ECOLOGY OF PLANT HUMMINGBIRD INTERACTIONS IN VERDECOCHA, 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 Verdecocha reserve lies between 3346 and 3432 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 Verdecocha we collaborated with Jorge Enrique Maldonado and our assistants Wilson Hipo and Rolando Hipo where of crucial help.

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 Verdecocha we sampled the transects from March 2017 to March 2020.

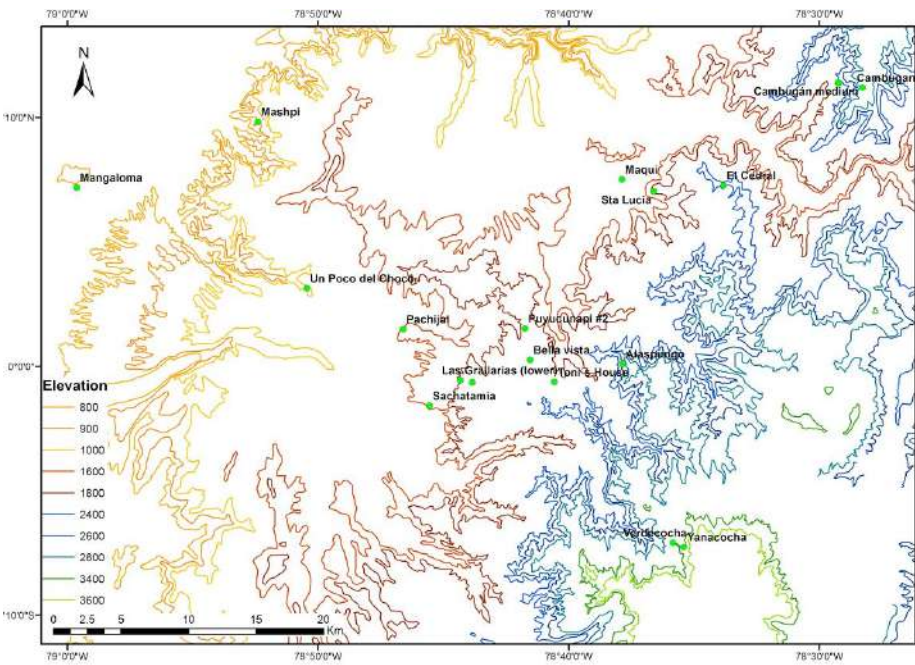

Figure 1: Location of the site in the elevation gradient.

Field transects

In Verdecocha we have 1 transect of 1.5 km. The access to the Verdecocha transect is through the Inca Trail at Yanacocha reserve, walking around 2,5 km from the entrance to the hummingbird garden. From here, the access trail continues for few meters until a sign indicating the boundary with the Verdecocha reserve. The access trail continues upwards through a steep slope to the mountaintop and then begins a 15 minute descent to the start of the transect. This transect starts about 3400 m of elevation and is located along a mountain ridge where there is a well conserved forest with many epiphytes and scattered suro areas. There is a section of about 150 meters of dwarf forest with mainly bush vegetation and orchids (Figure 2).

