nets there are some restrictions, (morphological and/or phonological) that make impossible some connections (Bascompte & Jordano 2007). This concept of “forbidden links” has been used to explain the structure in ecological networks in opposition to the neutral models where phenotypic traits of interacting species are considered irrelevant (Bascompte & Jordano 2007, Santamaría & Rodríguez-Gironés 2007). Phenotypic coupling in hummingbird-plant systems, and the importance of the morphological traits on this process has been described previously (Stiles 1975, Gutierrez & Rojas 2001). Forbidden links can be the more reasonably explanation to many of the non-observed interactions. The Reddish Hermit (exposed culmen =  $23.38 \pm 0.60$  mm) for example, did not visited flowers of *Heliconia stricta* (total corolla = 68.35mm) in spite of being present at the same time and at the same place (Rodríguez-Flores & Stiles 2005).

Network architecture (measure as its heterogeneity and nestedness) can have huge implications in the robustness of the network, in other words, its ability to resist species loss (Bascompte & Jordano 2007). When a network fitted better to the power law function (like the one studied here) is resistant to random losses of species, but

fragile to the extinction of generalist species (Albert *et al.* 2000, Bascompte & Jordano 2007). The study of complex networks has the ability of predicting the possible outcomes of species extinctions on the structure and functionality of the network (Srinivasan *et al.* 2007). The extinction simulations highlight the importance of generalist hummingbirds as core species in the structure of this mutualistic network (Fig. 5A). Same results were found in another study regarding bats and dispersed plants, where plants were highly fragile to the elimination of a few generalist bats (Castaño Salazar 2009). However, in difference to the facilitation network studied by Verdú & Valiente-Banuet (2008), in our network was impossible to assume that the species of one group are strongly dependent of the species in the other to survive and that such dependence is species specific, because we did not take into account the other non-hummingbirds pollinators, and did not have information about hummingbird’s pollination efficiency. If we take into account the generalist behavior of the hummingbirds, is highly probable that if we eliminate one hummingbird species, and by consequence some plant species lost their connections to the network, another hermit will use the flowers that the previous species visited, opening the possibility that these species to be reconnected to the network. Furthermore, facing this network to a random extinction process, we would predict that this will remain stable even if we remove an important number of nodes, this because the most part of the species are specialist (in our case principally plant species) and the probability of remove a generalist node from the network is low (Castaño Salazar 2009). However, although nested networks are robust to species loss, this tolerance has a limit before the collapse (Bascompte & Jordano 2007), and with the simulation of the species extinction like we used here, we can have an idea of the network tolerance.

We could illustrated that a community approximation to the hummingbird-plant interaction, that goes forward the traditional pairwise perspective, gives new perspectives about the mechanisms

that organize and structure the ecological communities. At the same time, this approximation opens new and interesting possibilities to move a step forward and study the ecological communities in terms of the species' evolutionary history and of the effect that can have the extinction of the species and the interactions in the conservation and the preservation of the ecosystems. For future studies it is necessary to include information about contemporary and historical climate, temporal and spatial variability and their effect on the network structure, factors that are also relevant to understand the processes that are driving and structuring biotic specializations (Vázquez *et al.* 2009, Dalsgaard *et al.* 2012).

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