ECOLOGY OF PLANT HUMMINGBIRD INTERACTIONS IN MAQUIPUCUNA, ECUADOR

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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 Maquipucuna reserve lies between 1534 and 1726 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. At Maquipucuna we collaborated with Rebeca Justicia, and Rodrigo Ontaneda from Maquipucuna Fundation.

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 Maquipucuna we sampled the transects from April 2017 to June 2019.

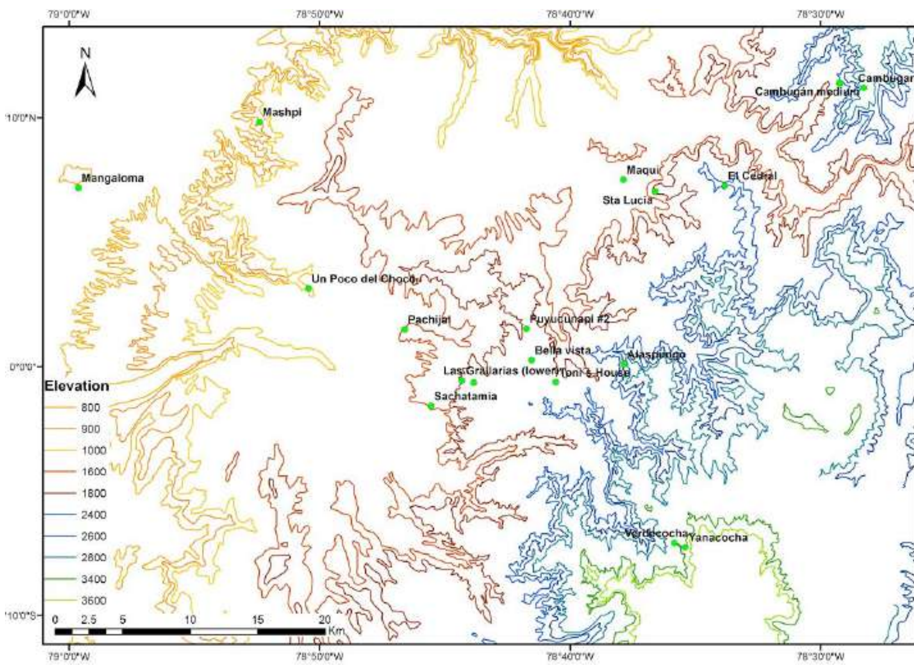

Figure 1: Location of the site in the elevation gradient.

Field transects

In Maquipucuna we have 1 transect of 1.5 km. The transect starts about 2,5 km from the Maquipucuna lodge and follows a part of the main trail where tourists hardly ever go. Following the soft slope through a mature secondary forest, the transect reaches a plateau at an elevation of 1600 masl. From here on the trail is characterized by a steep climb and several sharp bends. The forest matures as the transect continues. Natural disturbances such as landslides and tree falls are common in this part. Following a ridge where trees of the Melastomataceae family dominate, the trail reaches its last part with primary forests (sightings of Andean Bears are not uncommon in this area). Passing a vantage point with a beautiful view at around 1750 m of elevation the trail descents for about 150 meters. Here - surrounded by giant fig trees and dense primary forest vegetation - the transect ends (Figure 2).

