ECOLOGY OF PLANT HUMMINGBIRD INTERACTIONS IN YANACOCHA, 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 Yanacocha reserve lies between 3467 and 3541 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 Yanacocha in particular we collaborated with Martin Schaefer, Adela Espinosa, Michael Moens, Efraín Cepeda, Santiago Arroyo, Luis Hipo and Silvio Calderón from Jocotoco Fundation. Additionally, Wilson Hipo and Rolando Hipo from the communitites of Yanacocha and Alambi respectively, provided field assistance.

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 Yanacocha we sampled the transects from February 2017 to December 2019.

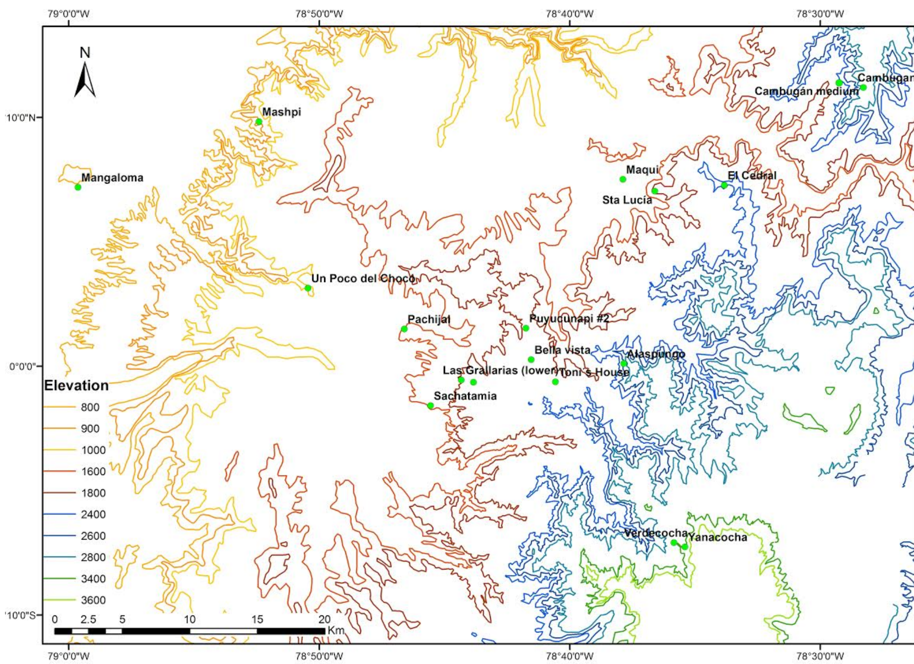

Figure 1: Location of the site in the elevation gradient.

Field transects

In Yanacocha we have 1 transect of 1.5 km. The transect starts at around 3500 m of elevation and runs parallel to the Inca trail. It begins about 20 meters below the Masked Trogon trail and continues along the Spectacled Bear trail until it reaches a flat and more open terrain, which is about 20 meters away before beginning the ascent to the hummingbird garden where the hummingbird feeders are located. This transect has little altitudinal variation and mostly runs through the interior of a well maintained forest with suro patches and crosses several small creeks by the end (Figure 2).

