ECOLOGY OF PLANT HUMMINGBIRD INTERACTIONS IN UN POCO DEL CHOCÓ, ECUADOR

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Contents

1. Introduction and project overview

One of the main hypotheses for how so many related species can co-occur is resource -partitioning where species use different resources, which limits competition among species and allows them to co-exist. In the case of hummingbirds and plants, each hummingbird species forages on a distinct set of flowers and each flowering plant species is visited by a subset of hummingbirds. Interactions between plants and hummingbirds are mutually beneficial. These mutualistic hummingbird-plant interactions are important from a hummingbird perspective because hummingbirds require nectar to fuel their high-energy lifestyles where they often hover – an energetically costly behavior – to take nectar. From a plant perspective most hummingbirds pollinate flowers as they forage on nectar, though some hummingbirds take nectar from the base of the flower, cheating the flower from this service of pollination. The intricate web of interactions between hummingbirds and their food plants evolved over millennia as a result of diffuse co-evolution which yielded a remarkable array of morphological forms and functions. On-going human activities, such as deforestation and climate change threaten these interaction webs, yet little is known as to how hummingbirds and their food plants will respond. To understand the influence of humans on this complex relationship, accurate, high quality data on hummingbird and flowering plant occurrence and hummingbird-plant interactions are required across broad regions and over an elevation range.

The Northwest slope of the Andes of Ecuador is an ideal place to study plant-hummingbird interactions because it is among the most biodiverse places on earth where multiple co-occurring species rely on each other for survival. There are ~360 species of hummingbirds on earth with the highest diversity in the Andes where up to 30 species can be found at a single site and ~1600 vascular plant species have been recorded in the region. Our study region was in the Pichincha Province (latitude 0°12′ N to 0°10′ S, longitude 78°59′ W to 78°27′ W) and covers 107 square kilometers with an elevation range from 800 to 3500 meters. Our sampling location in Un poco del Chocó reserve lies between 988 and 1202 meters along this gradient.

The goal of the project was to determine the abiotic and biotic factors driving variation in hummingbird-plant interaction networks across elevation and land-use gradients. By evaluating these mutualistic interactions we are able to predict how diversity of both hummingbirds and plants will be influenced by elevation and anthropogenic activities. The project is led by Dr. Catherine Graham from the Swiss Federal Research Institute and executed by Aves y Conservación/BirdLife in Ecuador, Santa Lucía, Maquipucuna, and Un Poco del Chocó with collaboration of several reserves including Mashpi, Las Grallarias, Amagusa, Sachatamia, Yanacocha (Fundación Jocotoco), Verdecocha, Puyucunapi (Mindo Cloud Forest), Rumisitana, Pontificia Universidad Católica del Ecuador, and Alaspungo community. In Un poco del Chocó in particular we collaborated with Willo Vaca reserve's co-owner, and Christian Montalvo and Leo Montalvo were our field assistants.

2. Methodological Approach

To monitor abundance patterns, flowering phenology and hummingbird flower visitation we used a combination of field transects and time-lapse cameras. These transects were 1.5 km in length and were spread across the elevation and land-use gradient with 1 to 2 transects per site. We visited each of the 18 transects (11 in forest and 7 in disturbed sites) one time per month during a two year period. In Un poco del Chocó we sampled the transects from March 2017 to March 2020.