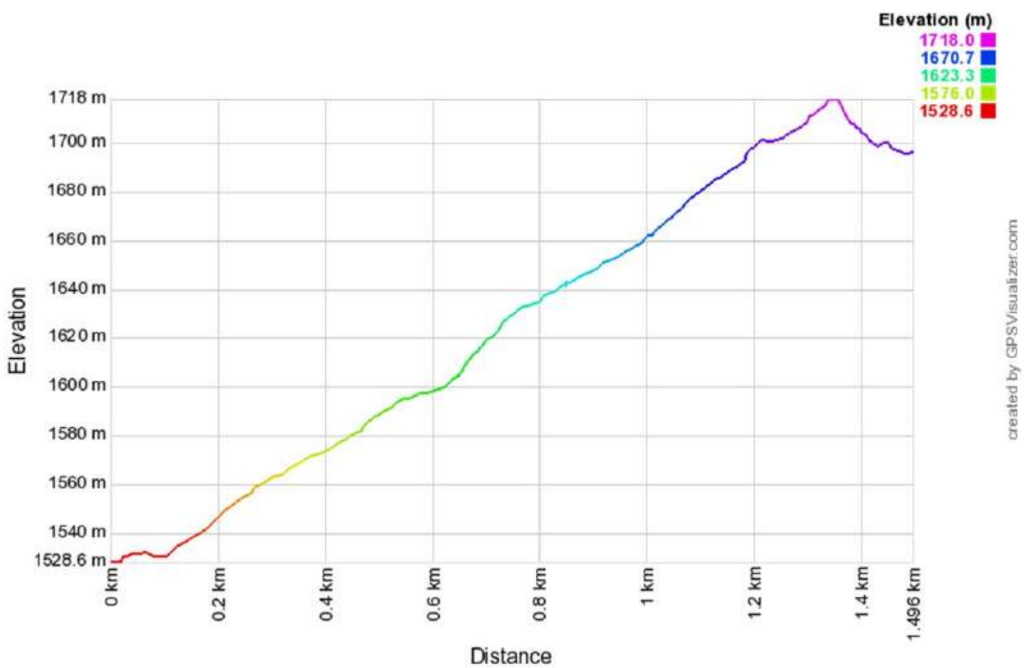

Figure 2: Elevation gradient of the transect.

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

Maquipucuna reserve is one of the largest private properties that protects 66 plant species used by hummingbirds according to our project results (Annex 1). However, in our cameras we recorded 164 different interactions between 12 hummingbirds and 47 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**
Aglaiocercus coelestis	518	28
Phaethornis syrmatophorus	478	27
Phaethornis yaruqui	175	24
Phaethornis striigularis	410	23
Coeligena wilsoni	306	21
Ocreatus underwoodii	272	20
Urosticte benjamini	32	8
Doryfera ludovicae	31	4
Heliodoxa jacula	7	4
Thalurania colombica	4	3
Colibri coruscans	1	1
Heliodoxa rubinoides	4	1

The most common hummingbird recorded was *Aglaiocercus coelestis* and the most common plant was *Renealmia sessilifolia*. Although they are the most common species, they are not necessarily the species that interact with more species. The hummingbird that interacts more is *Aglaiocercus coelestis* and the plant that has more interactions is *Cavendishia grandifolia*. 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
Cavendishia grandifolia	103	9
Centropogon solanifolius	136	7
Gasteranthus quitensis	165	7
Heliconia impudica	86	7
Columnea kucyniakii	33	6
Palicourea demissa	29	6
Psammisia ulbrichiana	42	6
Renealmia sessilifolia	313	6
Burmeistera multiflora	59	5
Columnea ciliata	49	5
Columnea eburnea	134	5
Costus pulverulentus	87	5
Glossoloma purpureum	99	5
Guzmania jaramilloi	136	5
Palicourea sodiroi	29	5
Burmeistera crispiloba	6	4
Columnea sp.	37	4
Guzmania rhonhofiana	58	4
Macleania smithiana	15	4
Psammisia sodiroi	43	4
Renealmia dolichocalyx	231	4
Bomarea pardina	43	3
Columnea picta	17	3
Erythrina megistophylla	37	3
Guzmania lehmanniana	7	3
Guzmania xanthobractea	24	3
Heliconia sclerotricha	9	3
Heliconia sp.	7	3
Psammisia aberrans	18	3
Besleria solanoides	8	2
Dicliptera scabra	35	2
Drymonia tenuis	7	2
Elleanthus robustus	86	2
Heliconia virginalis	7	2
Kohleria spicata	4	2
Podandrogyne sp1	5	2
Tillandsia cyanea	5	2
Wercklea ferox	4	2

Centropogon nigricans	5	1
Cuatresia riparia	4	1
Drymonia brochidodroma	3	1
Fuchsia macrostigma	1	1
Justicia secunda	1	1
Kohleria villosa	2	1
Microchilus sp.	4	1
Psammisia cordifolia	3	1
Sobralia tamboana	2	1

Plants information and phenology

We recorded the abundance of flowers from April 2017 to June 2019. The months with higher abundance of flowers are November and May (Figure 6).

