ECOLOGY OF PLANT HUMMINGBIRD INTERACTIONS IN SANTA LUCÍA, 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 Santa Lucía reserve lies between 1732 and 2478 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 Santa Lucía we collaborated with the community, especially Noé Morales and Edison Tapia who 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 Santa Lucía we sampled the transects from February 2017 to June 2019.

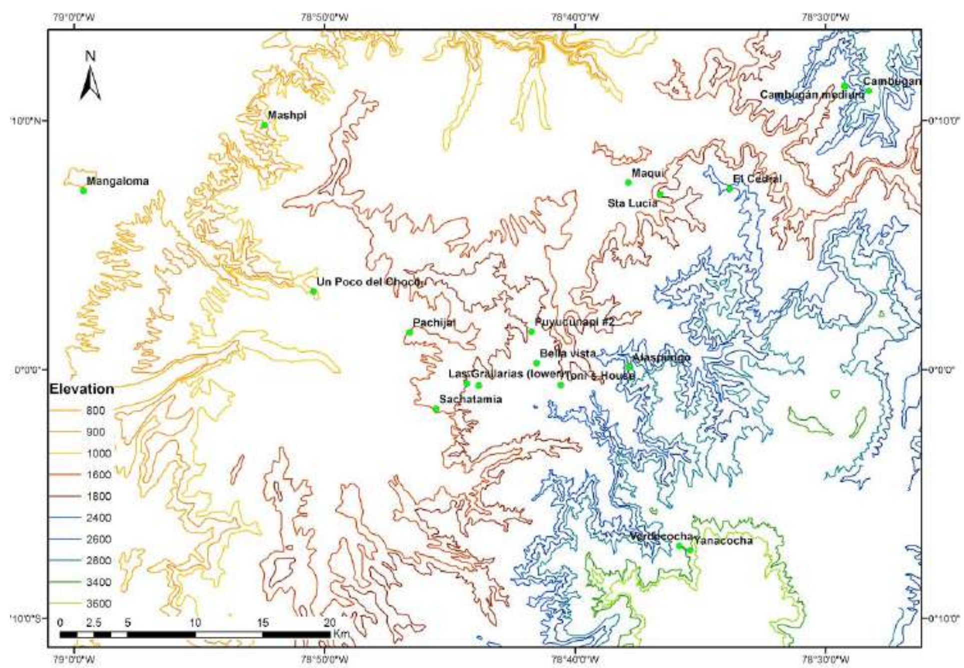

Figure 1: Location of the site in the elevation gradient.

Field transects

In Santa Lucía we have 2 transects of 1.5 km each. The transect (composed by two sub transects) starts about 15 minutes from Santa Lucía's Cock-of-the-Rock lek near a small stream at around 1730 m of elevation. The first trail crosses a bridge which allows for observation in a riparian habitat. Then it winds up to 1.880 m (in most parts steeply) through a mature forest with gigantic trees (e.g. Myrtaceae and Lauraceae). Understory plants in the Rubiaceae family make this transect hummingbird-rich. The trail is narrow and during most parts there is a deep creek on one side which allows for good views (Figure 2).

The second trail is located in the upper part of the reserve. Here the forest is less dense, but still lined with old primary growth. The transect end at an elevation of just above 2000 m (Figure 3).