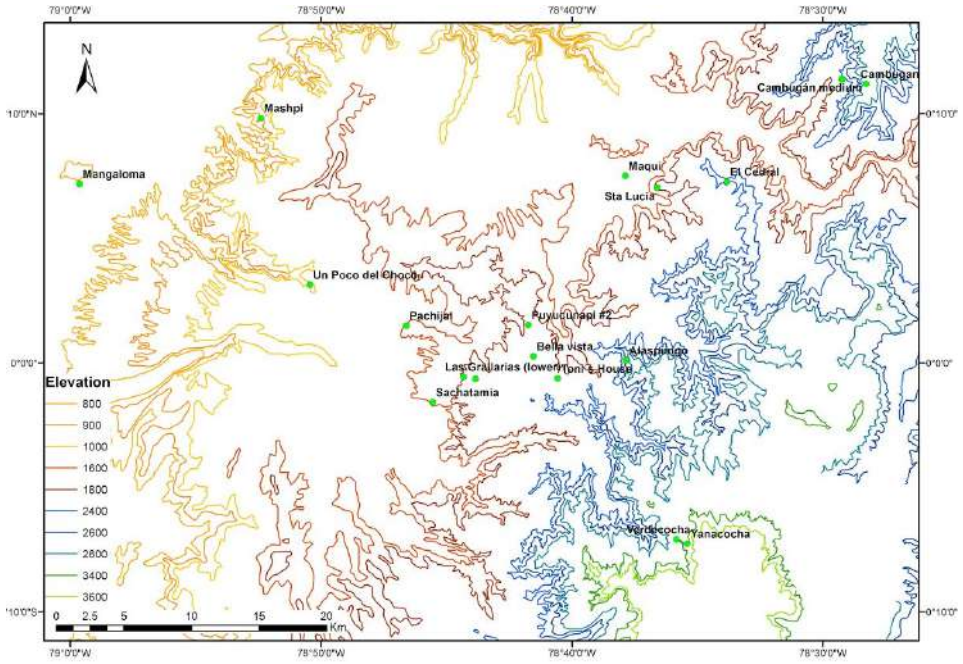

Figure 1: Location of the site in the elevation gradient.

Field transects

In Un poco del Chocó we have 1 transect of 1.5 km. The transect starts on the blue trail in the northwestern border of the reserve at an elevation of 1200 m. First it traverses over 20 year old secondary forest with Miconia trees, then continuous in mature secondary forest at similar elevation for 800 m. At the end of the blue trail the transect continues on the green trail towards the northeastern border of the reserve where it descends down the slope reaching into primary forest, where the green trail meets the red trail. Continuing on the red trail, about 100 m of trail cross a steep slope which was affected by a landslide in 2015. The transect passes one small waterfall and winds down through primary forest where it ends at an elevation of 990 m (Figure 2).