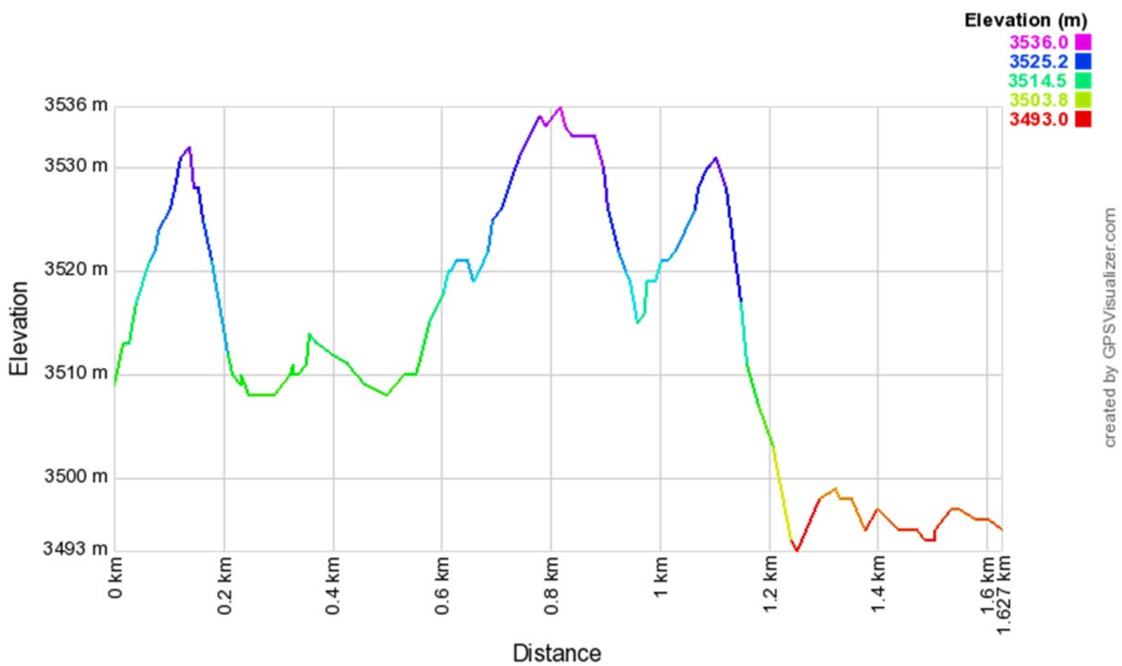

Figure 2: Elevation gradient of the transect.

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

Yanacocha is the highest site in our study area and we have identified 44 plant species used by hummingbirds according to our project (Annex 1). However, in our cameras we recorded 102 different interactions between 11 hummingbirds and 33 plants (Figure 5).

Metallura tyrianthina (Tyrian Metaltail)
Coeligena lutetiae ♂ (Buff-winged Starfrontlet)
Eriocnemis luciani (Sapphire-vented Puffleg)
Lafresnaya lafresnayi ♀ (Mountain Velvetbreast)

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	665	27
Coeligena lutetiae	1356	21
Eriocnemis luciani	561	20
Lafresnaya lafresnayi	805	14
Eriocnemis mosquera	174	8
Pterophanes cyanopterus	89	4
Chalcostigma herrani	14	3
Ensifera ensifera	7	2
Adelomyia melanogenys	1	1
Aglaeactis cupripennis	1	1
Lesbia nuna	1	1

The most common hummingbird recorded was *Coeligena lutetiae* 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 *Bomarea hirsuta*. 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**
Bomarea hirsuta	76	7
Barnadesia spinosa	183	5
Centropogon pichinchensis	315	5
Fuchsia ayavacensis	79	5
Heppiella repens	264	5
Nasa grandiflora	194	5
Palicourea fuchsioides	157	5
Tropaeolum tuberosum	152	5
Bomarea lutea	139	4
Bomarea multiflora	50	4
Centropogon dissectus	469	4
Macleania rupestris	469	4
Passiflora cumbalensis	19	4
Salvia pichinchensis	345	4
Siphocampylus rupestris	128	4
Columnea dielsii	282	3
Siphocampylus giganteus	82	3
Tillandsia polyantha	33	3
Disterigma noyesiae	38	2
Fuchsia sp.	9	2
Fuchsia vulcanica	38	2
Gaultheria insipida	14	2
Jaltomata viridiflora	6	2
Racinaea tetrantha	43	2
Saracha quitensis	30	2
Vaccinium floribundum	18	2
Berberis grandiflora	12	1
Bomalera lutea	2	1
Brachyotum gracilescens	7	1
Elleanthus gastroglottis	1	1
Miconia bracteolata	8	1
Pernettya prostrata	7	1
Rubus roseus	5	1

Plants information and phenology

We recorded the abundance of flowers from February 2017 to December 2019. The months with higher abundance of flowers are June and July (Figure 6).