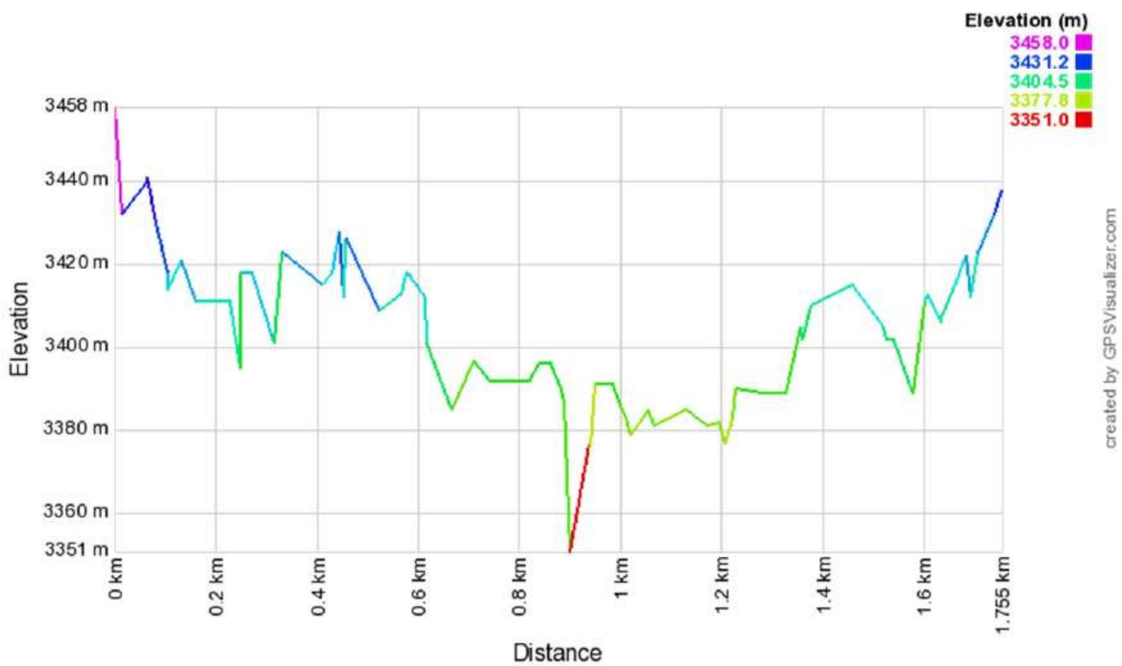

Figure 2: Elevation gradient of the transect.

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

Verdecocha contains an important sample of high montane forest where hummingbird forage on an array of 53 plant species according to our project results (Annex 1). However, in our cameras we recorded 138 different interactions between 14 hummingbirds and 46 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**
Metallura tyrianthina	1567	39
Coeligena lutetiae	489	21
Eriocnemis luciani	834	20
Eriocnemis nigrivestis	588	20
Lafresnaya lafresnayi	218	11
Eriocnemis mosquera	114	10
Adelomyia melanogenys	85	7
Pterophanes cyanopterus	4	3
Heliangelus strophianus	21	2
Aglaeactis cupripennis	1	1
Chalcostigma herrani	1	1
Coeligena torquata	1	1
Ensifera ensifera	8	1
Lesbia nuna	2	1

The most common hummingbird recorded was *Metallura tyrianthina* and the most common plant was *Macleania rupestris*. Although they are the most common species, they are not necessarily the species that interact with more species. The hummingbird that interacts more is *Metallura tyrianthina* and the plant that has more interactions is *Heppiella repens*. 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**
Heppiella repens	204	8
Macleania rupestris	580	7
Guzmania bakeri	557	6
Palicourea amethystina	226	6
Palicourea fuchsioides	307	6
Tillandsia polyantha	115	6
Centropogon pichinchensis	119	5
Gaiadendron punctatum	174	5
Bomarea hirsuta	79	4
Columnea dielsii	215	4
Elleanthus gastroglottis	39	4
Fuchsia corollata	32	4
Fuchsia sp.	25	4
Racinaea tetrantha	189	4
Salvia pichinchensis	78	4
Bomarea patacocensis	136	3
Burmeistera glabrata	7	3
Centropogon dissectus	24	3
Elleanthus aurantiacus	27	3
Miconia corymbiformis	57	3
Nasa grandiflora	11	3
Salvia pauciserrata	24	3
Thibaudia floribunda	305	3
Tropaeolum adpressum	4	3
Aetanthus macranthus	18	2
Berberis grandiflora	17	2
Centropogon llanganatensis	10	2
Columnea strigosa	19	2
Elleanthus amethystinoides	12	2
Elleanthus gracilis	11	2
Epidendrum mesogastropodium	8	2
Fuchsia ayavacensis	31	2
Gaultheria glomerata	2	2
Gaultheria insipida	26	2
Siphocampylus rupestris	8	2
Sphyrospermum grandifolium	5	2

Bomarea lutea	36	1
Cleome anomala	7	1
Clethra ovalifolia	3	1
Deprea glabra	82	1
Disterigma noyesiae	74	1
Glossoloma altescandens	4	1
Miconia sp3	11	1
Rubus roseus	2	1
Schefflera lasiogyne	2	1
Vallea stipularis	11	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 August and May (Figure 6).