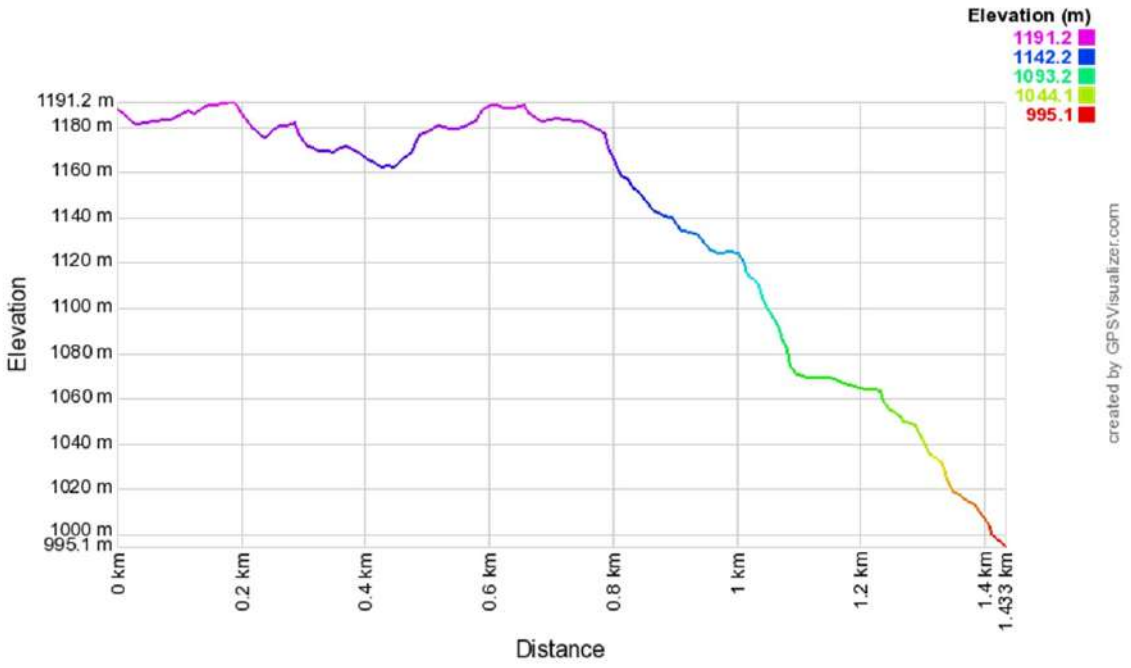

Figure 2: Elevation gradient of the transect.

Along each transect, four to five kinds of data were taken:

Figure 3: Team researcher, Andreas Nieto, counts flowers along a transect.

- **Flower counts**: Any plant with hummingbird syndrome flowers within a distance of ~5 meters of the transect was counted and identified to species. Characteristics of a flower with the hummingbird syndrome include brightly colored flowers (purple, red, orange or yellow) with medium to long corollas. While most species hummingbirds use have these characteristics we were conservative and monitored any questionable species or plants we have seen hummingbirds feeding. For each plant either all flowers were counted or in the case of bushes with more than ~100 flowers, total flowers on 5 representative branches were counted and used to extrapolate the number of flowers on the plant. Each species was collected once and pressed in order to archive our work and/or verify identification with an expert. Plant specimens were deposited at the Herbarium of Catholic University in Quito and Ibarra.

- **Interaction observations**: During the flower census, any interaction of a hummingbird with a flower was noted.

- **Hummingbird counts**: Any hummingbird heard or seen at a distance of 20 meters was also noted.

- **Flower morphology**: Several flower morphological features were measured on at least three individuals per species wherever possible. The Flower traits included were: a) flower corolla length, the distance from the flower opening to the back of corolla, b) effective corolla distance by cutting open flowers and measuring the corolla length extending back to the flower nectarines, c) corolla opening, d) stigma and anther length.

- **Nectar concentration**: This data was taken only at three sites corresponding to low, medium and high transects. Sugar concentration was collected at flowering species for up to 12 flowers per species using a refractometer (a capillary tube is used to extract nectar).

Time-lapse cameras

We used time-lapse cameras to monitor hummingbird-plant interactions. Time-lapse cameras, which take a picture every second, were placed at individual flowers along the above described transects to capture visitation by hummingbird species. We placed cameras on all flowering plants along the transect roughly proportional to their abundance. The cameras turn on at dawn and record an image every second for several days, resulting in a dataset of millions of images. These images are efficiently processed using Motion Meerkat or Deep Meerkat which can be used to sort out images with hummingbirds which can be manually identified (in the past we have been able to identify 95% of birds in images). This approach minimizes reliance on time-consuming human flower observations, greatly increasing data collection in time and space permitting a rigorous test of network theory.

Figure 4: Team researcher Holger Beck shows how a camera is set up in order to film a flower.

3. Resulting patterns

Plant-hummingbird interactions

Un poco del Chocó reserve and surroundings protect over 90 plant species used by hummingbirds according to our project results (Annex 1). However, in our cameras we recorded 120 different interactions between 13 hummingbirds and 43 plants (Figure 5).

Figure 5: Examples of some of the hummingbirds and plants we caught in cameras.

Table 1: List of hummingbirds and number of interactions.

Hummingbird	**No of interactions**	**No plants interacting**
Phaethornis yaruqui	1466	35
Phaethornis striigularis	510	27
Thalurania fannyi	155	17
Heliodoxa jacula	131	11
Schistes geoffroyi	121	8
Coeligena wilsoni	40	7
Ocreatus underwoodii	38	5
Eutoxeres aquila	34	3
Florisuga mellivora	2	2
Urosticte benjamini	5	2
Amazilia tzacatl	3	1
Heliothryx barroti	1	1
Phaethornis syrmatophorus	1	1

The most common hummingbird recorded was *Phaethornis yaruqui* and the most common plant was *Heliconia harlingii*. Although they are the most common species, they are not necessarily the species that interact with more species. The hummingbird that interacts more is *Phaethornis yaruqui* and the plant that has more interactions is *Heliconia sclerotricha*. In table 1 and 2 we can observe the number of interaction for each species.