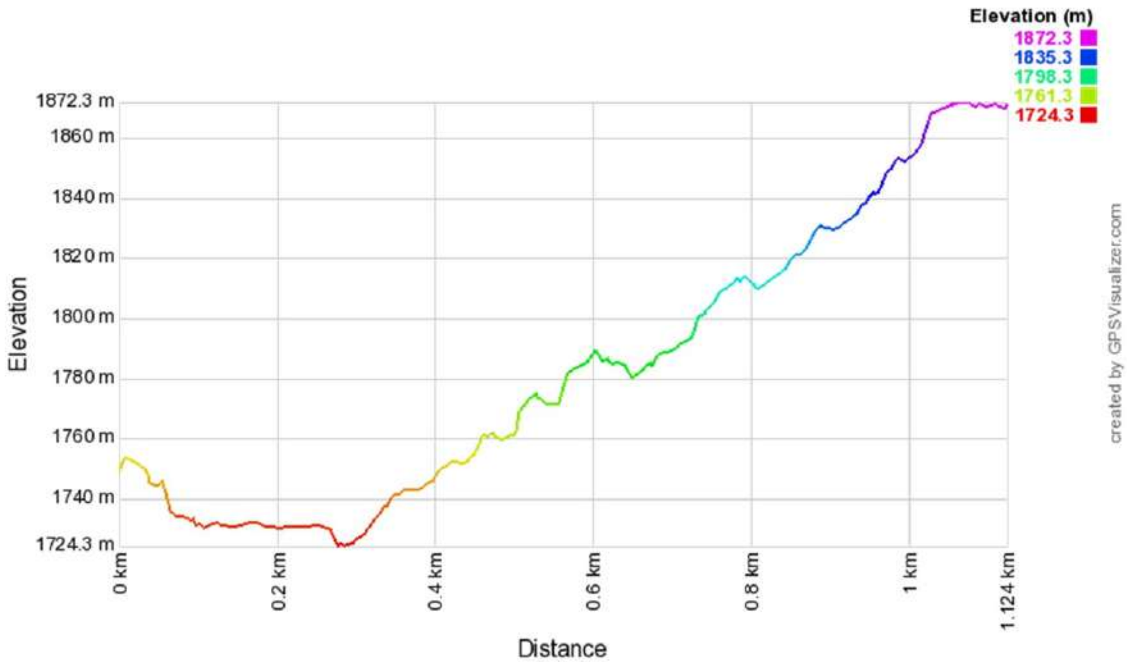

Figure 2: Elevation gradient of the transect.

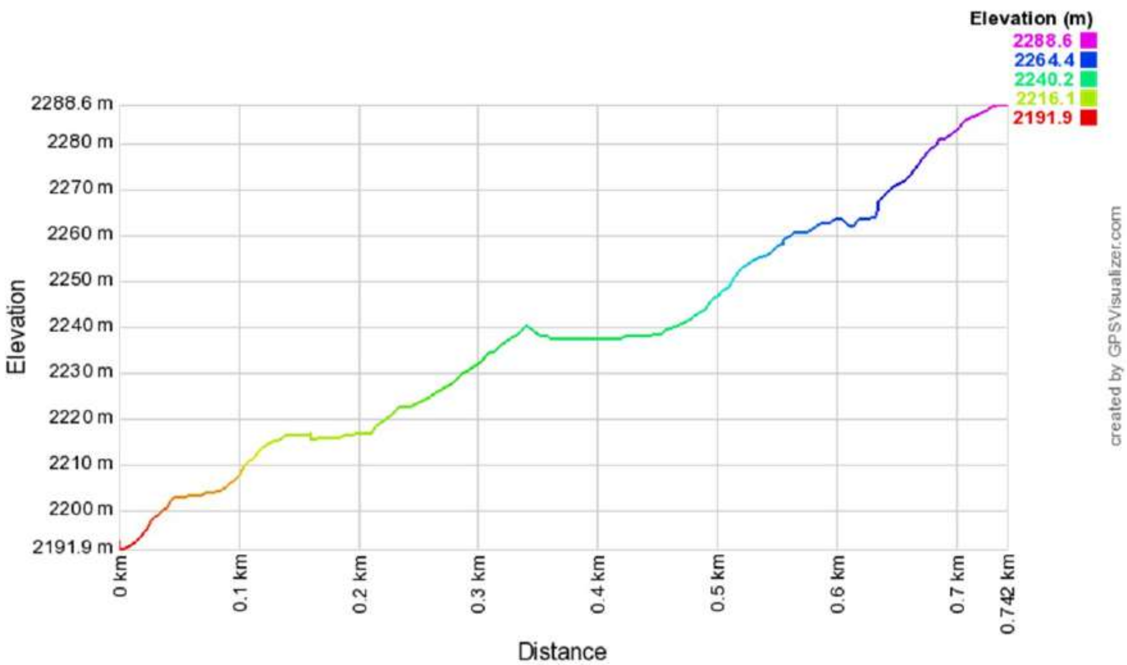

Figure 3: Elevation and location of the second transect.