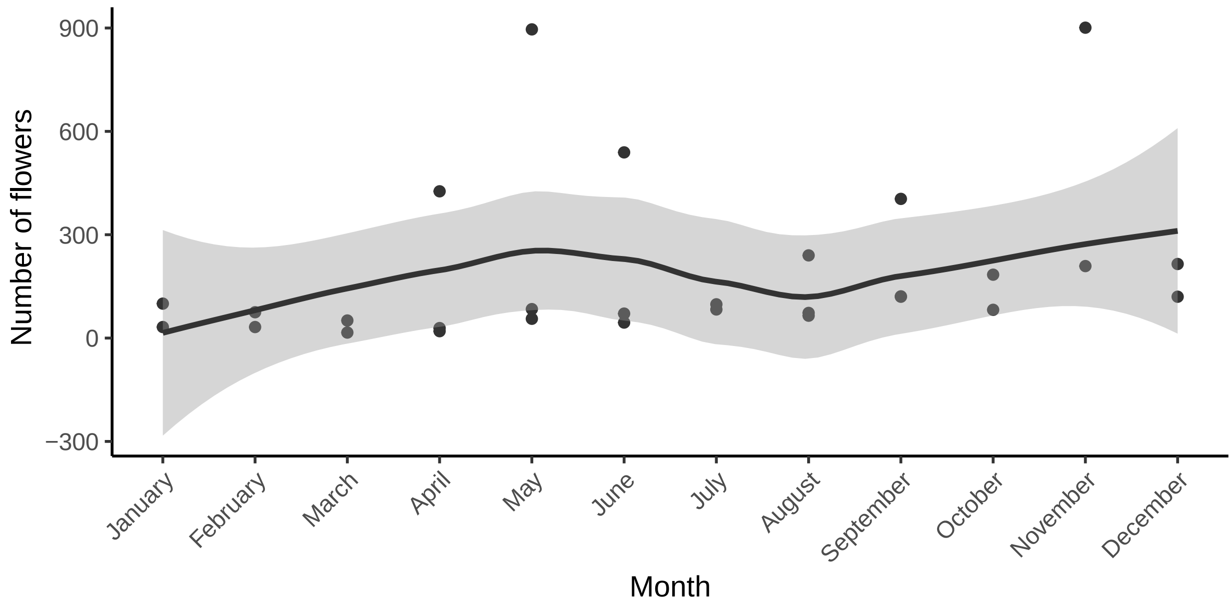

Figure 6: Abundance of flowers by month. Points represent the sum of flowers at each month and the black line represents the mean trend.

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.