Table 2: List of plants and number of interactions.

Plant	**No of interactions**	**No hummingbirds interacting**
Heliconia sclerotricha	91	8
Heliconia harlingii	165	7
Guzmania wittmackii	45	6
Hoffmannia killipii	54	6
Pitcairnia nigra	417	6
Costus pulverulentus	75	5
Guzmania scherzeriana	113	5
Palicourea guianensis	61	5
Psammisia sodiroi	30	5
Besleria solanoides	56	4
Chevaliera magdalenae	353	4
Columnea picta	42	4
Aphelandra pepe-parodii	26	3
Columnea eburnea	37	3
Gasteranthus pansamalanus	13	3
Gasteranthus quitensis	80	3
Guzmania remyi	140	3
Pitcairnia elliptica	227	3
Renealmia thyrsoidea	72	3
Columnea rubriacuta	2	2
Columnea spathulata	15	2
Drymonia teuscheri	60	2
Drymonia turrialvae	34	2
Glossoloma sprucei	31	2
Heliconia stricta	34	2
Heliconia virginalis	68	2
Kohleria villosa	73	2
Palicourea asplundii	9	2
Pitcairnia palmoides	25	2
Cavendishia grandifolia	5	1
Drymonia chiribogana	2	1
Guzmania angustifolia	1	1
Guzmania glomerata	2	1
Guzmania rosialba	6	1
Paradrymonia splendens	6	1
Pitcairnia barrigae	2	1
Podandrogyne brevipedunculata	4	1
Psammisia aberrans	1	1

Renealmia sessilifolia	7	1
Renealmia sp.	17	1
Tillandsia cyanea	1	1
Trichodrymonia splendens	2	1
Tropaeolum adpressum	3	1

Plants information and phenology

We recorded the abundance of flowers from March 2017 to March 2020. The months with higher abundance of flowers are October and May (Figure 6).