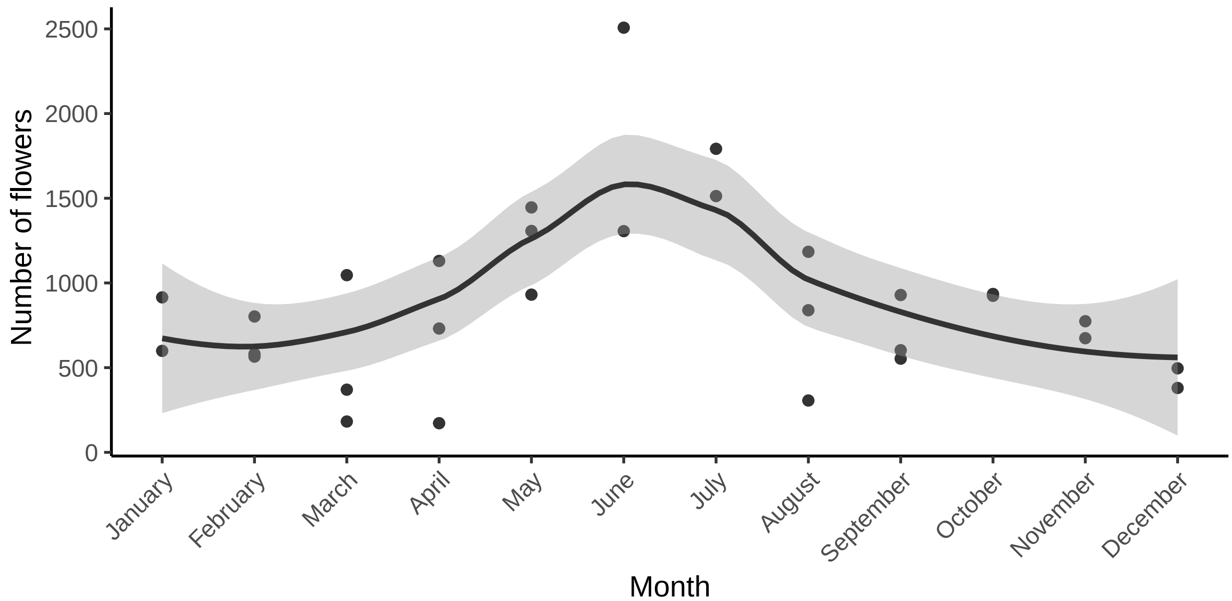

Figure 6: Abundance of flowers by month. Points represent the sum of flowers at each month and the black line represents the mean trend.

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.