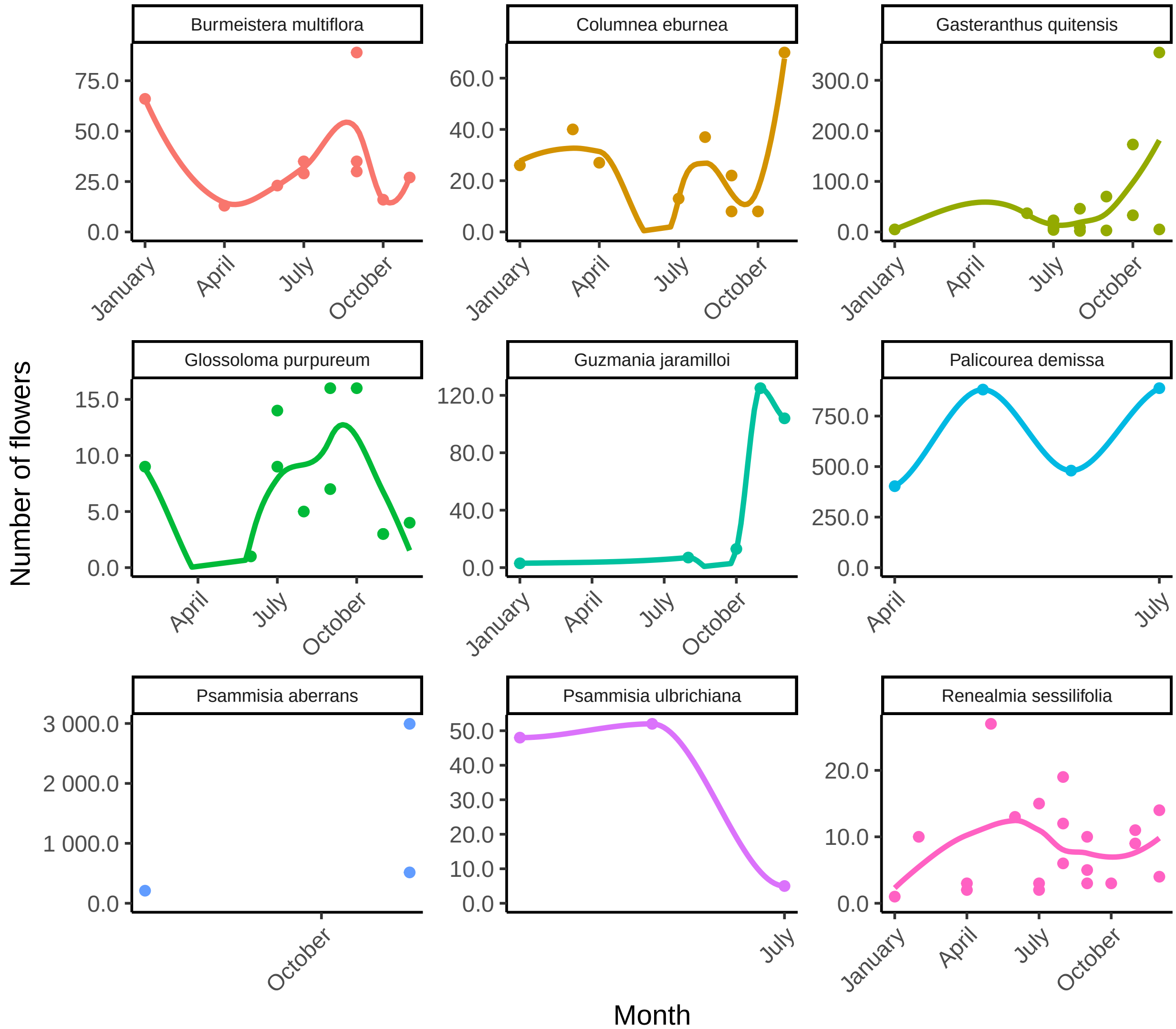

Figure 7: Phenology of most common flowers by month. Points represent the number of flowers counted in each month and the line represents the mean trend. Each color represents a different plant species.

Below we describe the most representative plant families present in Maquipucuna.

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. Maquipucuna has 15 species being *Columnea* the most representative with six species. Additionaly, *Drymonia collegarum* is endemic and vulnerable of extinction (VU), and there is also a new *Columnea* species shared with Las Gralarias, Puyucunapi and Sachatamia.

ERICACEAE

Ericaceae also known as the blueberry family as "mortiño" is represented by 125 genera and 4000 species, widely distributed in temperate, subarctic, and also at high elevations in tropical regions. In Ecuador 21 genus and 240 species have been reported. Life forms include woody shrubs (*Cavendishia*, *Macleania*), trees (*Bejaria*, *Thibaudia*), or suffrutex (small plants with woody stems and soft branch as *Gaultheria*, *Disterigma*). Plants could be erect, prostrate or climbers with coriaceous leaves. Flowers are perfect (containing anther and stigma), mostly tubular with 4 to 7 lobes, anthers in twice number than the petals, often enlarger in one or two terminal tubes. Fruit usually is a capsule, berry or drupe. In Pichincha province there are 13 genus and 73 species. During EPHI project 45 species were registered and 18 are endemic: one is critically endangered (CR), four are endangered (EN), and 10 species are vulnerable (VU). *Macleania tropica* is the first record for Pichincha area, it was only known from Esmeraldas and Colombia. *Antoptherus ecuadorensis*, and *Macleania alata* are the first records made since the type collection in 1979 and 1986 respectively (these two species were collected nearby the study transects).. Maquipucuna has 15 species being *Psammisia* and *Macleania* the genus with more species. Only *Macleania recumbens* is endemic and vulnerable (VU).