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

Figure 4: 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 5: Team researcher Holger Beck shows how a camera is set up in order to film a flower.

3. Resulting patterns

Plant-hummingbird interactions

Santa Lucía forest is run by the local community where 102 plant species are used by hummingbirds according to our project results (Annex 1). However, in our cameras we recorded 266 different interactions between 18 hummingbirds and 68 plants (Figure 6).

Figure 6: 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	2635	54
Phaethornis syrmatophorus	1615	43
Coeligena wilsoni	563	41
Adelomyia melanogenys	535	24
Heliangelus strophianus	543	21
Coeligena torquata	431	20
Ocreatus underwoodii	294	19
Heliodoxa rubinoides	98	8
Diglossa albilatera	14	7
Doryfera ludovicae	173	6
Heliodoxa imperatrix	31	6
Schistes geoffroyi	19	6
Boissonneaua flavescens	34	4
Urosticte benjamini	7	3
Amazilia tzacatl	1	1
Colibri coruscans	1	1
Phaethornis striigularis	1	1
Phaethornis yaruqui	1	1

The most common hummingbird recorded was *Aglaiocercus coelestis* and the most common plant was *Centropogon solanifolius*. 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 *Fuchsia macrostigma*. 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**
Fuchsia macrostigma	166	11
Centropogon solanifolius	710	9
Heliconia burleana	65	9
Palicourea sodiroi	470	9
Psammisia ulbrichiana	50	9
Bomarea pardina	188	8
Mezobromelia capituligera	306	8
Besleria solanoides	429	7
Glossoloma oblongicalyx	268	7
Guzmania squarrosa	174	7
Macleania bullata	66	7
Macleania recumbens	116	7
Palicourea lineata	383	7
Pitcairnia sodiroi	329	7
Psammisia sodiroi	179	7
Guzmania gloriosa	46	6
Centropogon nigricans	112	5
Drymonia teuscheri	307	5
Heliconia impudica	260	5
Kohleria affinis	181	5
Psammisia oreogenes	90	5
Renealmia fragilis	64	5
Tillandsia complanata	89	5
Centropogon llanganatensis	26	4
Columnea kucyniakii	132	4
Columnea medicinalis	50	4
Columnea strigosa	59	4
Gasteranthus pansamalanus	14	4
Gasteranthus quitensis	80	4
Guzmania jaramilloi	118	4
Pitcairnia nigra	161	4
Renealmia sessilifolia	251	4

Bomarea multiflora	35	3
Burmeistera cylindrocarpa	11	3
Calathea ischnosiphonoides	65	3
Columnea ciliata	146	3
Columnea leopardus	22	3
Columnea picta	24	3
Drymonia collegarum	85	3
Elleanthus robustus	26	3
Gasteranthus lateralis	47	3
Gasteranthus leopardus	27	3
Guzmania xanthobractea	47	3
Palicourea demissa	80	3
Renealmia aurantifera	16	3
Burmeistera pterifolia	7	2
Burmeistera pterofolia	3	2
Drymonia tenuis	14	2
Erythrina edulis	155	2
Mikania sp.	2	2
Podandrogyne sp1	63	2
Sertifera purpurea	10	2
Tropaeolum adpressum	7	2
Abutilon sp.	13	1
Begonia longirostris	2	1
Centropogon comosus	9	1
Columnea aff picta	2	1
Drymonia brochidodroma	2	1
Elleanthus aurantiacus	1	1
Erythrina megistophylla	89	1
Faramea calyptrata	2	1
Faramea quinqueflora	3	1
Manettia trianae	10	1
Meriania tomentosa	1	1
Pachycaulos nummularium	1	1
Psammisia aberrans	19	1
Psammisia ecuadorensis	1	1
Psammisia sp.	10	1

Plants information and phenology

We recorded the abundance of flowers from February 2017 to June 2019. The months with higher abundance of flowers are October and July (Figure 7).