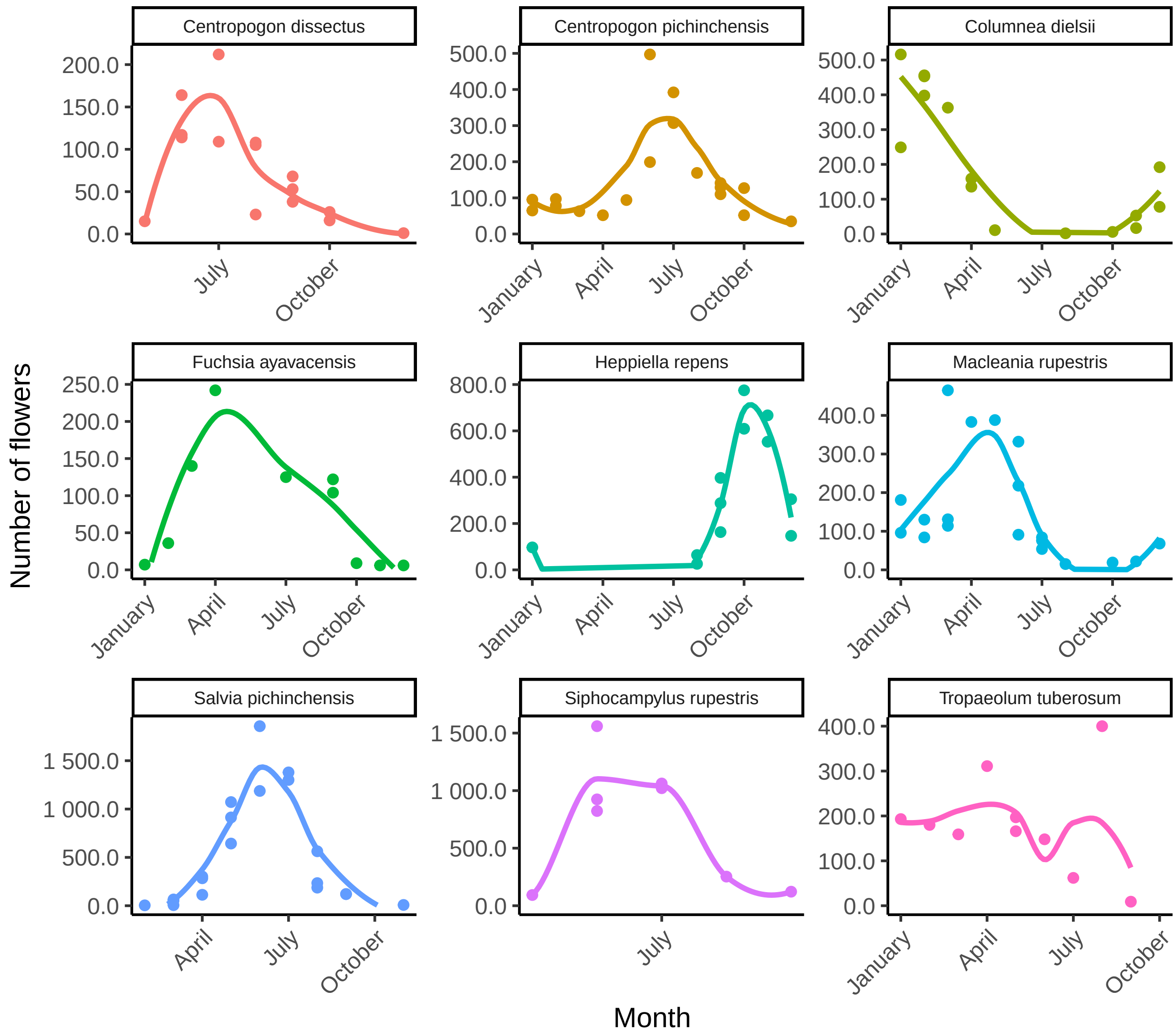

Figure 7: Phenology of most common flowers by month. Points represent the number of flowers counted in each month and the line represents the mean trend. Each color represents a different plant species.

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

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). Eleven species have been recorded in Yanacocha. *Disterigma* and *Gaultheria* are the most diverse genus with three species each one. Only *Disterigma noyesiae* is endemic and also vulnerable (VU).

MELASTOMATACEAE

Melastomataceae also known as May flowers or Inca earrings. It is represented by 200 genera and 4500 species, widely distributed in tropical and temperate regions. In Ecuador 38 genus and 550 species have been reported. Melastomataceae are woody shrubs (*Tibouchina*, *Brachyothum*), trees (*Miconia*, *Meriania*) or rarely herbs (*Monolema*). This family is mainly characterized by having the major leaf veins usually 3 or 5 palmate running in a parallel fashion from the base to near the leaf tip. Flowers are bisexual, actinomorphic or zygomorphic; corolla with 4 to 6 petals free or sometimes overlapping to form a tube; stamens generally in two whorls doubling the number than the petals. Fruits could be a capsule or berry with numerous seeds. In the Pichincha province there are 20 genera and 120 species, among them 20 species were registered in our project. Most do not show hummingbirds interactions and this is not a very important group in our study sites with the exception of Yanacocha, Verdecocha and Alaspungo. Only two species are endemic and both are endangered. There are also two new species: *Blakea sp*.nov. from Alaspungo and *Meriania sp*. nov. collected near Un Poco del Chocó. In Yanacocha five species of Melastomataceae are present: *Brachyotum gleasonii* and *Brachyotum gracilescens* are vulnerable (VU).