The Network of Interactions

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

By analyzing the network structure, we found that the plant *Cavendishia grandifolia* and the hummingbird *Aglaiocercus coelestis* are the key species that holds the network together. If they are lost, the network will become less stable. By contrast, *Tillandsia cyanea* and *Heliodoxa rubinoides* are very specialized species which means they interact with a small group of specialized species.

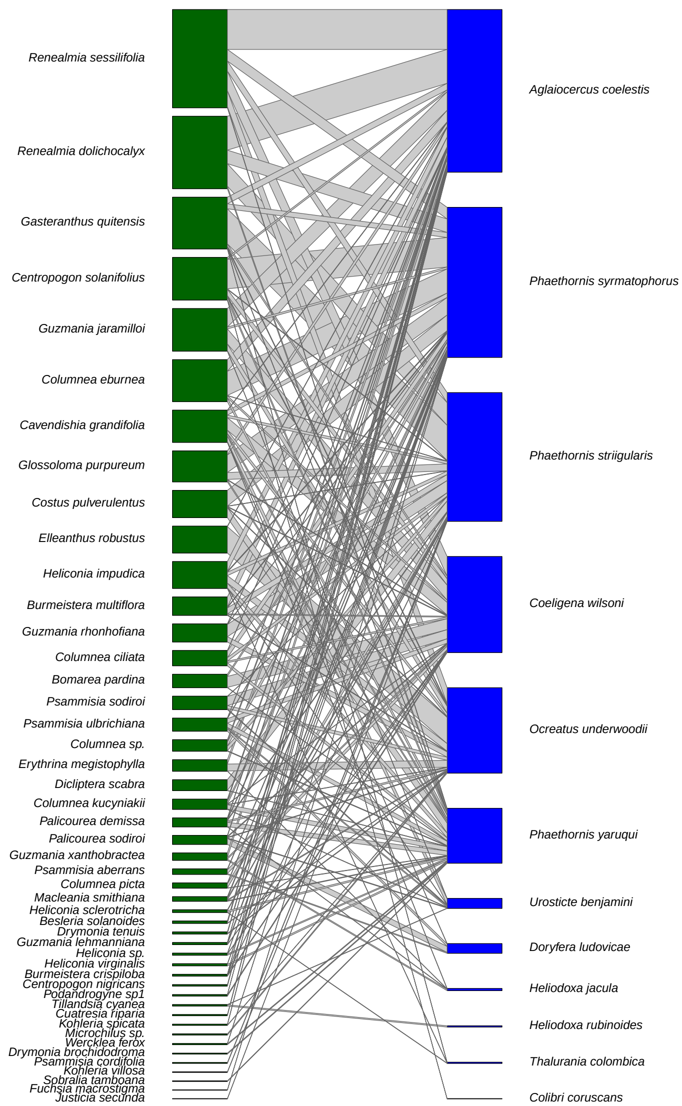

Figure 8: Network of interactions. Blue represents hummingbirds and green plants. Each line represents an interaction between a hummingbird and a plant obtained from our camera observations. Thicker lines indicate that the interaction was common while very thin lines indicate that the interaction occurred 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 *Cavendishia grandifolia* and *Centropogon solanifolius* can be used in restoration in Maquipucuna. These species offer resources to more hummingbirds than the other plants where we recorded hummingbirds foraging (10 species).
- *Heliodoxa rubinoides* is the most specialized hummingbird. Species such as *Tillandsia cyanea* is key to maintaining this hummingbird in Maquipucuna.
- In Maquipucuna we recordered one new species of *Columnea sp.nov*. This species is also present in Las Gralarias, Puyucunapi and Sachatamia.
- The hummingbird *Colibri coruscans*, typical of disturbed areas, was only recorded in Maquipucuna and Santa Lucía.
- Maquipucuna does not have a clear flowering peak. However, some years more flowers are present from April to June.

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