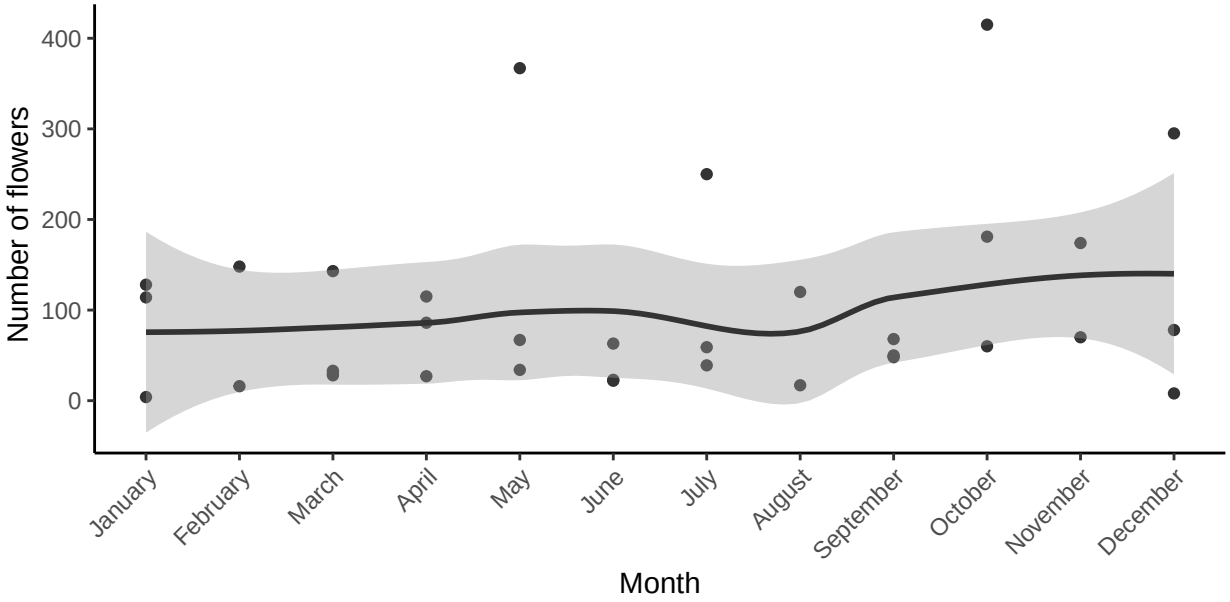

Figure 6: Abundance of flowers by month. Points represent the sum of flowers at each month and the black line represents the mean trend.

However, not all plant produces flowers at the same time. In figure 7 we can observe the phenology of the four most common plant species.