The Network of Interactions

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

By analyzing the network structure, we found that the plant *Bomarea hirsuta* and the hummingbird *Coeligena lutetiae* are the key species that holds the network together. If they are lost, the network will become less stable. By contrast, *Pernettya prostrata* and *Chalcostigma herrani* are very specialized species which means they interact with a small group of specialized species. In table 3 we can observe the plants interacting with each hummingbird.

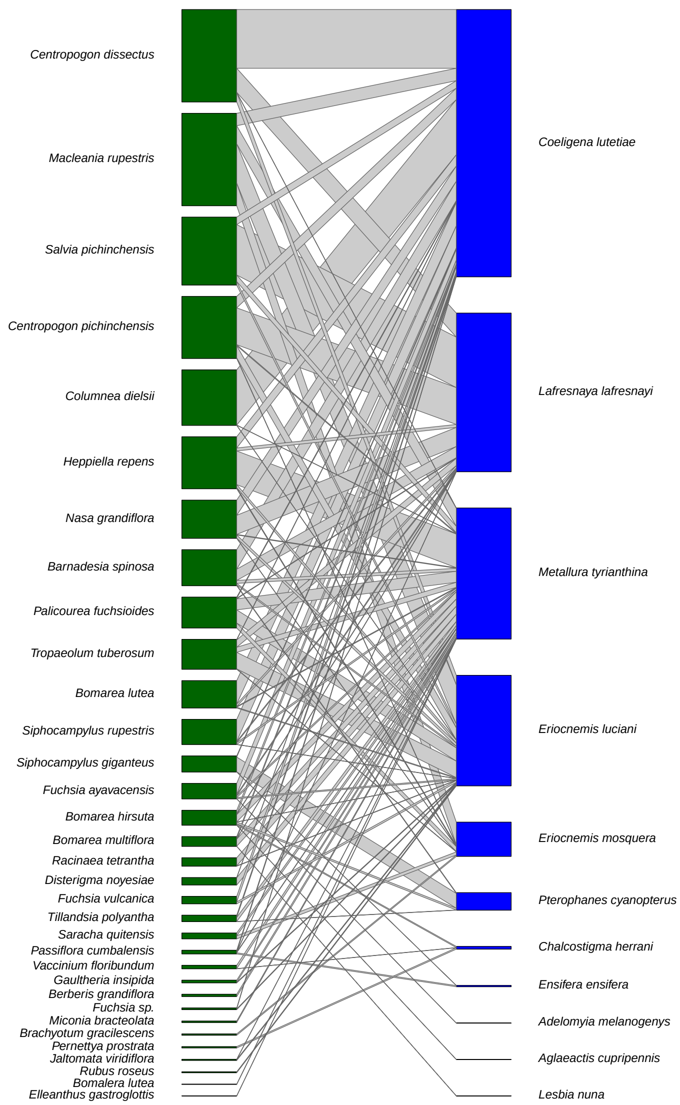

Figure 8: Network of interactions. Blue represents hummingbirds and green plants. Each line represents an interaction between a hummingbird and a plant obtained from our camera observations. Thicker lines indicate that the interaction was common while very thin lines indicate that the interaction occurred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

Table 3: List of Hummingbirds with the plant species they visited.