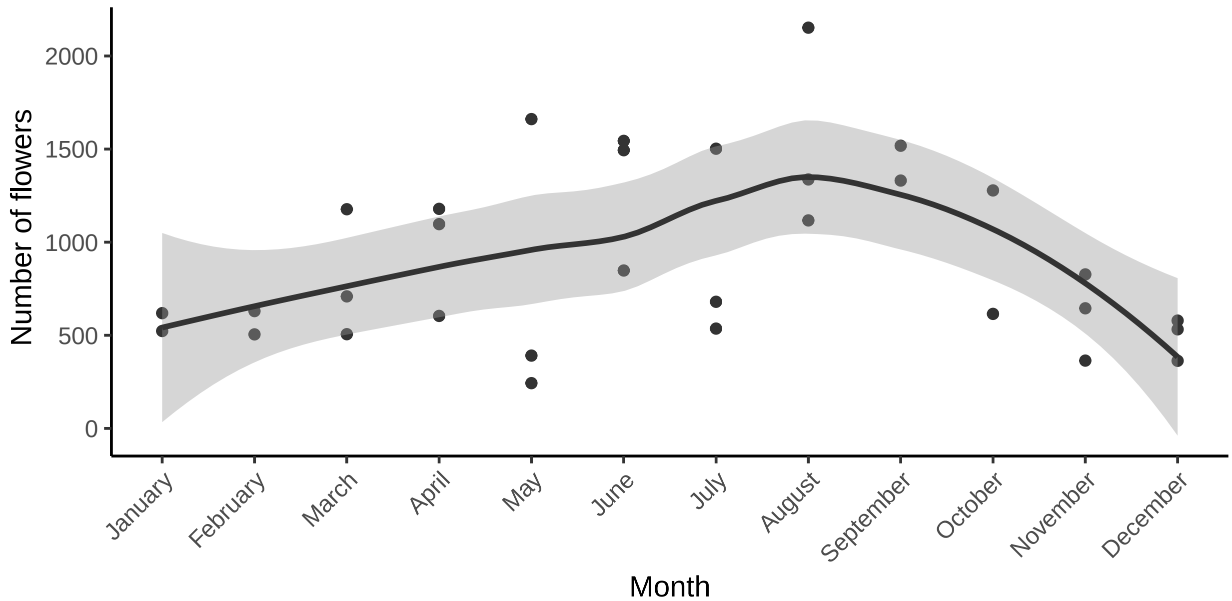

Figure 6: Abundance of flowers by month. Points represent the sum of flowers at each month and the black line represents the mean trend.

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.