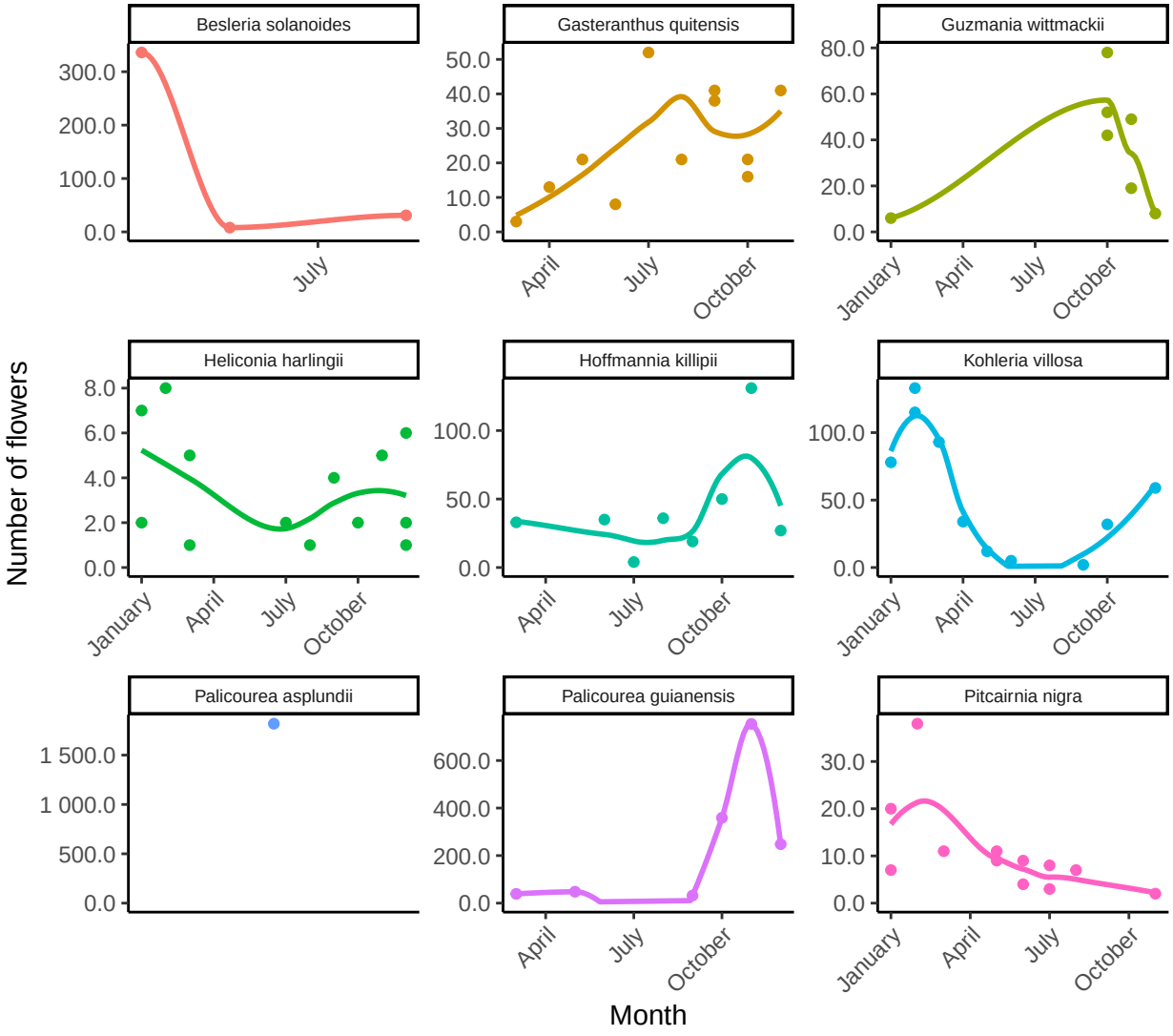

Figure 7: Phenology of most common flowers by month. Points represent the number of flowers counted in each month and the line represents the mean trend. Each color represents a different plant species.

Below we describe the most representative plant families present in Un poco del Chocó.

GESNERIACEAE

Gesneriaceae, the African violet family has around 3000 species, distributed mainly in Central and South America, East and South Asia, Europe and Oceania. In Ecuador there are 200 species grouped in 25 genera. They could be herbs (*Kohleria*, *Diastema*), shrubs (*Glossoloma*, *Columnea*) or very rarely small trees (*Shuaria*, *Besleria*). Gesneriaceae usually have opposite leaves, axillary or terminal inflorescence (cyme, raceme or fascicles), flowers with five petals joined to form a colorful tube with 4 or 5 lobes. Four didynamous stamens (two longer and two shorter) generally fused together and located at the dorsal part of the flower, a simple elongated style with the stigma usually bilobed. In the Pichincha province 15 genera and 89 species have been reported. In our study 64 species were registered, 12 are endemic, 6 are endangered (EN), and 6 are vulnerable (VU). Additionally, we found 3 species that were not previously reported for Pichincha, 2 new records for Ecuador, and 5 new species. Un poco del Chocó has 23 species of Gesneriaceae registered. *Columnea* (8 spp.), and *Drymonia* (6 spp.) contain the greatest number of species. Two species are endemic and threatened: *Gasteranthus crispus* is endangered (EN), and *Drymonia chiribogana* is vulnerable (VU). * Columnea ferruginea* is the first record for Ecuador.

BROMELIACEAE

Bromeliaceae belongs to the pineapple family, it is represented by 50 genera and 2000 species, restricted mainly to tropical America. Seventeen genus and 450 species have been reported in Ecuador. They are epiphytic, lithophytic or terrestrial herbs. Leaves are spirally arranged, usually rosulate (similar distribution to the rose petals), sessile (without petiole), simple, and with parallel veins. Inflorescence terminal or lateral in panicle, raceme or spike, floral bracts usually brightly colored. Flowers are bisexual or sometimes unisexual. Sepals, and petals 3, sometimes fussed forming a tube. Stamens 6 in 2 whorls of 3. The style is terminal and often 3 parted. Fruits could be berries o less often capsules. Seeds are little usually winged or plumose. In the Pichincha province 13 genera and 90 species have been reported. As part of our study 48 species were registered and 17 are endemic. One is critically endangered (CR), two are endangered (EN), and six are vulnerable (VU). One species of *Pitcairnia* is probably new and it is restricted to Mashpi area. Un poco del Chocó, with 19 species of Bromeliaceae is the most diverse place in the study area. *Guzmania* 10 spp., and *Pitcairnia* include the highest number of species with 10 and 5 respectively. Six are endemic and most of them endangered: *Pitcairnia elliptica* (CR), *Tillandsia acosta-solisii* (EN), *Guzmania alborosea* (VU), *Pitcairnia stevensonii* (VU), *Tillandsia cyanea* and *Guzmania jaramilloi*.

The Network of Interactions

The interaction data we collected can be used to explore how the interactions network is organized at Un poco del Chocó. In figure 8 we show the structure of the network.