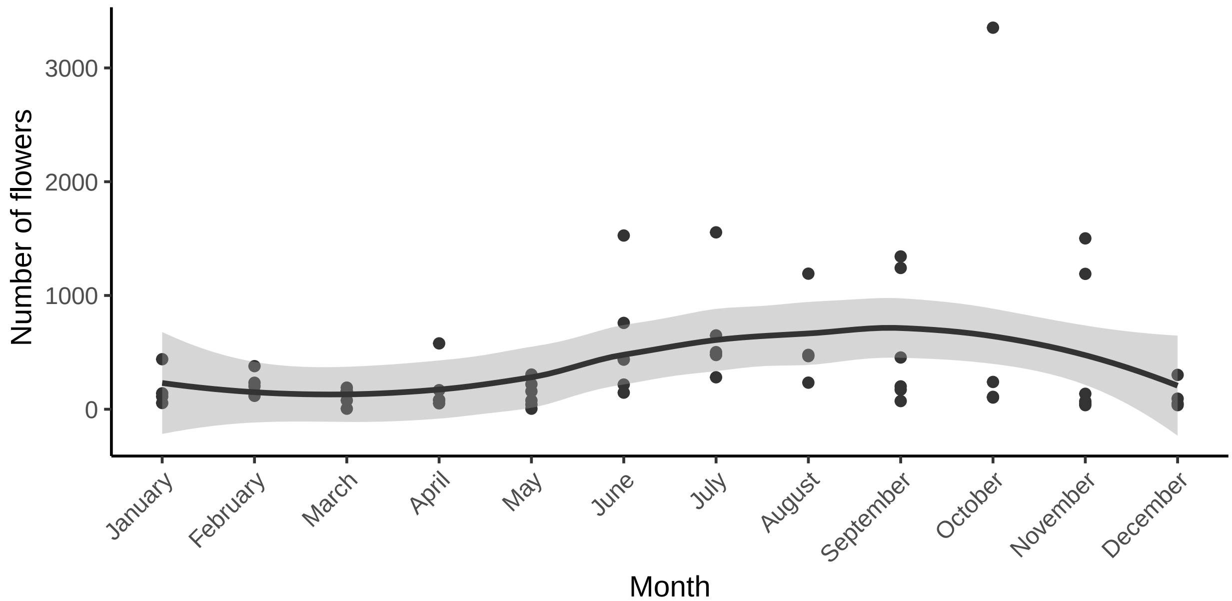

Figure 7: Abundance of flowers by month. Points represent the sum of flowers at each month and the black line represents the mean trend.

However, not all plant produces flowers at the same time. In figure 8 we can observe the phenology of the four most common plant species.