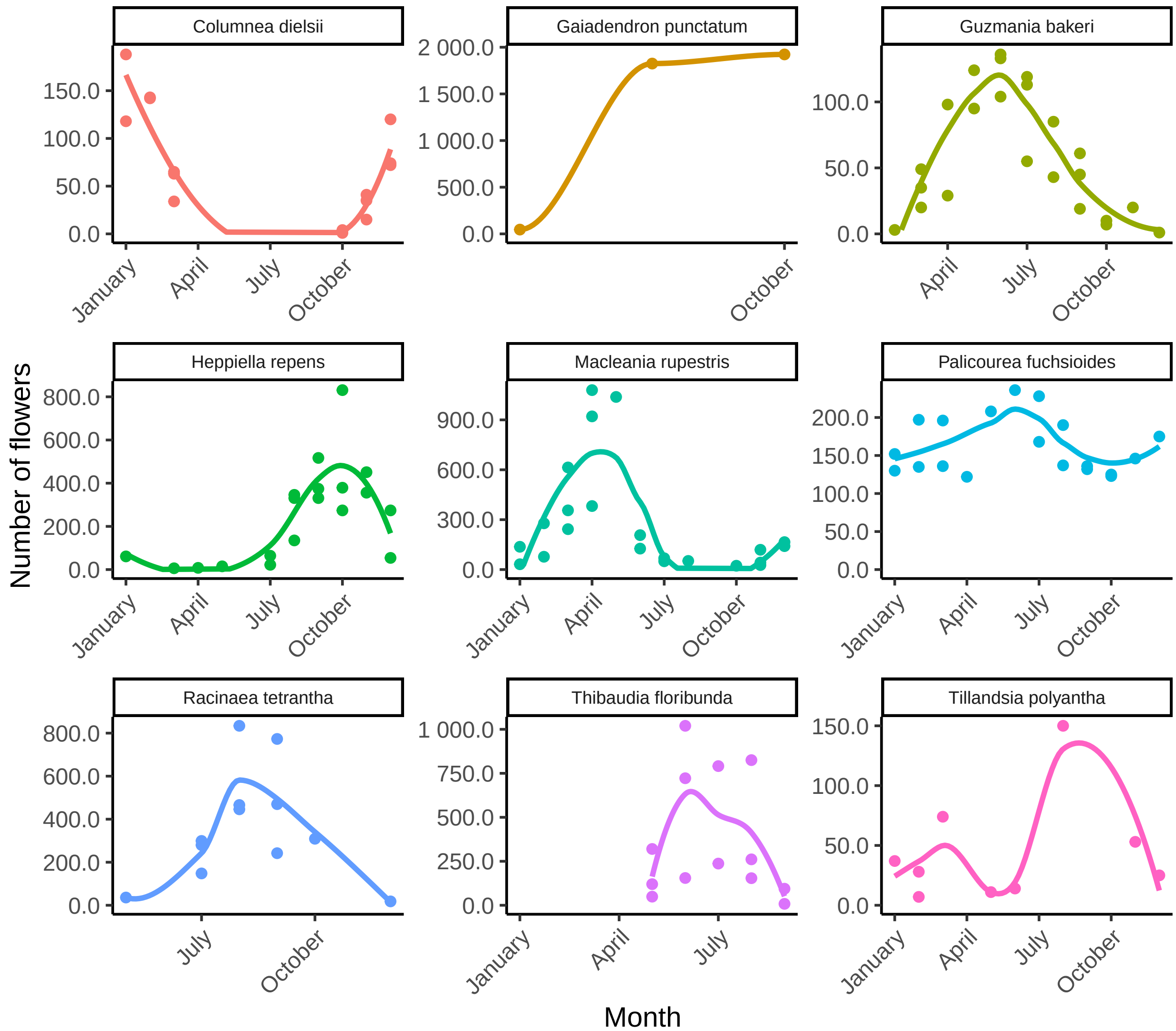

Figure 7: Phenology of most common flowers by month. Points represent the number of flowers counted in each month and the line represents the mean trend. Each color represents a different plant species.

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

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). There are 9 species in Verdecocha, the genus *Gaultheria* and *Disterigma* are the most diverse with 3 and 2 species respectively but *Macleania* and *Thibaudia* are the most visited. *Disterigma noyesiae* is the only endemic and also vulnerable (VU) representative.

CAMPANULACEAE

Campanulaceae includes lobelias and “pucunero” plants. It is represented by 70 genera and near 2000 species, it is considered as a cosmopolitan (spread around the world) family. Ten genus and 148 species have been reported from Ecuador. Campanulaceae are manly terrestrial plants, rarely epiphytic, there are shrubs (*Centropogon*, *Siphocampylus*), vines (*Siphocampylus*, *Burmeistera*) or herbs (*Lobelia*) with latex. Flowers are perfect (anthers and stigma are present), petals fussed forming a tubular bilabiate corolla (base and top petals are larger than the laterals). Filaments and anthers joined forming a slightly curved tube generally longer than the corolla, stigma emerging between the anthers. In the Pichincha province 6 genus and 39 species have been reported, and in the scope of this project 23 species were registered. There are 11 endemic species, one is critically endangered (CR), five are endangered (EN), and three species are vulnerable (VU). Two species of *Burmeistera* are new and restricted to Mashpi area, and there is also a potential new *Centropogon* species from Alaspungo. Verdecocha has five species of Campanulaceae. Four are endemic, and among them *Siphocampylus rupestris* is endangered (EN), and *Centropogon dissectus* and *Centropogon llanganatensis* are vulnerable (VU).