Hummingbird Species	*Visited plant species*
	Barnadesia spinosa
	Berberis grandiflora
	Bomalera lutea
	Bomarea hirsuta
	Bomarea lutea
	Bomarea multiflora
	Centropogon dissectus
	Centropogon pichinchensis
	Columnea dielsii
	Disterigma noyesiae
	Elleanthus gastroglottis
	Fuchsia ayavacensis
	Gaultheria insipida
	Heppiella repens
	Jaltomata viridiflora
	Macleania rupestris
	Miconia bracteolata
	Nasa grandiflora
	Palicourea fuchsioides
	Passiflora cumbalensis
	Racinaea tetrantha
	Salvia pichinchensis
	Saracha quitensis
	Siphocampylus rupestris
	Tillandsia polyantha
	Tropaeolum tuberosum
Metallura tyrianthina	*Vaccinium floribundum*
	Barnadesia spinosa

	Bomarea hirsuta
	Bomarea lutea
	Bomarea multiflora
	Centropogon dissectus
	Centropogon pichinchensis
	Columnea dielsii
	Disterigma noyesiae
	Fuchsia ayavacensis
	Fuchsia sp.
	Fuchsia vulcanica
	Heppiella repens
	Macleania rupestris
	Nasa grandiflora
	Palicourea fuchsioides
	Passiflora cumbalensis
	Salvia pichinchensis
	Siphocampylus giganteus
	Siphocampylus rupestris
	Tillandsia polyantha
Coeligena lutetiae	*Tropaeolum tuberosum*
	Barnadesia spinosa
	Bomarea hirsuta
	Bomarea lutea
	Centropogon dissectus
	Centropogon pichinchensis
	Columnea dielsii
	Fuchsia ayavacensis
	Fuchsia sp.
	Fuchsia vulcanica
	Gaultheria insipida

	Heppiella repens
	Jaltomata viridiflora
	Macleania rupestris
	Nasa grandiflora
	Palicourea fuchsioides
	Racinaea tetrantha
	Rubus roseus
	Salvia pichinchensis
	Siphocampylus rupestris
Eriocnemis luciani	*Tropaeolum tuberosum*
	Barnadesia spinosa
	Bomarea hirsuta
	Bomarea lutea
	Bomarea multiflora
	Centropogon dissectus
	Centropogon pichinchensis
	Fuchsia ayavacensis
	Heppiella repens
	Nasa grandiflora
	Palicourea fuchsioides
	Passiflora cumbalensis
	Salvia pichinchensis
	Siphocampylus rupestris
Lafresnaya lafresnayi	*Tropaeolum tuberosum*
	Brachyotum gracilescens
	Centropogon pichinchensis
	Heppiella repens
	Macleania rupestris
	Nasa grandiflora
	Palicourea fuchsioides

	Saracha quitensis
Eriocnemis mosquera	*Tropaeolum tuberosum*
	Barnadesia spinosa
	Bomarea hirsuta
	Siphocampylus giganteus
Pterophanes cyanopterus	*Tillandsia polyantha*
	Bomarea hirsuta
	Pernettya prostrata
Chalcostigma herrani	*Vaccinium floribundum*
	Passiflora cumbalensis
Ensifera ensifera	*Siphocampylus giganteus*
Lesbia nuna	*Bomarea multiflora*
Aglaeactis cupripennis	*Bomarea hirsuta*
Adelomyia melanogenys	*Fuchsia ayavacensis*

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 *Bomarea hirsuta* and *Barnadesia spinosa* can be used in restoration in Yanacocha. These species offer resources to more hummingbirds than the other plants where we recorded hummingbirds foraging (7 species).
- *Chalcostigma herrani* is the most specialized hummingbird. Species such as *Bomarea hirsuta* and *Pernettya prostrata* are key to maintaining this hummingbird in Yanacocha.
- The plant phenology in Yanacocha is very marked with a peak of floration in the middle of the year.
- Yanacocha has five species of Melastamataceae used by hummingbirds, the greatest diversity of this family among all our study sites.
- Yanacocha and Verdecocha harbor a hummingbird community composed of species not found in mid or low elevations.

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