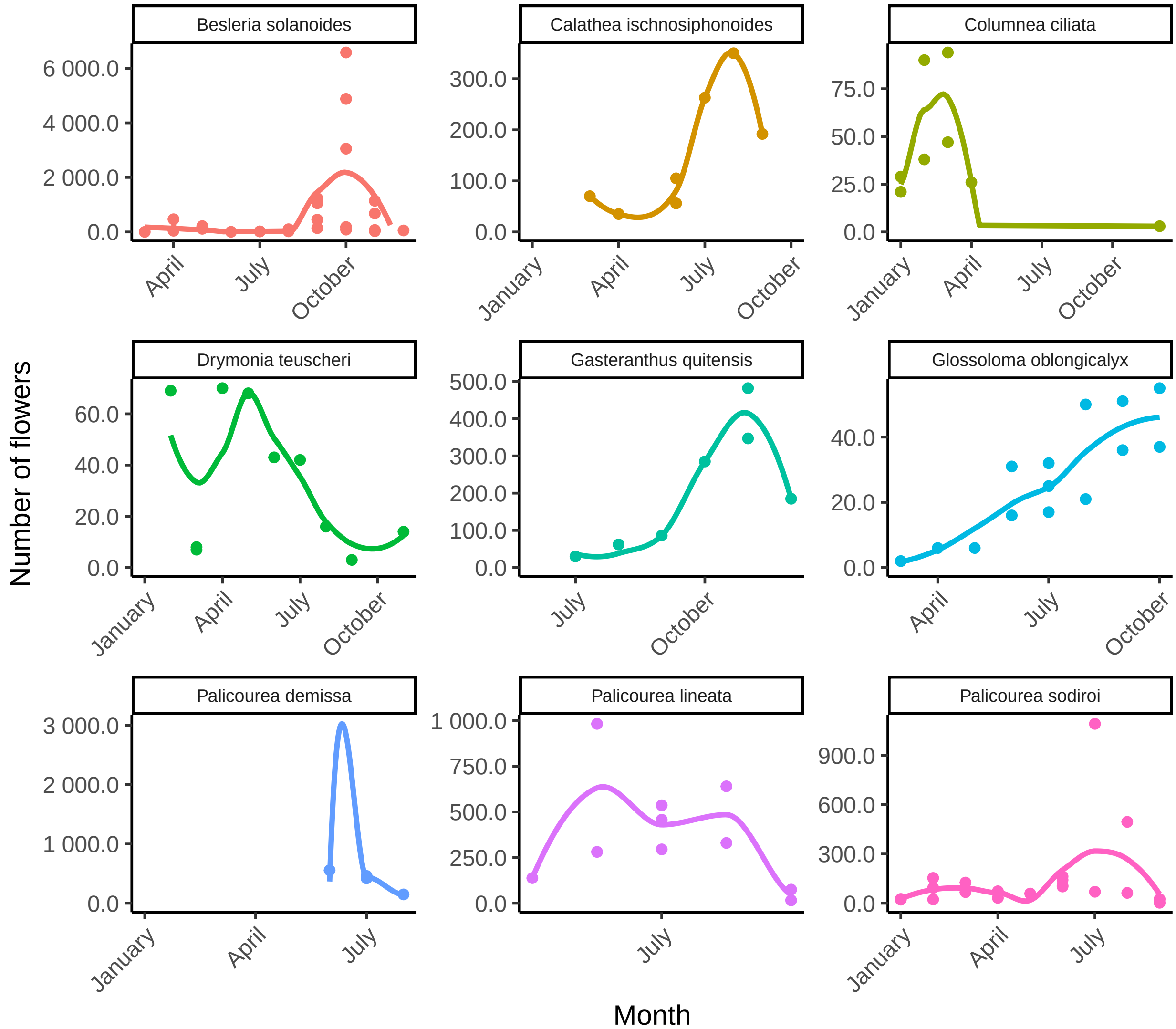

Figure 8: Phenology of most common flowers by month. Points represent the number of flowers counted in each month and the line represents the mean trend. Each color represents a different plant species.

Below we describe the most representative plant families present in Santa Lucía.

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. There are 22 specie in Santa Lucía, *Columnea* (6 spp.), and *Gasteranthus* (4spp.) have more species. Four species are endemic and threatened: *Columnea ovatifolia* is endangered (EN) and *Columnea katzensteiniae*, *Drymonia collegarum*, *Gasteranthus lateralis* are vulnerable (VU). There is also a new *Columnea* species which is shared with Las Gralarias, Puyucunapi and Sachatamia.

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. Fourteen species are present in Santa Lucía. *Guzmania" is the most diverse genus with 8 species. Four species are endemic:* Guzmania bakeri* also vulnerable (VU), *Pitcairnia sodirio*, *Guzmania jaramilloi* and *Pitcairnia fusca*.