The Network of Interactions

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

By analyzing the network structure, we found that the plant *Heppiella repens* and the hummingbird *Metallura tyrianthina* are the key species that holds the network together. If they are lost, the network will become less stable. By contrast, *Gaiadendron punctatum* and *Ensifera ensifera* are very specialized species which means they interact with a small group of specialized species.

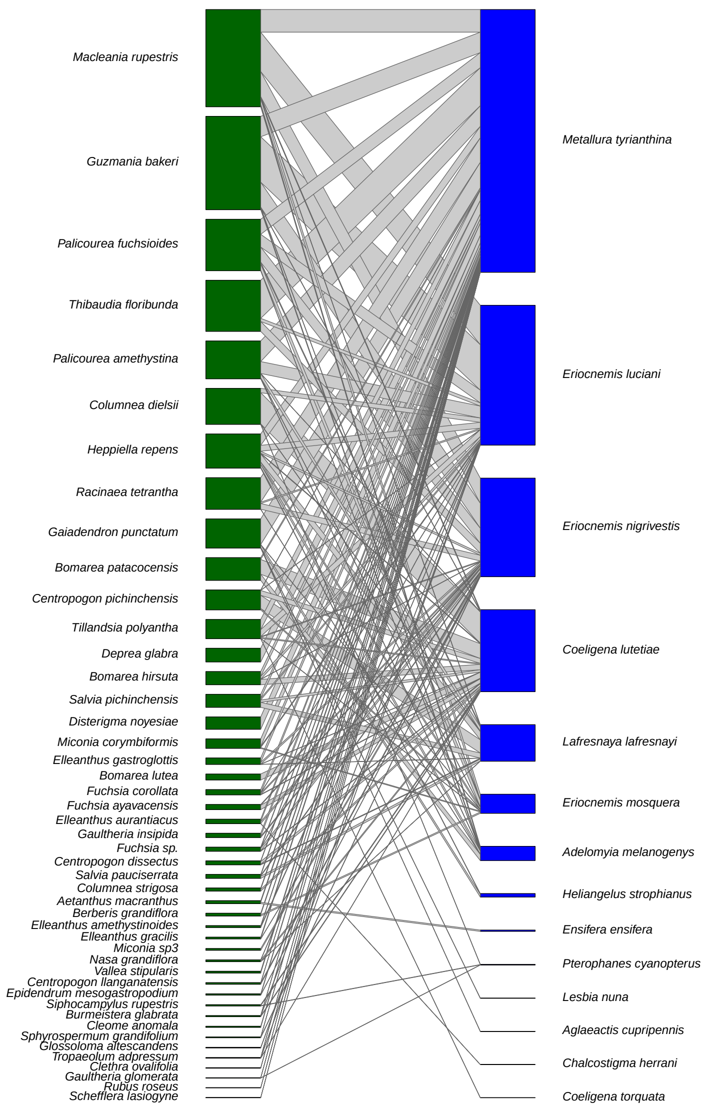

Figure 8: Network of interactions. Blue represents hummingbirds and green plants. Each line represents an interaction between a hummingbird and a plant obtained from our camera observations. Thicker lines indicate that the interaction was common while very thin lines indicate that the interaction occurred 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 *Heppiella repens* and *Macleania rupestris* can be used in restoration in Verdecocha. These species offer resources to more hummingbirds than the other plants where we recorded hummingbirds foraging (8 species).
- *Ensifera ensifera* is the most specialized hummingbird. Species such as *Aetanthus macranthus* is key to maintaining this hummingbird in Verdecocha.
- Plant phenology shows a peak of flower production in June and September.
- Verdecocha is the most important site for the conservation of the critically endangered Black-breasted Puffleg.
- Verdecocha and Yanacocha harbor a hummingbird community composed of species not found in mid or low elevations.

Acknowledgements

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