By analyzing the network structure, we found that the plant *Heliconia sclerotricha* and the hummingbird *Phaethornis yaruqui* are the key species that holds the network together. If they are lost, the network will become less stable. By contrast, *Tillandsia cyanea* and *Florisuga mellivora* are very specialized species which means they interact with a small group of specialized species.

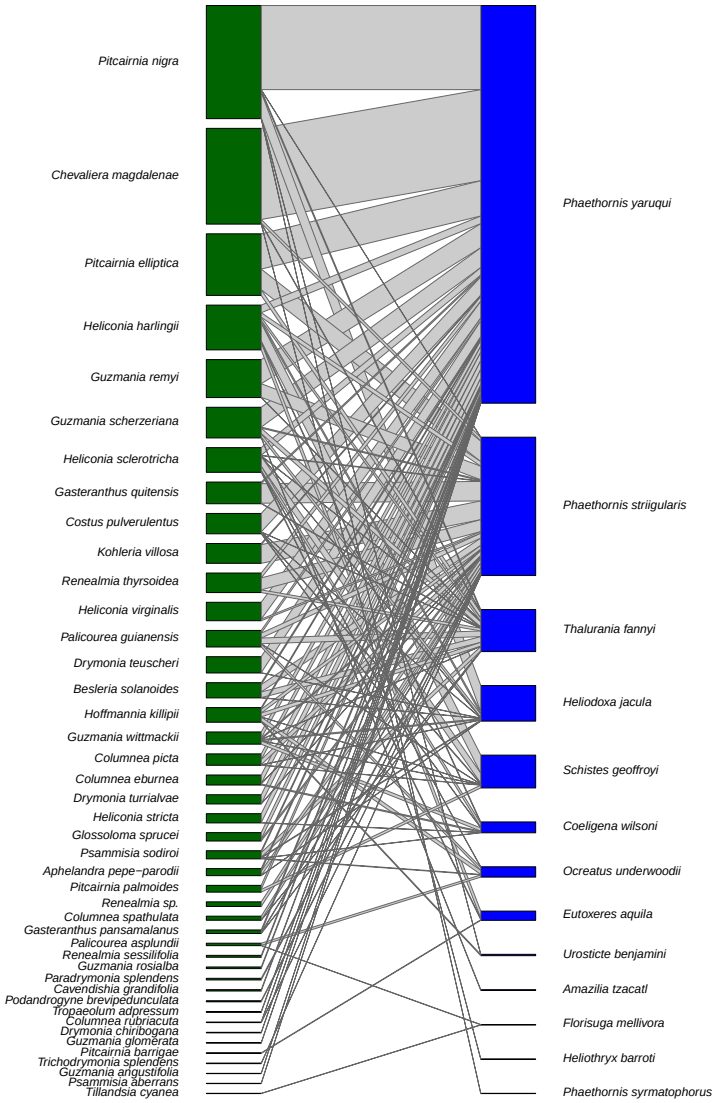

Figure 8: Network of interactions. Blue represents hummingbirds and green plants. Each line represents an interaction between a hummingbird and a plant obtained from our camera observations. Thicker lines indicate that the interaction was common while very thin lines indicate that the interaction occurred rarely. The size of the colored bar shows the number of interactions of a hummingbird or plant participated in an interaction.

4. Conclusions:

- Many similar species can occur in the same place because they use different resources.
- Conservation efforts should consider not only species but interactions among species.
- Key hummingbird plants such as *Heliconia sclerotricha* and *Heliconia harlingii* can be used in restoration in Un poco del Chocó. These species offer resources to more hummingbirds than the other plants where we recorded hummingbirds foraging (8 species).
- *Florisuga mellivora* is the most specialized hummingbird. Species such as *Palicourea asplundii* and *Tillandsia cyanea* are key to maintaining this hummingbird in Un poco del Chocó.
- Un Poco del Chocó has the highest diversity of Bromelias of all the study areas.
- In Un poco del Chocó the first record for Ecuador of *Columnea ferruginea* was observed.
- The hummingbird *Florisuga mellivora* was only recorded in Un poco del Chocó.

Acknowledgements

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