The Network of Interactions

The interaction data we collected can be used to explore how the interactions network is organized at Santa Lucía. In figure 9 we show the structure of the network.

By analyzing the network structure, we found that the plant *Fuchsia macrostigma* 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, *Meriania tomentosa* and *Phaethornis striigularis* are very specialized species which means they interact with a small group of specialized species.

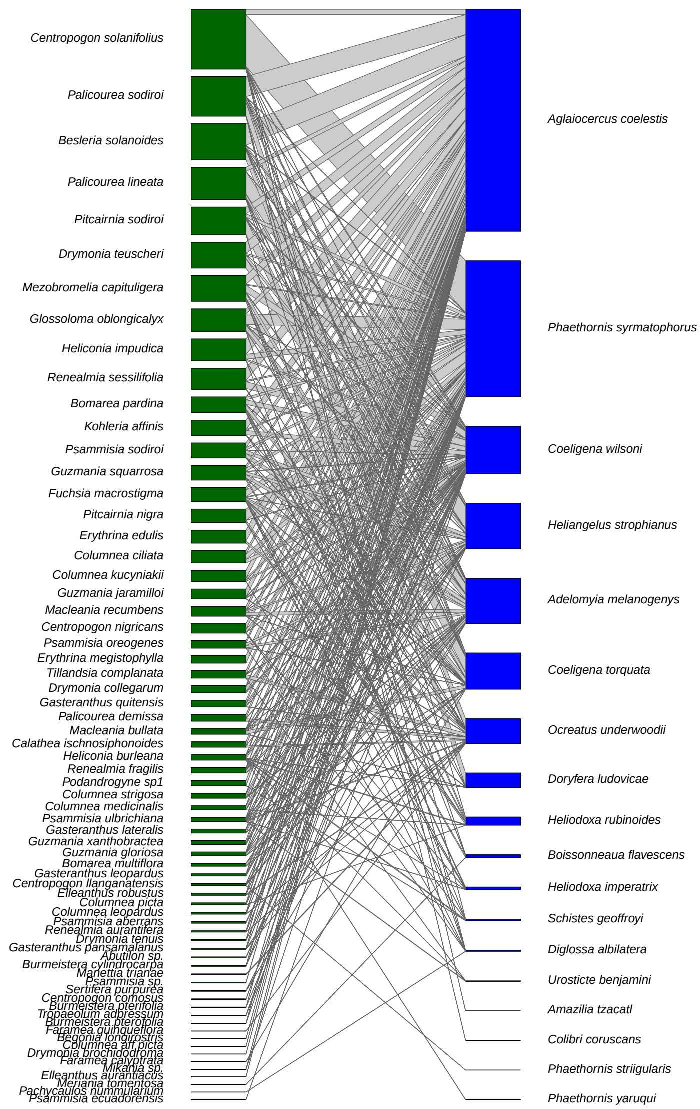

Figure 9: Network of interactions. Blue represents hummingbirds and green plants. Each line represents an interaction between a hummingbird and a plant obtained from our camera observations. Thicker lines indicate that the interaction was common while very thin lines indicate that the interaction occurred 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 *Fuchsia macrostigma* and *Centropogon solanifolius* can be used in restoration in Santa Lucía. These species offer resources to more hummingbirds than the other plants where we recorded hummingbirds foraging (12 species).
- *Phaethornis striigularis* is the most specialized hummingbird. Species such as *Centropogon llanganatensis* is key to maintaining this hummingbird in Santa Lucía.
- Santa Lucía shows a clear flowering peak during June and July.
- Santa Lucía has a hummingbird community composed of some species from the highlands. Besides, the hummingbird *Colibri coruscans*, typical of disturbed areas, was also recorded in Santa Lucía.
- In Santa Lucía a new species of plant,*Columnea sp.nov* was recorded. This species is also present in Sachatamia, Puyucunapi, and Las Gralarias.

Acknowledgements

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